

# Multiple Systems of Spatial Memory: Evidence From Described Scenes

Marios N. Avraamides  
University of Cyprus

Jonathan W. Kelly  
Vanderbilt University

Recent models in spatial cognition posit that distinct memory systems are responsible for maintaining transient and enduring spatial relations. The authors used perspective-taking performance to assess the presence of these enduring and transient spatial memories for locations encoded through verbal descriptions. Across 3 experiments, spatial reasoning about immediate and remote environments was influenced by enduring, allocentric spatial memories. In contrast, transient, egocentric spatial memories influenced participants' spatial reasoning about immediate, but not remote, environments unless participants received specific imagery instructions. These findings provide support for theories proposing multiple spatial memory systems. Furthermore, these findings closely replicate previous results from studies with purely visual scenes, thereby providing converging evidence for functional equivalence between spatial representations maintaining visual and described locations.

*Keywords:* spatial cognition, spatial memory, verbal descriptions, perspective taking

*Supplemental materials:* <http://dx.doi.org/10.1037/a0017040.supp>

An everyday task like driving home from work requires on-line processing of perceptually available spatial information (e.g., avoiding pedestrians and negotiating turns) as well as off-line reasoning about remembered spatial relationships (e.g., determining an alternative route to avoid traffic congestion). Spatial cognition research suggests that on-line and off-line tasks rely on the encoding and retrieval of different types of spatial information and are subserved by distinct neuroanatomical structures (Byrne, Becker, & Burgess, 2007). In the present study, we provide behavioral evidence for the presence of two different types of spatial representations used when reasoning about space in the context of on-line and off-line tasks. Previous evidence for this distinction has typically focused on visually learned spatial information and visually controlled spatial behavior. In the current experiments, we extend the dual-representation account to spatial information acquired through language, thereby examining whether spatial representations for locations acquired through different sensory modalities are functionally equivalent.

On one hand, on-line spatial tasks governing the control of moment-to-moment spatial activity are thought to rely on spatial relations that are briefly maintained in memory in an egocentric format containing self-to-object directions and distances (Amorim, Glasauer, Corpinot, & Berthoz, 1997; Farrell & Thomson, 1999;

Wang & Spelke, 2000). This conclusion is supported by studies in which researchers examined spatial updating—the mechanism that allows moving observers to continuously track the locations of surrounding objects (Loomis, Lippa, Golledge, & Klatzky, 2002). In spatial updating studies, participants memorize the locations of one or more objects and then point to them without vision, first from the initial observation standpoint and again after moving to a novel standpoint. A common finding is that pointing to remembered locations is equally fast and accurate from the initial learning standpoint and a novel standpoint adopted by physical translation, rotation, or both (e.g., Presson & Montello, 1994; Rieser, 1989; Rieser, Guth, & Hill, 1986), indicating successful spatial updating. However, many studies have shown that pointing is slower and less accurate when the novel standpoint is adopted through imaginal, rather than physical, movements (e.g., Presson & Montello, 1994; Rieser, 1989). This finding has led scientists to argue that proprioceptive and vestibular information as well as copies of efferent commands, which are present with physical but not imagined movement, are prerequisites for on-line spatial updating of egocentric relations (Rieser, 1989). Studies from neuroscience highlight the posterior parietal cortex as the part of the brain supporting execution of on-line tasks. Parts of posterior parietal cortex are believed to encode spatial information using various egocentric frames (Colby, 1998), while the precuneus has been suggested as the structure in which egocentric representations of the immediate environment are maintained and updated (Byrne et al., 2007; Wolbers, Hegarty, Büchel, & Loomis, 2008). The fact that the precuneus exhibits dense connections with premotor areas corroborates its central role in performing motor actions toward objects in immediate surroundings (e.g., pointing). Furthermore, the retrosplenial cortex has been recently proposed as a system that integrates egocentric environmental information with self-motion cues, allowing the formation of long-term spatial memories (Wolbers & Büchel, 2005).

On the other hand, off-line spatial tasks seem to rely on allocentric representations containing interobject directions and dis-

---

Marios N. Avraamides, University of Cyprus, Nicosia, Cyprus; Jonathan W. Kelly, Department of Psychology, Vanderbilt University.

Jonathan W. Kelly is now at the Department of Psychology, Iowa State University.

The present research was supported by a grant from the European Research Council (ERC-2007-StG 206912-OSSMA) to Marios N. Avraamides. We thank Melina-Nicole Kyranides and Stephanie Pantelidou for help with the data collection.

Correspondence concerning this article should be addressed to Marios N. Avraamides, Department of Psychology, University of Cyprus, P.O. Box 20537, Nicosia 1678, Cyprus. E-mail: mariosav@ucy.ac.cy

tances (McNamara, 2003; Mou & McNamara, 2002). This evidence stems from spatial memory studies in which participants first encode a spatial layout in memory and then, after moving to a different environment (e.g., a different laboratory), retrieve spatial relations from the stored representation. A popular task in these studies is the judgments of relative directions task in which participants respond to statements of the form "Imagine standing at  $x$  facing  $y$ . Point to  $z$ ," where  $x$ ,  $y$ , and  $z$  are learned objects. McNamara and colleagues (e.g., McNamara, 2003; Mou & McNamara, 2002) have argued that upon studying a spatial layout, participants encode object locations using a reference frame intrinsic to the layout. The layout is then stored in memory from a preferred orientation determined by a variety of factors including egocentric experience, layout structure, experimenter instruction, and salient environmental cues like room walls. In a series of studies, McNamara and colleagues (e.g., McNamara, 2003; Mou & McNamara, 2002) have shown that judgments of relative directions performance is superior when the imagined perspective is aligned, compared to misaligned, with the orientation in which the memory was presumably stored. According to the reference direction theory, interobject relations aligned with a reference direction are directly represented within the spatial memory, and so imagining aligned perspectives is relatively easy. In contrast, misaligned interobject relations need to be inferred, and this inference process is cognitively effortful, resulting in greater latencies and errors when imagining misaligned perspectives (see McNamara, 2003, for a discussion). However, the question of orientation dependence is not without controversy, and some evidence points toward orientation independence (Presson & Hazelrigg, 1984; Sun, Chan, & Campos, 2004).

The seminal work of O'Keefe and Nadel (1978) on place cells in rats implicated the medial temporal lobe and the hippocampus in particular as the neural basis of forming and maintaining stable, viewpoint-invariant spatial representations of environments. Place cells, whose firing fields are established upon experiencing a novel environment, fire to represent the animal's allocentric location within the environment. Neuroimaging studies indicate hippocampal activity when navigating within familiar environments. For example, Maguire et al. (1998) used positron emission tomography to identify increased activation in the right hippocampus of adults navigating within a familiar virtual town. Based on their findings, Maguire et al. (1998) argued that the right hippocampus serves to form allocentric representations of space, which can be used to compute metric spatial relations like distances and directions between two landmarks. However, using fMRI technology, Wolbers and Büchel (2005) provided evidence that hippocampal involvement in spatial memory formation gradually decreases during learning, suggesting that its role might be limited to incorporating newly acquired information into an emerging memory representation.

Because spatial information is experienced egocentrically through the senses, formation of allocentric memories must depend on a system that converts information from egocentric to allocentric reference frames. Recent research suggests that the retrosplenial cortex might be the neural substrate underlying the translation of egocentric information from parietal areas to allocentric information in medial temporal areas and vice versa (Epstein, 2008; Epstein, Parker, & Feiler, 2007; Wolbers & Büchel, 2005).

In line with evidence from cognitive neuroscience, increasing behavioral evidence suggests that egocentric and allocentric spatial

representations are both formed when learning a spatial layout (Kelly, Avraamides, & Loomis, 2007; Mou, McNamara, Valiquette, & Rump, 2004; Waller & Hodgson, 2006; see also Byrne et al., 2007). Moreover, a number of researchers with theories proposing multiple systems of spatial memory attempt to account for results from spatial updating and spatial memory studies (Easton & Sholl, 1995; Mou, McNamara, et al., 2004; Waller & Hodgson, 2006; Wang & Spelke, 2000). These theories posit that egocentric and allocentric relations are maintained by two distinct spatial memory systems. According to Mou, McNamara, et al. (2004), egocentric relations are represented in a transient system supported by visual and idiothetic cues, which allows interaction with the environment by continuously updating locations within one's immediate surroundings. This transient representational system supports visually guided behaviors like reaching and walking toward objects and can also operate efficiently without concurrent visual support (Rieser et al., 1986). In addition, allocentric relations are maintained in an orientation-specific system that is coarser but more enduring than the transient egocentric system (Mou, McNamara, et al., 2004; Waller & Hodgson, 2006). Importantly, the spatial information in this enduring system is not updated with observer movement, allowing maintenance of stable representations to support off-line tasks like route planning over larger distances.

Empirical support for these distinct spatial memory systems is provided by recent studies using visual scenes (Kelly et al., 2007; also see Mou, McNamara, et al., 2004). In these studies, participants first studied a spatial layout from one perspective and then made spatial judgments, without vision, after turning to adopt a different physical perspective. Spatial judgments involved adopting imagined perspectives within the remembered layout and locating target objects by pointing from those imagined perspectives. Furthermore, this task was performed while participants stood either in the center of the learning room or in a neighboring room. When perspective taking occurred in the learning room, performance was (a) superior when responding from imagined perspectives aligned, compared to misaligned, with the learning perspective (the *encoding alignment effect*) and (b) was also superior for imagined perspectives aligned, compared to misaligned, with participants' physical perspective (the *sensorimotor alignment effect*). In contrast, when perspective taking occurred in the neighboring room, only the encoding alignment effect occurred, and the sensorimotor alignment effect was absent. The encoding alignment effect was attributed to the organization of the enduring memory system. It was hypothesized that participants represented the spatial layout in the enduring system relative to an intrinsic reference frame aligned with the learning perspective, and they retrieved this enduring spatial memory when performing the task in the learning room and the neighboring room. The sensorimotor alignment effect was attributed to the organization of the transient, or sensorimotor, memory system. It was argued that participants established egocentric codes in the sensorimotor system when studying the layout. This sensorimotor representation was updated when participants turned to adopt a new physical perspective, and it facilitated responding from imagined perspectives aligned with the body when participants stood within the learning environment (May, 2004). However, upon participants' walking to the neighboring room, the transient egocentric system encoded participants' new surroundings and ceased to update the originally learned egocentric relations (also see Wang & Brockmole, 2003).

While the findings of Mou, McNamara, et al. (2004) and Kelly et al. (2007) support the idea of distinct systems for representing egocentric and allocentric relations, both studies involved responding to visual objects. Locations, however, are often encoded in memory through other learning modalities such as audition, touch, and proprioception, and also through symbolic media such as language. Before embracing a theory with multiple systems of spatial memory, it seems imperative that we examine whether multiple systems are also involved in representing spatial information encoded through nonvisual modalities.

There is increasing empirical evidence that spatial representations acquired through different perceptual modalities are functionally equivalent (Avraamides, Loomis, Klatzky, & Golledge, 2004; Noordzij & Postma, 2005; for a review, see Loomis, Klatzky, Avraamides, Lippa, & Golledge, 2007) or even amodal (Bryant, 1997). In the case of language, the literature on mental models (Johnson-Laird, 1983, 1996) or situation models (Van Dijk & Kintsch, 1983) has documented that spatial representations derived from language preserve many of the properties of real environments (see Zwaan & Radvansky, 1998, for a review). In a study by Avraamides et al. (2004), for example, participants used a pointer to indicate relative directions between pairs of objects learned through vision or spatial language. Responses were equally fast and accurate for targets encoded through vision and spatial language. However, a number of other findings indicate differences between spatial representations derived from vision and other input modalities. For example, Wang (2004) reported that object locations learned visually were automatically updated during participant rotation, but this was not the case for object locations that were only described. Furthermore, Péruch, Chabanne, Nesa, Thinus-Blanc, and Denis (2006) found faster and more accurate spatial reasoning about scenes learned visually than scenes through verbal description. However, as Millar and Al-Attar (2004) pointed out external cues that can serve to achieve allocentric coding of locations are readily available with vision but typically not when other modalities are used. Also, it is well known that the learning rate for representations acquired through language and vision differs markedly: It takes longer with language than vision to form a representation of comparable quality (e.g., Avraamides et al., 2004; Klatzky, Lippa, Loomis, & Golledge, 2002). As a result, even when performance differences are found between learning modalities, it is unclear whether these differences are caused by retrieval of information from fundamentally different representations or whether they reflect differences in the level of learning. On the other hand, as with any other null effect, the absence of any differences reported by various studies can be potentially accounted for by factors other than functional equivalence.

Due to this limitation, it is often not very useful to simply compare overall response latency and accuracy after learning from different sources. An alternative way to assess functional equivalence is to examine whether specific effects that are well documented with one input source can be also observed with other input sources. In the present experiments, we used the paradigm used by Kelly et al. (2007) in which participants performed imagined perspective taking while standing either within the learned layout or in a different room. The goal was to examine whether distinct encoding and sensorimotor alignment effects (facilitated performance for imagined perspectives aligned with the learning perspective and participants' actual perspective, respectively)

could be observed when participants recalled verbally described locations. Evidence of alignment effects similar to those found using purely visual scenes would represent converging evidence for functional equivalence between spatial representations maintaining visual and described objects. It should be noted that in all of the following experiments participants memorized described locations within a room that was previously examined visually. This was done (a) to allow usage of verbal descriptions that combined egocentric and allocentric terms, (b) to provide access to the same environmental reference frames available when learning a scene visually, and (c) to allow participants to place the described objects in a mental representation of comparable vividness to representations formed in visual experiments.

## Experiment 1

Our goal for Experiment 1 was to examine whether encoding and sensorimotor alignment effects would occur when imagining perspectives within a layout of objects learned through spatial language. Following Kelly et al. (2007), we predicted that a sensorimotor alignment effect would occur when participants were tested while standing within the learned environment (immediate condition) but not after walking to a neighboring environment (nonimmediate condition). In addition, we expected that an encoding alignment effect would occur in both testing conditions.

## Method

**Participants.** Forty students from the University of Cyprus participated in the experiment in exchange for course credit.

**Design.** The study followed a 2 (testing location: immediate, nonimmediate)  $\times$  3 (imagined perspective: 0° encoding aligned, 90° sensorimotor aligned, 270° misaligned) mixed factorial design. Testing location was manipulated between-subjects, whereas imagined perspective varied within subjects. Pointing error and latency were the primary dependent measures.

**Procedure.** The procedure of the experiment was divided into a learning and a testing phase.

**Learning phase.** Learning was identical for participants in both testing conditions. Participants entered the learning room and were given unlimited time to visually inspect the various objects it contained. Typical laboratory objects (computers, desks, etc.) were visible around the room, and participants' attention was directed toward those objects by the experimenter. Participants then donned a blindfold and headphones and were positioned in the center of the learning room facing 0° (see Figure 1); we refer to this orientation as the *learning perspective*. Participants wore the blindfold in a way that occluded vision toward the room and its objects but allowed participants to view a joystick mounted on a tripod in front of them. Participants were told that the experimenter would place six objects at various locations around them. Participants learned the locations of the objects by listening to recorded messages delivered over the headphones. These messages described the object locations in a naturalistic manner, using a combination of egocentric and allocentric reference frames. The allocentric frames selected were centered on objects that participants had viewed earlier. For example, the following description was used to indicate where the telephone was placed (see Figure 1): "Behind you there is a large bookcase. In front of the bookcase there is a

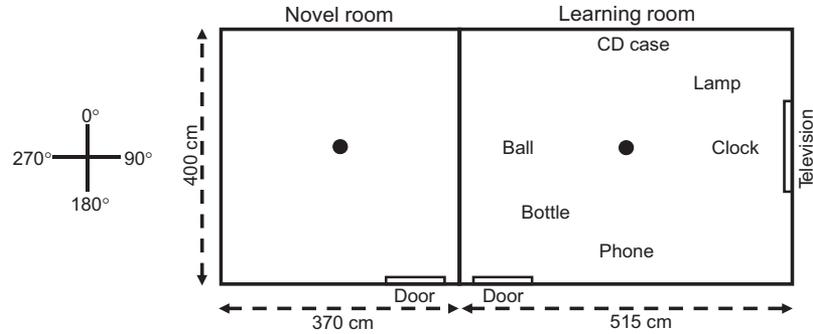


Figure 1. Schematic representation of the spatial layout and the environment used for the experiments. Filled circles indicate participants' standing locations in the learning room and the novel room.

chair. On this chair we have placed a telephone." While no telephone was present during the visual inspection of the lab, both the bookcase and the chair were pointed out to participants before they were blindfolded. We provided visual details about the appearance of the objects to enhance the vividness of the resulting mental representation. The descriptions that were used were based on pilot work in which five naive research assistants were asked to provide descriptions for objects placed in the room. The learning phase continued and descriptions were repeated until participants indicated that they had memorized the locations of all six described objects. Participants' memories were not tested at this point. Instead, when participants indicated that they had memorized all locations they were asked to mentally attend to each object's location one more time. Even after participants reported remembering all locations, we repeated descriptions once more to allow for a final check.

**Testing phase.** Once the learning phase ended, participants assigned to the nonimmediate condition were guided to the adjacent room. Participants continued to wear the blindfold but could look downward toward their feet to keep track of their movement. Participants were positioned in the center of the adjacent room facing the direction shown in Figure 1. This facing direction (herein referred to as the *testing orientation*) deviated 90° from the learning orientation. Participants in the immediate condition were also guided outside of the room but then returned to the position they occupied during learning. However, they were turned to a new facing orientation which, as in the nonimmediate condition, deviated 90° from the learning orientation. In both conditions, a joystick was placed in front of them and was aligned with their facing direction. Participants in both conditions performed the same task of locating remembered object locations from imagined perspectives. On each trial participants heard a statement of the form "Imagine standing in the center of the layout facing  $x$ ," where  $x$  was one of the objects learned through spatial language. Participants were instructed to press a button on the joystick once they had imagined facing toward that object (this was the orienting phase of the task). Participants then heard a statement of the form "Point to  $y$ ," where  $y$  was a different object from the layout. Participants attempted to deflect the joystick in the direction of  $y$  as if they were facing  $x$  and then pressed a button to log their response (this was the response phase of the task). Participants completed one practice block and one experimental block of 30 trials each. The large number of practice trials was used because

participants often find this task counterintuitive and express confusion as to how they should respond (see also Presson & Montello, 1994). Different sets of objects were used in each block with the mapping of set to block counterbalanced across participants.

Pointing error, orientation latency, and response latency constituted the dependent measures. Pointing error was operationalized as the unsigned angular deviation of the joystick response from veridical. *Orientation latency* referred to the latency for pressing a joystick key to indicate that the imagined perspective was adopted. Timing began when the orientation instruction was provided and ended when participants pressed the button to request the target object. Response latency was measured from the time the target object was requested until participants pressed a button to enter their response after deflecting the joystick. Latency analyses only included responses that deviated less than 22.5° from the correct direction response (i.e., responses considered to be correct).

## Results

In this experiment and all subsequent experiments, we focused on pointing error as the primary dependent measure. In all cases, orienting latencies and response latencies displayed the same general pattern found in pointing errors, and there was no evidence of speed-accuracy trade-offs. Latencies are provided in the supplementary online material.

Following Kelly et al. (2007), we calculated encoding and sensorimotor alignment effects by comparing performance at the 0°, 90° and 270° imagined perspectives. Superior performance from 90° compared to 270° indicates a sensorimotor alignment effect, since 90° and 270° are aligned and misaligned with the body, respectively, and both are equally misaligned with the learning perspective. Superior performance from 0° compared with 270° indicates an encoding alignment effect, since 0° and 270° are aligned with the learning perspective and misaligned with the body, respectively, and both are misaligned with the body. Magnitudes of the encoding and sensorimotor alignment effects were calculated as follows:

### Encoding effect

$$\text{Accuracy}(270^\circ) - \text{Accuracy}(0^\circ) \quad (1)$$

### Sensorimotor effect

$$\text{Accuracy}(270^\circ) - \text{Accuracy}(90^\circ) \quad (2)$$

As performance on other perspectives was not considered particularly diagnostic, and for the sake of simplicity, in the following analyses we only included data from the three imagined perspectives (0°, 90°, and 270°) needed to assess encoding and sensorimotor alignment effects. Nevertheless, performance from all imagined perspectives is depicted in the figures for interested readers. Pointing errors were analyzed in repeated measures analyses of variance (ANOVAs) with terms for testing location (immediate or nonimmediate) and imagined perspective (0°, 90°, or 270°). Data from three participants were removed due to very low accuracy (<20%).

Results revealed a significant main effect of imagined perspective and a nonsignificant interaction between imagined perspective,  $F(2, 70) = 4.30, p < .05, \eta^2 = .11$ , and testing location,  $F(2, 70) = 2.91, p = .06, \eta^2 = .08$ . The main effect of test location was not significant,  $F(1, 35) = 0.6, p = .81, \eta^2 = .002$ . Pair-wise comparisons showed that in both testing locations pointing error was lower when imagining the 0° perspective than the 270° perspective ( $ps < .05$ ). Furthermore, in the immediate testing condition error was lower for the 90° perspective than the 270° perspective ( $p < .05$ ). In contrast, there was no performance difference between 90° and 270° when testing occurred in the nonimmediate location ( $p = .34$ ). The pattern of errors for all perspectives as a function of testing condition is shown in Figure 2.

We used Equations 1 and 2 to compute the encoding and sensorimotor alignment effects for the two testing locations (see Figure 3). A reliable encoding alignment effect (for which the 95% confidence interval does not include 0°) was present for both testing conditions. However, a sensorimotor alignment effect was present only in the immediate testing condition.

**Discussion**

The results of Experiment 1 indicate the presence of an encoding alignment effect when reasoning about immediate or nonimmediate spatial locations and a sensorimotor alignment effect only when reasoning about immediate locations. The presence of an encoding alignment effect in both testing locations shows that participants formed orientation-dependent memories when encoding the layout. Indeed, performance was superior when participants adopted an imagined perspective aligned with the learning perspective. This perspective was also aligned with the primary axis of the room that was previously observed by participants.

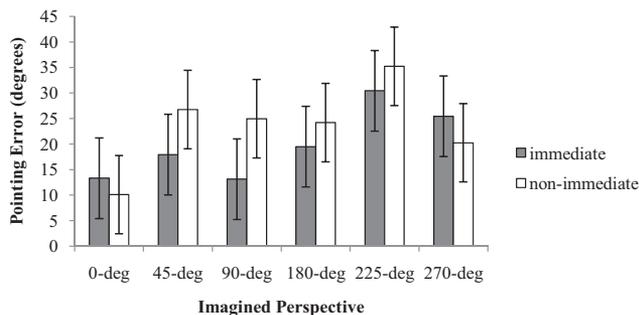


Figure 2. Pointing error as a function of imagined perspective and testing condition in Experiment 1. Error bars indicate 95% confidence intervals.

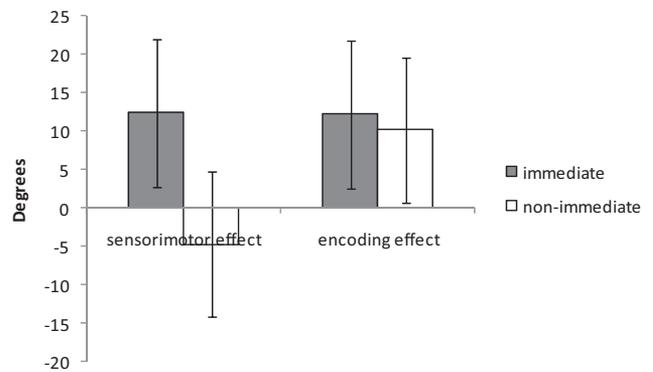


Figure 3. Encoding and sensorimotor alignment effects in pointing error in Experiment 1. Error bars indicate 95% confidence intervals.

Although our findings do not indicate whether these memories were egocentric or allocentric, we argue based on previous studies that the memories were allocentric but stored in a preferred orientation determined by egocentric experience (Mou & McNamara, 2002). Interestingly, the encoding alignment effect was smaller in the nonimmediate than the immediate condition. However, this was not caused by inferior performance from the encoding perspective. Instead, the smaller effect was due to superior performance from the misaligned 270° perspective in the nonimmediate condition. As suggested by Avraamides and Kelly (2008), reasoning about nonimmediate environments is free of sensorimotor interference, which could account for the better performance from the misaligned perspective. As a result, in the current analyses we might overestimate the magnitude of the encoding alignment effect in cases where a sensorimotor alignment effect also occurs. We return to this issue in the General Discussion.

As predicted, a sensorimotor alignment effect was observed only in the immediate condition. This replicates the findings of Kelly et al. (2007), who reported the same result with visual scenes. Our conjecture is that this sensorimotor alignment effect is caused by the egocentric relations stored in the transient memory system, which are updated continuously during movement within the represented environment. This transient egocentric representation facilitates reasoning from one’s actual perspective and interferes when egocentric codes must be inhibited in order to respond from a misaligned imagined perspective (May, 2004). Following this logic, the absence of a sensorimotor encoding effect in the nonimmediate condition stems from a combination of decreased facilitation for the sensorimotor-aligned perspective and decreased interference for the misaligned perspective. The bases for encoding and sensorimotor alignment effects are discussed further in the General Discussion.

In summary, Experiment 1 replicates findings from previous studies using visual scenes and provides support for the functional equivalence account. The presence of sensorimotor and encoding alignment effects indicates that participants formed egocentric and allocentric representations of the described object locations, a striking parallel to previous findings using visually learned scenes. Also similar to findings using visual learning, the egocentric representation was transient, and its associated sensorimotor alignment effect disappeared when participants left the learning envi-

ronment. The allocentric representation was more enduring, and the associated encoding alignment effect persisted even after participants left the learning environment.

In Experiment 2, we further tested the functional equivalence account by examining whether a sensorimotor alignment effect can be observed in a nonimmediate environment by providing imagery instructions. Imagery instructions may serve to bring remote spatial relations into focus and promote reencoding within a sensorimotor framework. Indeed, previous studies with visual scenes (Kelly et al., 2007; May, 2007) have shown that sensorimotor alignment effects can occur in a remote environment when participants are instructed to visualize the remote objects. In the present experiment, we examined whether this effect of imagery extends to scenes encoded through language.

## Experiment 2

Previous researchers employing imagery instructions have found evidence for sensorimotor alignment effects under both immediate and remote testing conditions. In a study by May (2007), participants visually encoded a spatial layout of eight objects in one room and were subsequently tested either in the same room (similar to the immediate testing condition in Experiment 1) or in a room on a different floor of the building (similar to the remote testing condition in Experiment 1 but farther removed from the learning environment). Prior to testing, participants in both conditions were asked to imagine as if they were standing in the learning room and to recall the locations of the eight objects. Unlike the results from Experiment 1, May (2007) found similar perspective-taking performance in the two testing locations. However, because participants adopted a testing perspective identical to (in immediate testing) or aligned with (in remote testing) the learning orientation, it cannot be determined whether the alignment effect was an encoding, a sensorimotor, or a combined effect. The findings of May (2007) were replicated by Kelly et al. (2007). By dissociating the learning and testing perspectives, Kelly et al. found an encoding and a sensorimotor alignment effect in both immediate and nonimmediate testing conditions. Thus, based on

the findings of Kelly et al., we expected that both types of alignment effects would be found in the present experiment. We anticipated that imagery instructions would encourage participants to recode object locations in a sensorimotor framework even when standing in the nonimmediate environment, thereby overcoming the spatial decontextualization that normally occurs during nonimmediate testing.

In pursuit of further evidence for functional equivalence for locations learned through vision and language, we designed Experiment 2 to test whether a sensorimotor alignment effect would occur in a nonimmediate environment if participants were given imagery instructions. The task was identical to the nonimmediate condition of Experiment 1 with one notable exception: When participants assumed the testing perspective but before any trials were presented, they were asked to imagine the previously learned scene around them (“Now imagine all the objects that were earlier described as being around you”). Participants were given unlimited time to do so. The immediate testing condition from Experiment 1 was not included in Experiment 2. Twelve participants were recruited for this experiment.

## Results

Absolute pointing error (see Figure 4) was analyzed in a one-way repeated measures ANOVA. Results showed a significant main effect of imagined perspective,  $F(2, 22) = 6.99$ ,  $p < .01$ ,  $\eta^2 = .39$ . Pair-wise comparisons showed pointing errors were lower when responding from  $0^\circ$  than from either  $90^\circ$  or  $270^\circ$  ( $p < .05$  and  $p = .057$ , respectively). Furthermore, pointing error was lower when pointing from  $270^\circ$  than from  $90^\circ$  ( $p < .05$ ).

We used Equations 1 and 2 to compute encoding and sensorimotor alignment effects. As seen in Figure 5, an encoding alignment effect was present. Surprisingly, a reverse sensorimotor alignment effect was found.

## Discussion

Despite the imagery instruction used in Experiment 2, results replicated those of the nonimmediate condition of Experiment 1

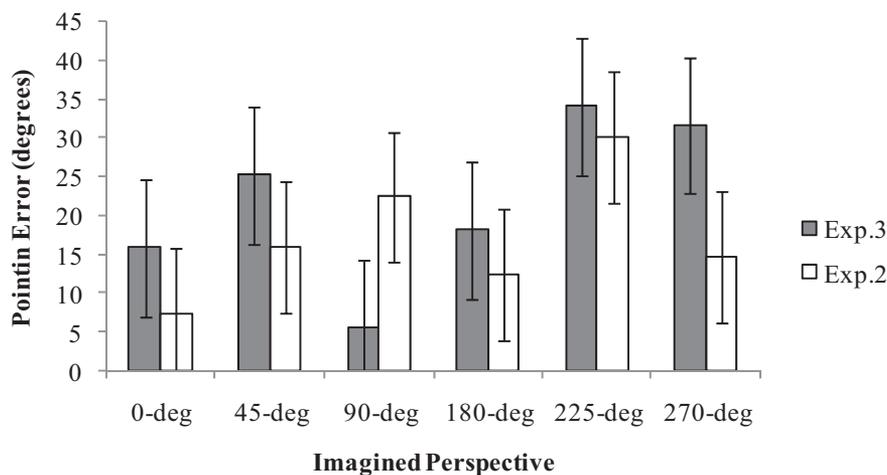


Figure 4. Pointing error as a function of imagined perspective and testing condition in Experiments 2 and 3. Error bars indicate 95% confidence intervals.

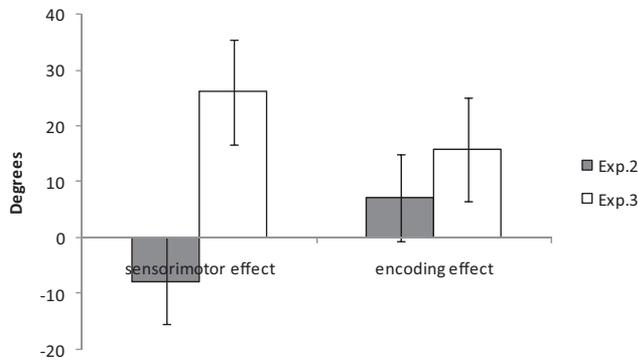


Figure 5. Encoding and sensorimotor alignment effects in pointing error in Experiments 2 and 3. Error bars indicate 95% confidence intervals.

and contradicted previous findings (Kelly et al., 2007; May, 2007). Although a clear encoding alignment effect was found in pointing error, no sensorimotor effect was found. If anything, a reverse sensorimotor effect was found, indicating that participants pointed more accurately when adopting the misaligned than the sensorimotor aligned perspective. While it is not clear how a reverse sensorimotor alignment effect came about, there is no doubt that the findings from this experiment did not conform to the predictions.

Although these results seem to argue against the functional equivalence account, an observation made during this experiment may provide an explanation. When asked to imagine the remembered scene, most participants made spontaneous gestures toward imagined locations and overtly rehearsed the object names. It was obvious from these spontaneous verbal protocols and gestures that participants imagined the scene as if they had adopted the learning perspective despite the fact that they were actually facing 90° clockwise from that perspective. In other words, participants imagined the scene such that there was no longer a discrepancy between the learning perspective and their actual facing orientation.

One possibility is that participants became disoriented while moving to the adjacent room. Disorientation has been previously shown to reduce the effect of sensorimotor codes (May, 1996). Furthermore, Mou, McNamara, Rump, and Xiao (2006) showed that many disoriented participants assumed the learning perspective. In the present study, disorientation seems rather unlikely because the path toward the testing location was simple, and previous studies have shown that people can update their allocentric position and orientation quite efficiently even on the basis of vestibular signals and kinesthetic cues alone (e.g., Klatzky, Loomis, Beall, Chance, & Golledge, 1998). A more plausible hypothesis is that the influence of the transient system was so reduced when participants moved away from the learning environment that they were able to construct an egocentric representation for the remembered scene from any subjective orientation they wished. A good strategy, in that case, would be to adopt a subjective perspective aligned with the perspective in which the enduring representation of the layout is maintained.

A second possibility is that, in contrast to objects learned through vision, objects learned through spatial language cannot be attached to a sensorimotor representation through imagery instructions, and direct perceptual experience is required. Compatible

with this hypothesis are findings reported by Wang (2004), where participants encoded a layout of objects within the laboratory and also imagined standing in their kitchens. They then pointed to lab objects after turning to face other laboratory objects (update-real condition) or after turning to face kitchen objects (update-imagined condition). When the laboratory objects were learned through either vision or touch, pointing latency in the update-imagined condition was comparable before and after rotation, suggesting that locations were automatically updated during rotation. However, when laboratory objects were encoded through verbal descriptions, pointing latency in the update-imagined condition was longer after rotation, suggesting that objects learned through spatial language are not automatically updated with self-motion. Since egocentric spatial updating is generally regarded as a mechanism operating on transient sensorimotor representations (Mou, McNamara, et al., 2004; Waller & Hodgson, 2006), the findings of Wang (2004) suggest that it is possible that no such representations are created from spatial language.

We designed Experiment 3 to evaluate whether participants became disoriented upon moving to the nonimmediate environment. Furthermore, we examined again whether sensorimotor effects can be obtained in a nonimmediate environment when imagery instructions are provided. In contrast to Experiment 2, in which participants adopted the testing perspective prior to imagining the objects around them, in Experiment 3 imagery instructions were given while participants occupied a perspective that was globally aligned with the learning perspective (despite the fact that they had walked to the novel environment). This was done to encourage participants to adopt a subjective heading aligned with the learning perspective and then update it when rotating to assume the testing perspective. If a sensorimotor representation is formed, then object locations should be updated during rotation, giving rise to a sensorimotor alignment effect.

### Experiment 3

The task was identical to that of Experiment 2 except for the procedures that occurred between learning and testing. Upon entering the nonimmediate testing room, participants faced 0°, globally aligned with the learning perspective. To test whether participants became disoriented when walking to the nonimmediate testing room, we asked them to point as fast as they could toward the television that was present in the learning room 90° to the right of the learning perspective. Pointing error was judged visually by the experimenter, and pointing responses within approximately  $\pm 15^\circ$  were judged as being correct. After pointing to the television, participants were instructed to imagine the objects from the previously learned spatial layout as being around them. Once they reported having imagined the scene, they were then asked to slowly rotate toward the direction of the television, which coincided with the 90° testing perspective. Sixteen participants were recruited for this experiment.

### Results

All participants pointed accurately and quickly toward the television, indicating that they accurately updated their position and orientation during the movement to the adjacent room. This ruled

out the disorientation account. Data from one participant were excluded from all analyses due to very low accuracy (<15%).

Pointing error (see Figure 4) was analyzed in a one-way repeated measures ANOVA. Results indicated a significant main effect of imagined perspective,  $F(2, 28) = 7.61, p < .01, \eta^2 = .35$ . Pair-wise comparisons showed that pointing error was lower when responding from  $0^\circ$  than  $270^\circ$  ( $p < .05$ ). Also, error was lower when responding from  $90^\circ$  than from  $270^\circ$  ( $p < .01$ ). Although average pointing error was lower for  $90^\circ$  than  $0^\circ$ , this difference was not statistically significant ( $p = .12$ ).

As in the previous experiments, we computed the encoding and sensorimotor alignment effects. As shown in Figure 5, both an encoding alignment effect and a sensorimotor alignment effect were present.

## Discussion

Results from Experiment 3 verified that sensorimotor alignment effects can occur even in a nonimmediate environment when imagery instructions are provided. These results replicate the findings from studies with visual scenes (Kelly et al., 2007; May, 2007), providing further support for functional equivalence between representations containing visual and described objects. These findings also suggest that spatial updating of remote locations is possible under some circumstances. In the present experiment, participants rehearsed the remembered locations from one perspective but then rotated  $90^\circ$  to adopt a novel perspective. The fact that performance when imagining the perspective aligned with their bodies was superior to performance when imagining the perspective directly behind them suggests that participants updated the egocentric object locations during rotation. Previous researchers have claimed that spatial updating is a dynamic process involving only a limited number of objects from one's surroundings (Wang & Spelke, 2000). While this seems to be the typical case for spatial updating, the present results suggest that if remote objects are brought into attentional focus (and presumably reencoded in a sensorimotor framework), they can be updated during observer movement. These findings have important implications for theories that propose multiple systems for transient and enduring spatial memories. While these systems are generally depicted to be separate, they are nevertheless linked; the present results show that attentional processes can provide an interface between the two systems, allowing for egocentric cognitive immersion within a remote environment.

Finally, the results from Experiment 3 rule out two hypotheses regarding the absence of a sensorimotor alignment effect in Experiment 2. Fast and accurate pointing toward a visually encoded object from the learning environment indicated that none of the participants became disoriented while moving to the adjacent room. Also, the presence of a sensorimotor alignment effect suggests that described objects can be encoded in sensorimotor representations. Our conjecture about Experiment 2 is that the absence of any sensorimotor influence allowed participants to flexibly assume any subjective heading when imagining the objects around them. Adopting a subjective heading coincident with the learning perspective seems an ideal choice, as it ensures that no reference frame conflicts arise.

## General Discussion

The results from three experiments using described scenes showed that (a) independent sensorimotor and encoding alignment effects occur when reasoning about immediate environments, (b) encoding but not sensorimotor alignment effects are present when reasoning about nonimmediate environments, and (c) sensorimotor alignment effects within nonimmediate environments can be induced through imagery instructions. These results replicate previous findings obtained from similar experiments using visually learned scenes (Kelly et al., 2007; May, 2007; Mou, McNamara, et al., 2004).

It is possible that these experiments overestimate the magnitude of the encoding alignment effect in conditions where a sensorimotor alignment effect also occurred. This is because the misaligned perspective served as the baseline for measuring both encoding and sensorimotor alignment effects, and performance on the misaligned perspective may have been worse due to (a) misalignment with the learning perspective and (b) misalignment with participants' actual perspective. However, conditions in which no sensorimotor alignment effect occurred (the nonimmediate conditions of Experiment 1 and Experiment 2) provide an unbiased indication of the presence of an encoding alignment effect.

Taken together with previous studies using visual scenes, the findings of the present study provide support for the functional equivalence hypothesis. Although the spatial scenes used in the present experiments were not purely linguistic, the similar sensorimotor and encoding alignment effects in previous studies using visual scenes suggest that spatial memories for visual and described targets share similar organizational properties. Whether learning locations primarily through vision or through spatial language, participants formed two types of spatial representations: a transient egocentric representation and an enduring allocentric representation. Based on previous neuroscience findings, we posit that transient egocentric representations are maintained in the precuneus (Wolbers et al., 2008) while enduring allocentric representations are maintained in the hippocampus (Maguire et al., 1998; O'Keefe & Nadel, 1978). The claim that representations of visually inspected and described targets are functionally equivalent is compatible with the model proposed by Loomis et al. (2007). Based on Bryant's (1997) argument for amodal representations, this model posits that both the linguistic processing of verbal information and the sensory processing of visual and auditory stimulation leads to construction of a spatial image that is independent of the input. This spatial image can be subsequently retrieved in order to produce responses or can be updated during observer movement.

Despite similarities between the current findings using described targets and previous findings using visual scenes, it is unclear whether spatial language is independently sufficient to generate comparable spatial representations. In the current experiments, participants visually experienced a real environment prior to closing their eyes and learning object locations through spatial language. The prior visual experience might have provided a visual scaffolding that encouraged formation of an allocentric representation. This is conceptually similar to the finding that blind children typically represent haptic locations egocentrically, whereas blindfolded sighted children represent those same haptic locations allocentrically, suggesting an important role for prior visual experience.

rience in creating allocentric representations (Millar, 1979). Future work is needed to determine whether spatial language by itself results in spatial memories similar to those found here, where participants had prior visual experience in the environment. Furthermore, the object locations were described in both egocentric and allocentric terms, and this may play an important role in generating both egocentric and allocentric spatial representations. Future experiments in which scenes are described purely egocentrically or purely allocentrically should shed light on this issue.

It is possible that participants in these experiments associated described object locations with previously viewed objects and recalled those visually learned objects when performing the task. Although we cannot rule out this possibility, anecdotal evidence from Experiments 2 and 3 suggests that this was not the case. In these experiments, participants were asked to imagine the described objects as being around them. Then, most of the participants spontaneously gestured toward described objects and rehearsed out loud their names. Importantly, no participant rehearsed the names of any of the visual objects during this imagery phase. This suggests that participants focused attention on the described rather than on the visual objects.

Two previous studies measuring brain activity during retrieval of information encoded from vision and language provided results that seem *prima facie* at odds with the functional equivalence hypothesis. First, experiments by Mellet et al. (2000, 2002) have shown that both visual and verbal learning of locations activated the same parieto-frontal areas of the brain (measured using PET) but that visual learning also activated the right medial temporal lobe and verbal learning selectively activated the language centers of the brain. Second, a more recent study by Tlauka, Keage, and Richard (2005) that recorded EEG signals at the scalp of participants when processing spatial information previously encoded through vision and language found differences among the two sources in terms of the latency, amplitude, and topography of various early brain waves.

The presence of common activation in such studies may be taken as evidence in favor of functional equivalence. However, the additional presence of selective activation by different modalities suggests that a trace of the input modality is present at retrieval. In our opinion, this does not undermine the functional equivalence account. At least for linguistic input, it seems reasonable that retrieving information from a spatial representation also activates linguistic areas of the brain, as it is well known that verbal descriptions can be encoded at multiple levels (Van Dijk & Kintsch, 1983). As a result, a representation maintaining surface information from the verbal description may be automatically activated upon retrieving spatial information from an amodal spatial image. Similarly, a visual percept can be primed when retrieving spatial relations from a spatial image formed after visual processing.

Overall, the findings from the three experiments reported here support the idea that spatial memories formed from verbal descriptions are stored in two separate representational systems, echoing recent theories based on spatial memories acquired through vision. This idea was first formally expressed in the two-system self-reference model proposed by Easton and Sholl (1995; Sholl, 2001). Their model proposes an orientation-independent allocentric system that maintains interobject spatial relations in long-term memory and an egocentric self-reference system that codes and updates self-to-object relations. According to Sholl (2001), the

self-reference system can operate at two levels. At the perceptual-motor level, it functions to maintain egocentric relations with objects from the immediate surroundings to support visually guided actions directed toward remembered objects. At the representational level, the self-reference system interfaces with the allocentric system to allow retrieval of information from long-term memory. Sholl's model predicts the presence of a sensorimotor alignment effect in the immediate environment by claiming that retrieval is mediated by the self-reference system operating at the perceptual-motor level. Moreover, the model can also accommodate the absence of a sensorimotor effect in the nonimmediate condition by claiming that retrieval in that case used only the allocentric system. However, the presence of an encoding alignment effect poses a problem for Sholl's model, which postulates that long-term memories are maintained in an orientation-independent manner. A number of recent researchers documented that spatial memories are maintained in an orientation-specific manner (e.g., Mou & McNamara, 2002); the presence of an encoding-alignment effect in the present study provides further support for this claim.

A similar model was proposed by McNamara and colleagues (McNamara, 2003; Mou, McNamara, et al., 2004). This model also provides for two representational systems. Like Sholl's (2001) model, an egocentric system is responsible for coding and updating information needed to support on-line actions in the remembered space. In addition, an allocentric system maintains object-to-object spatial relations. In contrast to Sholl's model, McNamara's (2003) model posits that spatial layouts are organized along intrinsic axes that are stored in memory from preferred orientations. According to Mou and McNamara (2002), a variety of cues, including layout symmetry, room structure, instructions, and learning perspective determine the preferred orientation. Thus, this model can readily account for encoding effects in the present study. We believe that the learning perspective in the present study was used to establish the orientation in which the spatial memory was stored as this perspective was also aligned with a primary room axis, and no other salient cues favored any other orientation.

Based on the models of Sholl (2001) and of McNamara and colleagues (McNamara, 2003; Mou, McNamara, et al., 2004), Avraamides and Kelly (2008) described a hybrid model to describe spatial reasoning about immediate and nonimmediate environments. Like Mou, McNamara, et al.'s (2004) model, this model claims that, upon experiencing a spatial scene, people simultaneously construct two representations (see also Waller & Hodgson, 2006). One representation is a dynamic sensorimotor representation containing self-to-object spatial relations of the immediate surroundings (Wang & Spelke, 2000). These relations are automatically updated during movement within the environment through vestibular and proprioceptive cues. Furthermore, the sensorimotor codes defining egocentric object locations are constantly active and available to the observer, as claimed by May (2004). A second representation is allocentric in nature and stores object-to-object relations in long-term memory. As claimed by McNamara (2003), this representation is organized on the basis of intrinsic axes stored in memory with a preferred orientation. Indeed, Mou, Zhang, and McNamara (2004) provided evidence that spatial memories acquired from language are also organized along intrinsic axes.

According to Avraamides and Kelly (2008), when reasoning about one's immediate surroundings, the two representations interface such that the origin of the egocentric representation is represented as a location within the allocentric representation. This is compatible with neuroscientific evidence showing that the hippocampus (in which allocentric representations are most likely stored) and the posterior parietal cortex (in which egocentric representation are presumably maintained) are both active when moving within a familiar environment (Maguire et al., 1998). This link between egocentric and allocentric representations has two consequences. First, as May (2004) has argued, when locating an object from one's current position and orientation, performance is facilitated due to the presence of a sensorimotor code priming the correct response. This is compatible with the findings of Wolbers et al. (2008) that motor programs specifying egocentric responses to remembered objects were continuously updated during simulated movement in a virtual environment. Second, when reasoning from an imagined perspective, performance suffers because the sensorimotor code automatically activates an incorrect response and must be suppressed (May, 2004). This account predicts that sensorimotor alignment effects result from both facilitation when reasoning from the aligned perspective and interference when reasoning from misaligned perspectives. Empirically, this account has been supported by studies showing that disorientation eliminates the sensorimotor alignment effect by reducing both facilitation and interference (e.g., May, 1996).

Avraamides and Kelly (2008) argued that the sensorimotor alignment effect does not typically occur when reasoning about nonimmediate environments because the two representations are not linked. The sensorimotor representation encodes spatial relations from the immediate surroundings, which are different from those maintained by the allocentric representation. As a result, neither facilitation from aligned perspectives nor interference from misaligned perspectives is experienced. In Experiment 1 of the present study, the sensorimotor alignment effect was eliminated in the nonimmediate condition. As shown in Figure 2 and Supplementary Figure S1, this seems to have occurred as a result of both reduced facilitation for the aligned perspective and diminished interference for the misaligned perspective. Similar to the findings of Kelly et al. (2007), Experiment 3 provided evidence that a sensorimotor alignment effect can occur in a nonimmediate environment through instructions promoting egocentric imagery of the remote scene within the local environment (see also May, 2007). Presumably this occurs because imagery serves to interface the allocentric and sensorimotor representations, thereby constructing egocentric codes to previously encoded locations. As a result, the beneficial spatial decontextualization that remote testing provides is eliminated (May, 2007). Results from Experiment 2 are compatible with the hypothesis that, when reasoning about a remote environment, participants can adjust the interfacing of the two representations so that reference frame conflicts are prevented. However, this hypothesis remains to be explored more thoroughly by future researchers.

In summary, using scenes learned through spatial language, we replicated some of the primary findings regarding spatial memories for visually learned scenes. The results suggest that visual learning is not required for constructing and maintaining spatial representations. In fact, the striking similarity between the current results and those of previous studies using visual learning provides

converging evidence that representations derived from different input modalities form functionally equivalent spatial representations. Unlike previous work, where similarity in average latencies or errors has been considered evidence for functional equivalence, the current experiments demonstrate common sensorimotor and encoding alignment effects (i.e., theoretically predicted facilitation patterns across different imagined perspectives) in layouts learned through spatial language and through vision, thereby providing stronger support for functional equivalence. Although this study did not include a direct comparison of described and visually encoded scenes, taken together with the results of Kelly et al. (2007), Mou, McNamara, et al. (2004), and May (2007), the present results suggest that a common, possibly amodal spatial representation might underlie spatial reasoning for visual and described objects. Future research with purely linguistic scenes may be useful in further examining this possibility.

## References

- Amorim, M. A., Glasauer, S., Corpinot, K., & Berthoz, A. (1997). Updating an object's orientation and location during nonvisual navigation: A comparison between two processing modes. *Perception & Psychophysics*, *59*, 404–418.
- Avraamides, M. N., & Kelly, J. W. (2008). Multiple systems of spatial memory and action. *Cognitive Processing*, *9*, 93–106.
- Avraamides, M. N., Loomis, J. M., Klatzky, R. L., & Golledge, R. G. (2004). Functional equivalence of spatial representations derived from vision and language: Evidence from allocentric judgments. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *30*, 804–814.
- Bryant, D. (1997). Representing space in language and perception. *Mind & Language*, *12*, 239–264.
- Byrne, P., Becker, S., & Burgess, N. (2007). Remembering the past and imagining the future: A neural model of spatial memory and imagery. *Psychological Review*, *114*, 340–375.
- Colby, C. L. (1998). Action-oriented spatial reference frames in cortex. *Neuron*, *20*, 15–24.
- Easton, R. D., & Sholl, M. J. (1995). Object-array structure, frames of reference, and retrieval of spatial knowledge. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*, 483–500.
- Epstein, R. A. (2008). Parahippocampal and retrosplenial contributions to human spatial navigation. *Trends in Cognitive Science*, *12*, 388–396.
- Epstein, R. A., Parker, W. E., & Feiler, A. M. (2007). Where am I now? Distinct roles for parahippocampal and retrosplenial cortices in place recognition. *The Journal of Neuroscience*, *27*, 6141–6149.
- Farrell, M. J., & Thomson, J. A. (1999). On-line updating of spatial information during locomotion without vision. *Journal of Motor Behavior*, *31*, 39–53.
- Johnson-Laird, P. N. (1983). *Mental models: Towards a cognitive science of language, inference, and consciousness*. Cambridge, United Kingdom: Cambridge University Press.
- Johnson-Laird, P. N. (1996). Space to think. In P. Bloom, M. A. Peterson, L. Nadel, & F. Garrett (Eds.), *Language and space* (pp. 437–462). Cambridge, MA: MIT Press.
- Kelly, J. W., Avraamides, M. N., & Loomis, J. M. (2007). Sensorimotor alignment effects in the learning environment and in novel environments. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *33*, 1092–1107.
- Klatzky, R. L., Lippa, Y., Loomis, J. M., & Golledge, R. G. (2002). Learning directions of objects specified by vision, spatial audition, or auditory spatial language. *Learning & Memory*, *9*, 364–367.
- Klatzky, R. L., Loomis, J. M., Beall, A. C., Chance, S. S., & Golledge, R. G. (1998). Spatial updating of self-position and orientation during

- real, imagined, and virtual locomotion. *Psychological Science*, 9, 293–298.
- Loomis, J. M., Klatzky, R. L., Avraamides, M. N., Lippa, Y., & Golledge, R. G. (2007). Functional equivalence of spatial images produced by perception and spatial language. In F. Mast & L. Jäncke (Eds.), *Spatial processing in navigation, imagery, and perception* (pp. 29–48). New York: Springer.
- Loomis, J. M., Lippa, Y., Golledge, R. G., & Klatzky, R. L. (2002). Spatial updating of locations specified by 3-d sound and spatial language. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 28, 335–345.
- Maguire, E. A., Burgess, N., Donnett, J. G., Frackowiak, R. S. J., Firth, C. D., & O'Keefe, J. (1998, May 8). Knowing where and getting there: A human navigation network. *Science*, 280, 921–924.
- May, M. (1996). Cognitive and embodied modes of spatial imagery. *Psychologische Beiträge*, 38, 418–434.
- May, M. (2004). Imaginal perspective switches in remembered environments: Transformation versus interference accounts. *Cognitive Psychology*, 48, 163–206.
- May, M. (2007). Imaginal repositioning in everyday environments: Effects of testing method and setting. *Psychological Research*, 71, 277–287.
- McNamara, T. P. (2003). How are the locations of objects in the environment represented in memory? In C. Freksa, W. Brauer, C. Habel, & K. K. Wender (Eds.), *Spatial cognition: III. Routes and navigation, human memory and learning, spatial representations and spatial reasoning* (Vol. LNAI 2685, pp. 174–191). Berlin: Springer.
- Mellet, E., Bricogne, S., Crivello, F., Mazoyer, B., Denis, M., & Tzourio-Mazoyer, N. (2002). Neural basis of mental scanning of a topographic representation built from a text. *Cerebral Cortex*, 12, 1322–1330.
- Mellet, E., Bricogne, S., Tzourio-Mazoyer, N., Ghaem, O., Petit, L., Zago, L., et al. (2000). Neural correlates of topographic mental exploration: The impact of route versus survey perspective learning. *NeuroImage*, 12, 588–600.
- Millar, S. (1979). Utilization of shape and movement cues in simple spatial tasks by blind and sighted children. *Perception*, 8, 11–20.
- Millar, S., & Al-Attar, Z. (2004). External and body-centered frames of reference in spatial memory: Evidence from touch. *Perception & Psychophysics*, 66, 51–59.
- Mou, W., & McNamara, T. P. (2002). Intrinsic frames of reference in spatial memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 28, 162–170.
- Mou, W., McNamara, T. P., Rump, B., & Xiao, C. (2006). Roles of egocentric and allocentric spatial representations in locomotion and reorientation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 6, 1274–1290.
- Mou, W., McNamara, T. P., Valiquette, C. M., & Rump, B. (2004). Allocentric and egocentric updating of spatial memories. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 30, 142–157.
- Mou, W., Zhang, K., & McNamara, T. P. (2004). Frames of reference in spatial memories acquired from language. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 30, 171–180.
- Noordzij, M. L., & Postma, A. (2005). Categorical and metric distance information in mental representations derived from route and survey descriptions. *Psychological Research*, 69, 221–232.
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford, United Kingdom: Oxford University Press.
- Péruch, P., Chabanne, V., Nesa, M. P., Thinus-Blanc, C., & Denis, M. (2006). Comparing distances in mental images constructed from visual experience or verbal descriptions: The impact of survey versus route perspective. *Quarterly Journal of Experimental Psychology*, 59, 1950–1967.
- Presson, C. C., & Hazelrigg, M. D. (1984). Building spatial representations through primary and secondary learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 10, 716–722.
- Presson, C. C., & Montello, D. R. (1994). Updating after rotational and translational body movements: Coordinate structure of perspective space. *Perception*, 23, 1447–1455.
- Rieser, J. J. (1989). Access to knowledge of spatial structure at novel points of observation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 15, 1157–1165.
- Rieser, J. J., Guth, D. A., & Hill, E. W. (1986). Sensitivity to perspective structure while walking without vision. *Perception*, 15, 173–188.
- Sholl, M. J. (2001). The role of a self-reference system in spatial navigation. In D. R. Montello (Ed.), *Spatial information theory: Foundations of geographic information science* (Vol. 2205, pp. 217–232). Berlin: Springer.
- Sun, H. J., Chan, G. S. W., & Campos, J. (2004). Active navigation and orientation-free spatial representations. *Memory and Cognition*, 32, 51–71.
- Tlauka, M., Keage, H., & Richard, C. C. (2005). Viewing a map versus reading a description of a map: Modality-specific encoding of spatial information. *Cognitive Science*, 29, 807–818.
- Van Dijk, T. A., & Kintsch, W. (1983). *Strategies of discourse comprehension*. New York: Academic Press.
- Waller, D., & Hodgson, E. (2006). Transient and enduring spatial representations under disorientation and self-rotation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 32, 867–882.
- Wang, R. F. (2004). Between reality and imagination: When is spatial updating automatic? *Perception & Psychophysics*, 66, 68–76.
- Wang, R. F., & Brockmole, J. R. (2003). Human navigation in nested environments. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 29, 398–404.
- Wang, R. F., & Spelke, E. S. (2000). Updating egocentric representations in human navigation. *Cognition*, 77, 215–250.
- Wolbers, T., & Büchel, C. (2005). Dissociable retrosplenial and hippocampal contributions to successful formation of survey representations. *The Journal of Neuroscience*, 25, 3333–3340.
- Wolbers, T., Hegarty, M., Büchel, C., & Loomis, J. (2008). Spatial updating: How the brain keeps track of changing object locations during observer motion. *Nature Neuroscience*, 11, 1223–1230.
- Zwaan, R. A., & Radvansky, G. A. (1998). Situation models in language comprehension and memory. *Psychological Bulletin*, 123, 162–185.

Received March 20, 2009

Revision received May 15, 2009

Accepted June 18, 2009 ■