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REVIEW

Multiple systems of spatial memory and action

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Abstract Recent findings from spatial cognition and cognitive neuroscience suggest that different types of mental representations could mediate the off-line retrieval of spatial relations from memory and the on-line guidance of motor actions in space. As a result, a number of models proposing multiple systems of spatial memory have been recently formulated. In the present article we review these models and we evaluate their postulates based on available experimental evidence. Furthermore, we discuss how a multiple-system model can apply to situations in which people reason about their immediate surroundings or non-immediate environments by incorporating a model of sensorimotor facilitation/interference. This model draws heavily on previous accounts of sensorimotor interference and takes into account findings from the stimulus–response compatibility literature.

Introduction

Many tasks of everyday life rely on the processing of spatial relations in perception and memory. In some cases relations must be processed in an on-line manner to support actions such as avoiding obstacles during locomotion, reaching for or pointing to objects in our immediate surroundings etc. In other cases, reasoning takes place in a rather off-line fashion. Examples of such off-line processing are the planning of a route prior to traveling in a familiar environment or the description of a remote environment to others.

It has been suggested that the representations supporting on-line and off-line tasks are subserved by distinct neuroanatomical systems in the brain (Milner and Goodale 1995; Norman 2002). On one hand, the dorsal stream of projection, which extends from the primary visual area (V1) to posterior parietal cortex (PPC), is assumed to process the information needed for the control and guidance of action in space. Consistent with this account is the finding that PPC cells fire to encode spatial locations in different egocentric reference frames (Snyder et al. 1997). These egocentric representations seem to be transient, as delays of even a few seconds have been shown in experimental settings to cause impairments on spatial action (Goodale et al. 1994). Furthermore, the information used by this system is believed to lie outside awareness. Recent data from fMRI work suggests that the precuneous (part of the parietal cortex) is involved in on-line tasks (Wolbers et al. 2007). On the other hand, the ventral stream, which extends from V1 to the inferior parietal cortex (IPC), has been regarded as a system responsible for processing and maintaining the enduring characteristics of objects and the environment. It builds representations that are maintained in an allocentric format and are available to conscious awareness (Milner and Goodale 1995). Tasks that rely on higher-order cognitive functions are believed to rely on this stream of processing. The distinction between dorsal and ventral systems has been also linked to the distinction between theories of direct and indirect perception (see Norman 2002 for a review). Gibson's (1979) ecological approach concerns tasks that are on-line in nature (e.g., negotiating a series of obstacles to arrive at a goal location;

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Fajen and Warren 2003; Loomis et al. 2006), and can therefore be served by the functions of the dorsal system (but see Loomis and Beall 2004 for a model-based account of locomotion). Constructivist/indirect perception theories (e.g., Rock 1983) deal with tasks that are more representational and cognitively mediated and are hence attributed to the workings of the ventral system.

Although the distinction between dorsal and ventral streams is discussed primarily in the context of visual perception, the functions attributed to the two systems seem to apply for spatial tasks executed without visual support. On-line tasks such as locomoting without vision and off-line tasks such as retrieving spatial relations from a non-immediate environment are primarily supported by different neuroanatomical systems (see Byrne et al. 2007 for an extensive discussion of the neural substrates of spatial memory and navigation).

For many years on-line and off-line tasks have been studied separately in the field of spatial cognition. Whereas on-line tasks have been the focus of researchers interested in spatial/egocentric updating, off-line tasks have been used by researchers studying the organizational structure of spatial memory. Over the years a number of influential models have been proposed in both concentrations of research but not until recently have unified theories emerged. To be successful, these theories of spatial cognition must be capable of explaining empirical findings from both spatial updating and spatial memory research. To that end, many of these theories posit multiple systems subserving on-line and off-line tasks.

The goal of the present work is twofold. On one hand, we aim at providing a critical review of the most recent multiple-system theories of spatial cognition. On the other hand we attempt to synthesize a model of sensorimotor facilitation/interference that can be integrated into a spatial cognition theory of this type. Our model is an extension of May's Sensorimotor Interference hypothesis (May 1996, 2004) and draws heavily from previous research on stimulus–response (S–R) compatibility. With this model we attempt to describe explicitly how spatial reasoning could take place about one's immediate surroundings or a distal environment.

We will begin by briefly discussing the main findings from the areas of spatial updating and spatial memory. Then, we will review evidence from recent studies documenting links between these two areas of research and discuss recent models of spatial cognition that propose multiple systems of memory (see also Burgess 2006, Hartley and Burgess 2005). Finally, we will review the basic findings from the field of S–R compatibility and present the sensorimotor facilitation/interference model. An important goal of this paper is to provide a detailed model of sensorimotor facilitation/interference whose predictions can be tested empirically in future research. We regard this model as a starting point for future experimentation.

Updating of egocentric relations

Spatial/egocentric updating refers to the mechanism that allows a moving observer to keep track of changing self-to-object relations (e.g., Rieser 1989; Wang and Spelke 2000). In a typical spatial updating experiment, participants encode in memory the location of one or more targets and then localize it/them from a novel standpoint (e.g., Klatzky et al. 1998). A common manipulation in these studies is the manner in which the novel standpoint is adopted. Movement to the novel standpoint may require translations, rotations, or a combination of the two, resulting in novel standpoints that differ in location and/or orientation from the learning standpoint. Additionally, movement to the novel standpoint can be achieved through physical movement, either active or passive, or through imaginal movement. After arriving at the novel standpoint, participants report the updated target locations using one of a variety of response methods, including body-based and verbal responses.

A typical result from these studies is that performance is best when responding from either the learning standpoint (i.e., no movement) or a novel standpoint adopted by physical movement (e.g., Rieser et al. 1986). In fact, performance is typically comparable from these two standpoints even when the movement towards the novel standpoint is done without vision (but see Hodgson and Waller 2006). Participants are also quite good at continually pointing to a target during physical movement (Loomis et al. 1992). These findings have led researchers to argue that an egocentric representation (i.e., a representation maintaining self-to-object relations) is formed at the learning standpoint and is updated during movement to the novel standpoint using non-visual cues (e.g., Farrell and Thomson 1999). Another important finding from these studies is that performance from a novel standpoint adopted by imagined, compared to physical, movement is severely impaired, especially when the novel standpoint implicates a change of facing direction by means of imagined rotation. In fact, many studies report decreasing accuracy and increasing response latency with increasing angular disparity between the actual and imagined perspective (e.g., Rieser 1989). The superior performance associated with physical movement has been interpreted as evidence for the importance of idiothetic cues (e.g., vestibular signals, proprioceptive information, copies of efferent commands) as input to the spatial updating process. This input presumably allows individuals to update their spatial representations in an effortless and on-line fashion while moving in the environment.

Empirical evidence in favor of such an on-line updating account is provided by Farrell and Thomson (1999). In one experiment, Farrell and Thomson instructed participants to walk to targets and place one of their feet (specified by the experimenter) on the exact target location. This was done both with and without visual input while walking, and the distances of the targets were chosen so that sometimes participants had to adjust their stride length at the final stages of the walk in order to land on the target with the correct foot. Results showed that these adjustments were made even when participants walked without vision. This result suggests that subjects walking without vision were updating their position as they moved with respect to a mental representation of the target's location, instead of executing a preformulated motor plan.

Although spatial updating studies typically report performance benefits for physical compared to imagined movements, it should be pointed out that performance after imagined movements is never at chance levels. It seems that participants are still able to update the positions of the targets; nevertheless, they must be doing so in a different manner. Rieser (1989) has suggested that, in the absence of proprioceptive signals, observers engage in deliberate computations to determine the new egocentric locations of targets. This type of spatial updating is rather effortful, as the computations are taxing to cognitive resources, and possibly takes place in an off-line manner after the imagined movement has been completed.

In contrast to Rieser's (1989) mental transformation hypothesis, May (2004) has proposed that difficulties associated with imagined movement are due to sensorimotor interference. According to this account, reasoning from imagined positions is impaired because it is prone to interference stemming from two sources. First, object-direction disparity (ODD) produces interference due the discrepant physical and imagined (i.e., relative to an imagined egocentric reference frame) object bearings. Compatible with this claim, May found a monotonic increase of pointing error and latency with increasing ODD after imaginal displacement. A second source of interference, termed head-direction disparity (HDD), occurs when the imagined egocentric reference frame is misaligned with the physical egocentric reference frame of the participant (as in the case of imagined movements that involve rotations). In Fig. 1 for example, the HDD (i.e., the angular difference between the observer's physical and imagined facing direction) is 135°. Even when the observer manages to overcome ODD conflicts in computing a response vector, the selected vector must be transformed to bodycentric coordinates. This could explain why imagined translations (in which no HDD conflicts are present) are typically easier than imagined rotations (e.g., Presson and Montello 1994; Rieser 1989). We adopt May's reasoning for our model of sensorimotor facilitation/interference in "Sensorimotor interference when reasoning about immediate environments".

Spatial memory

Experiments aimed at examining the organizational structure of spatial memory have used a somewhat different paradigm from spatial updating studies. In a typical spatial memory experiment, participants first study a spatial scene and are later tested on the learned spatial relations. One popular method of testing is to have participants perform judgments of relative direction (JRD's), in which they are asked to locate one remembered object from an imagined perspective defined by two other objects (e.g., "Imagine standing at X facing Y. Point to Z"). In contrast to spatial updating studies, participants in these experiments are usually tested in a location remote to the learned spatial layout.

In line with the results from spatial updating studies, early findings from a number of experiments concluded that spatial memories are influenced primarily by egocentric experience (e.g., Shelton and McNamara 1997). This conclusion was based on results showing superior

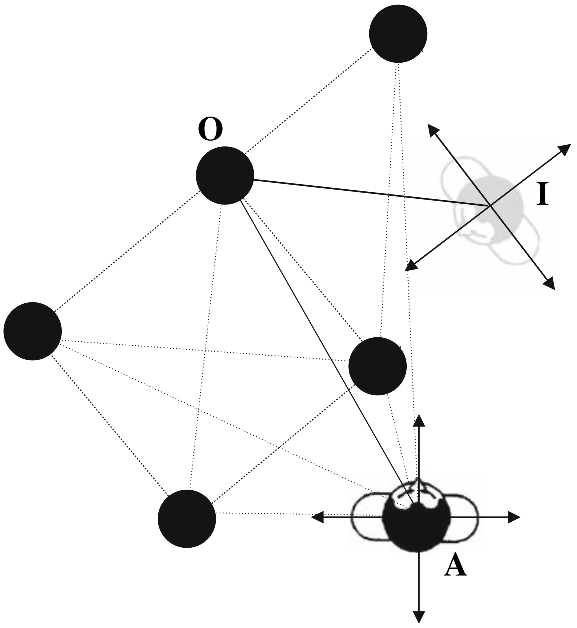

Fig. 1 A model describing spatial reasoning about one's immediate surroundings. *Black circles* represent objects in the immediate environment. *Dashed lines* indicate object-to-object spatial relations. A sensorimotor representation is embedded within an object-to-object system. Locating object *O* from the imagined perspective *I* is prone to interference stemming for the automatic activation of the spatial relation between *O* and the physical standpoint *A*

performance for locating targets from imagined perspectives that were aligned with the learning perspective (i.e., the perspective participants occupied at the time of studying the layout). Based on this finding researchers posited that the locations of objects were encoded in memory using a reference frame selected at the learning location (Shelton and McNamara 1997; but see Easton and Sholl 1995 for a different account). Thus, various accounts of viewpoint-dependent encoding have been formulated. For example, Franklin and Tversky (1990) proposed the Spatial Frameworks model in which locations are encoded relative to a reference frame defined by the extensions of the three body axes (head–feet, front–back, left–right). Shelton and McNamara (1997), on the other hand, argued that spatial memories are organized around reference directions selected from the experienced views.

Despite the ample experimental evidence demonstrating the importance of egocentric experience, recent findings have challenged this view. In one experiment, Shelton and McNamara (2001) had participants learn object locations in the presence of a salient environmental reference frame, redundantly provided by the room walls and a square mat on the floor. Learning occurred from multiple perspectives, but later testing showed that only perspectives aligned with the environmental reference frame axes were represented in memory. This result and others (e.g., Mou and McNamara 2002; Werner and Schmidt 1999) demonstrate the influence of environmental structure on spatial memory. A more complete description is that egocentric experience can dominate in the absence of environmental structure, but that environmental structure can dominate when it is sufficiently salient.

Based on these findings McNamara and colleagues (McNamara 2003; Mou and McNamara 2002; Shelton and McNamara 2001) proposed a new theory of spatial memory. They argued that spatial memories are not egocentric but are instead formed using environmentally defined reference frames. Although allocentric, these representations are stored in memory in a preferred orientation, which can be defined based on a variety of different cues (e.g., the structure of the scene, task instructions etc). However, lacking any cues egocentric experience can be used to determine the preferred orientation.

Memory systems functioning in parallel

The current state of affairs regarding findings from the spatial updating and spatial memory literatures is quite compatible with Milner and Goodale's (1995) theory of separable systems in support of on-line and off-line tasks. Based on this distinction, one may argue that the type of tasks studied in the context of spatial updating rely heavily on dorsal representations, whereas tasks examined in the context of spatial memory depend more on ventral representations. However, even if separate systems exist for spatial memory and spatial updating, this does not mean that only one of the systems can function at a given point in time. Instead, it is possible that the two systems operate in a parallel, even in synergy. If this is indeed the case then it should be possible to create experimental settings in which results independently associated with on-line and off-line tasks will both be obtained. Findings from a recent study by Mou et al. (2004) corroborate this expectation.

In their study, Mou et al. (2004) had participants study a layout of objects from one standpoint and then perform JRD's after moving to a novel standpoint. They independently manipulated: (1) the angle between the learning perspective and the imagined perspective adopted during the JRD task as well as (2) the angle between the participant's actual perspective and the imagined perspective adopted for the JRD task. Results revealed the presence of two independent effects. First, replicating the typical effect from spatial memory studies, performance was superior when the imagined perspective matched the orientation of the learning perspective. We will hereafter refer to this effect as the *memory-encoding alignment effect*. Second, replicating the well-known effect from spatial updating studies, they showed a benefit for imagined perspectives aligned with the participant's physical orientation at test. We will refer to this effect as the *sensorimotor alignment effect*.

The findings reported by Mou et al. (2004) are compatible with the hypothesis that two systems, a ventral and a dorsal one, are operating in parallel. The sensorimotor alignment effect could be due to dorsally mediated processes involved in spatial updating, whereas the memory-encoding alignment effect could be due to ventrally mediated processes involved in the encoding and storing of long-term memory. Findings reported by Sholl (2001), however, suggest that the functioning of the two systems might not be completely independent but instead rely on common resources.

Regardless of the validity of the dorsal-ventral distinction there seems to be a consensus among spatial memory researchers (e.g., Sholl 2001; Mou et al. 2004; Waller and Hodgson 2006) that a successful model of spatial memory must involve multiple systems in order to account for the wealth of empirical findings in the field of spatial cognition. In the next two sections we review four such models and the evidence that exists to support or challenge them.

Models of spatial cognition featuring multiple systems

A pioneering model of spatial memory is the two-system "self-reference" model proposed by Sholl (2001; Easton and Sholl 1995). In this model, one system stores an allocentric representation of object-to-object spatial relations in long-term memory. According to the model, this allocentric representation has no preferred orientation. A second system, the self-reference system, codes and updates egocentric relations to objects using the front–back and left–right axes of the body as reference (e.g., Franklin and Tversky 1990). The model postulates that this self-reference system can function at two levels: a perceptual-motor level and a representational level. At a perceptual-motor level it represents object locations in the immediate environment in order to support visually guided behaviors like reaching and walking toward objects. At a representational level, the self-reference system interfaces with the allocentric system to retrieve spatial information from long-term memory (as in the JRD task). According to Sholl's model, the allocentric system is itself orientation-free. An orientation is only determined at the time of retrieval by superposing the representational self-reference system onto the allocentric system. The model claims that in order to report the location of object *y* from the position of object *x*, one needs to center the representational self-reference system on object *x* (whose location is represented in the allocentric system) in the appropriate orientation and then compute the correct direction–distance vector.

Another well-known model of spatial cognition is the three-system model proposed by Wang and Spelke (2000, 2002). The heart of the model is the dynamic egocentric system that is used to maintain spatial relations between the observer and each of a limited number of objects from the surrounding environment. According to the model, these self-to-object relations are updated on an object-by-object basis as the observer changes position or orientation in the environment. A second system in the model is used to maintain allocentric representations in long-term memory. These representations code the geometric shape of the environment but contain no object-to-object spatial relations. Finally, a third subsystem is used for storing visual snapshots of the environment in a viewpoint-dependent manner.

A third model, consisting of two systems, was recently proposed by Mou et al. (2004). The model is quite similar to that proposed by Sholl (2001). Like Sholl's model, an egocentric system computes self-to-object relations needed for efficient locomotion. According to Mou et al. (2004), the spatial representations used by this system are transient and decay rapidly in the absence of perceptual support, particularly from vision. The second system of the model encodes object locations allocentrically in long-term memory. In contrast to Sholl's model, Mou et al. argue that this system is not orientation-free. Instead, object-to-object spatial relations are represented on the basis of environmental reference frames with preferred orientations, as posited by McNamara's theory (McNamara 2003).

Another two-system account has been recently proposed by Waller and Hodgson (2006). According to this account, spatial information about one's environment is coded simultaneously by two systems. A transient egocentric system, supported by visual and idiothetic cues, allows interaction with the environment by continuously updating egocentric relations to the objects of one's surroundings. This is similar to both the sensorimotor representation described by Mou et al. (2004) and the perceptual-motor representation described by Sholl (2001). In addition to the egocentric system, spatial relations are stored in a more long-term manner but at a coarser level than the egocentric system. According to this account, performance when fully oriented within the environment relies on the transient egocentric system. When egocentric information becomes unavailable or unreliable (as in the case of disorientation) reliance is shifted to the enduring system. Although this model is quite similar to the models of Sholl (2001) and Mou et al. (2004) differences exist in some of its details. For example, Waller and Hodgson (2006) leave open the possibility that the enduring system is also egocentric. Also, compared to the model of Mou et al. (2004), Waller and Hodgson?s argue that transient egocentric representations may remain active based on non-visual support (e.g., proprioceptive information and vestibular feedback).

Empirical evidence relating to models of multiple systems

Since all models reviewed in the preceding section include an egocentric system that is sensitive to the physical position and orientation of the observer, they can all account for the sensorimotor alignment effects reported in spatial updating studies. The Mou et al. (2004) model can also account for the presence of a memory-encoding alignment effect since it proposes that the representation used to store object locations is orientation-dependent. Wang and Spelke's (2000, 2002) model does not provide for the storage of object-to-object spatial relations in an enduring manner, but a memory-encoding alignment effect could presumably be accounted for through the model's viewpoint-dependent visual-snapshot subsystem. Memory-encoding alignment effects seem problematic for Sholl's model, which proposes that long-term spatial memory is represented in an orientation-free allocentric system. Finally, Waller and Hodgson (2006) do not specify whether the enduring system allows for orientation-dependent memories.

Models that include long-term storage of allocentric spatial relations seem to fare well in light of empirical findings from spatial memory studies (e.g., Mou and McNamara 2002). More challenging are findings reported by Wang and Spelke (2000). In these experiments, participants performed egocentric pointing (i.e., pointed directly to the studied locations of six target-objects from their actual orientation and position) under three experimental conditions. In a baseline condition, participants pointed to the non-visible targets with their eyes open from their physical standpoint. In the rotation condition, they pointed to objects without vision after a small rotation. Finally, in the disorientation condition, they pointed to locations without vision after they had been disoriented. Results from this study showed that configuration error (i.e., the standard deviation of the six signed pointing errors, indicating a lack of rigidity in the recalled locations) was greater after disorientation than in the other two conditions. Wang and Spelke (2002) interpreted this result as evidence for a transient egocentric representation that dominates spatial knowledge. Presumably, these egocentric relations could be efficiently updated after a small rotation, but not after disorientation. If participants relied on enduring allocentric representation after disorientation, they should have produced pointing errors consistent with errors in estimating their actual orientation within the environment. Such an error in estimating their own orientation would result in the same signed pointing error for each object, but would not produce the observed configuration error. The results are therefore at odds with models positing long-term allocentric representations, because the internal consistency of such a representation should be unaffected by disorientation.

Wang and Spelke's (2000) findings have sparked much interest in examining the effects of disorientation on the internal consistency of spatial representations. Subsequent studies have attempted to replicate this finding in order to examine various hypotheses that would reconcile the disorientation effect with models positing object-to-object systems.

Holmes and Sholl (2005) hypothesized that the disorientation effect might depend on whether the learned spatial layout is familiar or novel. They conducted a series of seven experiments but failed to replicate Wang and Spelke's (2000) disorientation effect. In fact, configurational error for a subset of participants was lower after disorientation than before disorientation.

Using an egocentric pointing task Mou et al. (2006) found that configuration error increased with disorientation when objects were arranged around the participant in an irregular shape, which did not provide a salient environmental reference frame. However, they found no such increase of configuration error when the layouts offered salient axes and were learned from a standpoint external to the layout. As a result, Mou et al. (2006) argued that egocentric representations control performance only when allocentric representations are of low fidelity.

Waller and Hodgson (2006) examined whether different response tasks were all equally affected by disorientation. Their results showed that configuration error increased after disorientation when pointing to targets egocentrically (a replication of Wang and Spelke 2000). However, configuration error *decreased* after disorientation when using a JRD task, which required retrieval of relative object locations (e.g., "Imagine standing at X, facing Y. Point to Z") rather than egocentric object locations. To account for these findings, Waller and Hodgson argued that a highly precise but transient egocentric representation and a coarser long-term representation are both formed when studying a spatial layout. When oriented to the environment, egocentric pointing performance relies on the egocentric transient representation. However, when disoriented, people switch to using the long-term representation. According to Waller and Hodgson, the increase of configuration error with egocentric pointing after disorientation reflects a switch to the coarser enduring representation. In contrast, performance on the JRD task can actually benefit from disorientation. Presumably this occurs due to a relaxation of interfering sensorimotor cues (see next section), allowing more flexible access to non-occupied perspectives.

The studies of Holmes and Sholl (2005), Mou et al. (2006) and Waller and Hodgson (2006) provide a few conflicting findings that need to be addressed by future research. Nevertheless, the three studies point toward the same conclusion: single-system egocentric models of spatial memory are no longer tenable. Instead, a long-term spatial representation is needed to support spatial reasoning. Although Waller and Hodgson (2006) take no position in terms of the structure of the long-term representation, other empirical findings suggest that this system maintains object-to-object relations (e.g., Easton and Sholl 1995) in an orientation-dependent manner (e.g., Mou et al. 2004). This conclusion is also compatible with the assumption that the ventral system of the brain operates on the basis of enduring representations that are organized around allocentric reference frames. In light of the evidence for dual-system models of spatial memory, we now focus on describing how these two systems might interact. Are they two distinct systems that operate in parallel or are they parts of a single system, sharing a single physical architecture? (see also Sholl 2001). In the next section we will review some recent results suggesting that the two systems can function either as a unified system or as distinct systems depending on whether one is reasoning about the immediate surrounding or a non-immediate environment.

Reasoning about non-immediate environments

While spatial updating experiments traditionally test participants within or in close proximity to the spatial layout, spatial memory studies often disengage participants from the learning environment by testing them in a remote location. In some cases this is done to prevent complicating effects due to participants' physical position and orientation in the scene (e.g., Avraamides and Kelly 2005). Indeed, it seems that when people reason about a remote environment, their physical position becomes irrelevant to spatial reasoning. Imagine, for example, that you are standing somewhere in the downtown area of your city. Does your current physical orientation as you are reading these words in your office or home influence your ability to adopt imagined perspectives in that downtown area, even ones misaligned with your current orientation? Probably not. Nevertheless, only recently have studies compared spatial performance in tasks requiring reasoning for immediate and non-immediate environments.

In one such study (Wang 2004), participants first learned the locations of objects in the laboratory and were also instructed to bring to memory the locations of objects from the kitchen of their homes. Depending on the condition, they were then asked to physically rotate to face a laboratory object or a kitchen object, and then point towards other laboratory objects or kitchen objects from this new perspective. The main question was whether participants would automatically update the locations of objects from both environments when performing the physical rotation. Successful updating would be signified by equal latencies and errors for pointing to objects before and after the physical rotation. Results revealed that when people turned to face a laboratory object they updated the locations of other laboratory objects but not the locations of kitchen objects. However, when they turned to face a kitchen object they updated object locations in both environments. Wang and Brockmole (2003a) found the same result using two nested environments (i.e., the laboratory and the campus in which the laboratory was situated). In both studies, the authors concluded that updating is automatic only for a limited number of egocentric locations contained within one's immediate environment. Locations in a remote environment can be updated in an effortful rather than automatic manner (see also Rieser et al. 1994). On a much larger scale, Gladwin (1970) also describes effortful updating of remote locations as part of a navigational strategy called "etak" used by pacific island dwellers travelling by boat.[1]

All four of the multiple-system models reviewed in "Models of spatial cognition featuring multiple systems" assume that the physical orientation of the participant at the time of test is critical when retrieving spatial locations from the immediate environment because task execution relies primarily on an egocentric representation. As a result, all four models are compatible with Wang's (2004) finding of equal performance for pointing to objects in the immediate environment before and after a physical rotation. If we assume that reasoning about a remote environment relies on a long-term object-to-object representation with a preferred orientation (like that proposed by Mou and McNamara 2002), then the performance advantage for responding to remote targets before than after the physical rotation toward an immediate object could then be explained as a memory-encoding alignment effect.

The question that remains is, however, how participants were able to update the remote locations when they were instructed to physically rotate toward a remote object. If spatial reasoning about a non-immediate environment relies on a long-term representation, why did the physical orientation of the participant at the time of test influence performance? One hypothesis is that the instruction to face a remote object prompted participants to bring the relation between their physical orientation and the stored orientation of the object-to-object system into their attentional focus. Evidence from the literature suggests that people often maintain separate representations about environments without keeping track of how these are oriented to each other (Wang and Brockmole 2003b). Physically orienting toward a remote location may have thus functioned to link the representation of the distal environment to the egocentric system.

To further understand how one's physical orientation influences spatial performance, we have recently conducted several experiments in which participants reason about spatial relations between objects in immediate and non-immediate environments (Kelly et al. 2007). In these experiments two adjacent rooms, identical in size and shape, served as the learning and testing environments. Participants studied the spatial layout of objects in one room and then performed JRD's either in the same room (learning environment) or after walking 3 m into an adjacent room (novel environment). Before testing, participants physically rotated 90° to adopt a new orientation in space. This was done to dissociate their physical perspective at the time of test from the learning perspective, and thereby dissociate sensorimotor alignment effects from memory-encoding alignment effects.

All four multiple-system models reviewed in "Models of spatial cognition featuring multiple systems" predict a sensorimotor alignment effect when participants are tested within the learning environment. However, the predictions are less clear when participants are tested in a different location. Sholl's (2001) model seems to predict an absence of a sensorimotor alignment effect. According to Sholl's model, when reasoning about a non-immediate environment, the egocentric self-reference system operates at a representational, rather than at a perceptual level. This implies that body orientation at the time of the test is

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[1] We thank David Waller for bringing this to our attention.

irrelevant when reasoning about a non-immediate environment and no sensorimotor influence will occur. Mou et al.'s (2004) model seems to make the same prediction. According to their account, the sensorimotor system automatically updates egocentric spatial locations, but only when visual support is present. Moving to a neighboring room should cause the sensorimotor representation to fade from lack of perceptual support. As a result, no advantage for the physical orientation at the time of test should be expected. Finally, both Wang and Spelke's (2000) model and Waller and Hodgson's (2006) model argue that the egocentric system updates self-to-object relations while being supported by either visual or idiothetic information. If the egocentric system continues to update these relations during movement to the adjacent room then these models predict the presence of a sensorimotor alignment effect. However, empirical evidence suggests the egocentric system only represents objects within the immediate environment (Wang and Brockmole 2003b). In light of this evidence it seems more reasonable to assume that these models also predict the absence of a sensorimotor alignment effect.

The Mou et al. (2004) model predicts a memory alignment effect in both the immediate and the non-immediate environment. Wang and Spelke's (2000) model could also account for the presence of a memory-encoding alignment effect. However, the presence of such an effect poses a challenge for the model proposed by Sholl (2001) as the model makes no provision for orientation-dependent encoding. Finally, Waller and Hodgson (2006) do not clarify whether orientation-dependent encoding is possible with their account.

Results from four experiments revealed a memory-encoding alignment effect when testing occurred in both the learning room and the neighboring novel room. Performance was faster and more accurate for imagined perspectives aligned with the first/last perspective participants experienced during the study phase. Presumably this perspective determined the preferred orientation of the long-term allocentric representation. Importantly though, our results also revealed a sensorimotor alignment effect, where performance was best when the imagined perspective was aligned with the participant's actual body orientation at test. However, this effect was only present when testing took place within the learning environment. We believe that this finding reflects the influence of an egocentric system used only when reasoning about the immediate environment but not when reasoning about a non-immediate environment.

Further experiments showed that the sensorimotor alignment effect returns when the participant re-enters the learning environment (while the objects are no longer present) after having completed a block of trials in the novel environment. This latter finding is compatible with Sholl's (2001) model but not with Mou et al.'s (2004) model, which posits that the sensorimotor representation fades in the absence of perceptual support.

Furthermore, the sensorimotor alignment effect occurred when reasoning about a non-immediate environment after participants were encouraged to interface their physical orientation with the stored representation for the non-immediate environment. In our case, this was achieved by asking them to egocentrically visualize the objects from the non-immediate environment as if they were standing in that environment. This latter finding is compatible with results reported in a recent study by May (2007) and in an earlier study by Rieser et al. (1994). Participants in May's experiments learned the locations of a number of objects and then, after being blindfolded, were tested in either the learning environment or a remote environment located on a different floor of the building. May also instructed participants to visualize the objects around them prior to testing, and found sensorimotor alignment effects in both test environments. This visualization instruction might have enabled participants to achieve greater cognitive immersion, by linking the stored object-to-object relations to the egocentric system.

A model of spatial memory and action

The empirical findings reported in the previous section show that when reasoning about an immediate environment the physical orientation of the individual is important. When reasoning about non-immediate environments the physical orientation is typically not important but it can influence performance under some circumstances.

It seems that the findings by Wang (2004), Wang and Brockmole (2003a), Mou et al. (2004), and Kelly et al. (2007) can be accounted for best by Sholl's (2001) model, provided that one modification is made: the allocentric system represents object-to-object locations in an orientation-dependent manner, determined by environmental reference frames (e.g., McNamara 2003).

The resulting model is depicted in Fig. 1. This system stores object-to-object locations in long-term memory using one or two primary reference frames (not shown in the figure) determined by egocentric experiences during learning and/or the structure of the environment itself (Shelton and McNamara 2001; Mou and McNamara 2002). The position of the observer in the layout is represented in this allocentric system just like the position of any other object (Mou et al. 2004; Sholl et al. 2006). In addition to inter-object locations that are represented in this system, a limited number of egocentric object locations are automatically activated (May 2004; Wang and Spelke 2000). In this way, the egocentric representation oriented with respect to the observer (hereafter referred to as a *sensorimotor egocentric representation*) interfaces with the allocentric system in long-term memory (Easton and Sholl 1995). This account allows the individual to orient him/herself in the immediate environment. Sholl et al. (2006) has argued that humans achieve spatial orientation with respect to their environment by computing an allocentric heading, that is, the angle between one's facing direction and an environmental reference axis. In the model depicted in Fig. 1, this axis is the reference frame used in the allocentric representation. The model allows for two types of spatial updating to occur when the position of the individual changes. Egocentric updating can occur by tracking the changing self-to-object relations in an on-line and rather effortless manner (e.g., Rieser et al. 1986; Wang and Spelke 2000). Also, allocentric updating can occur by keeping track of where the individual is positioned relative to the intrinsic reference axis (Mou et al. 2006). Based on this account allocentric updating is regarded as a consequence of egocentric updating.

When a participant in an experiment such as those of Mou et al. (2004), Wang (2004), and Kelly et al. (2007) is asked to adopt an imagined perspective within his/her immediate surroundings, s/he needs to establish an egocentric reference frame at a new position in the object-to-object representation and orient it according to the instruction. We will refer to this egocentric reference frame as the *imagined egocentric* reference frame to differentiate it from the sensorimotor egocentric reference frame specifying the participant's physical position and orientation. Positioning an imagined egocentric frame within the allocentric representation is analogous to what Sholl (2001) calls the self-reference system operating at a representational level. In line with May's (2004) theorizing, we argue here that the effectiveness with which such an imagined reference frame is used can be compromised due to interference stemming from the automatic activation of the sensorimotor representation. In the next section we describe the nature of this interference in more detail and in connection with findings form the S–R compatibility literature.

When reasoning about a non-immediate environment, body orientation at the time of test does not typically affect performance (Kelly et al. 2007; Wang 2004; Wang and Brockmole 2003a). As Fig. 2 shows, a sensorimotor egocentric representation of the immediate environment is again automatically activated. However, the allocentric representation of the non-immediate environment no longer represents self-location. Therefore, we propose that when reasoning takes place about a distal environment, the sensorimotor egocentric representation is disconnected from the allocentric representation and functions independently. This allows the participant to position an imagined egocentric reference frame at any position and orientation in the allocentric system and retrieve the necessary spatial relations without any interfering effects from the sensorimotor egocentric system.

We believe that the physical orientation of the participant influences spatial reasoning about a non-immediate environment only when the specific situation encourages setting up a link between the two systems of the model, such as when the participant is oriented relative to a distal object or s/he is asked to visualize distal objects in the immediate environment.

The section that follows discusses the possible nature of the influence of the egocentric system on spatial performance by reviewing theories and empirical findings from the S–R compatibility literature. This examination will allow us to offer a more concrete description of how a model like the one depicted in Figs. 1 and 2 can account for the presence and absence of a sensorimotor alignment effect.

Sensorimotor interference when reasoning about immediate environments

A long tradition of research on S–R compatibility effects has established that a particular task can be made easier or more difficult by manipulating the pairings of stimuli with

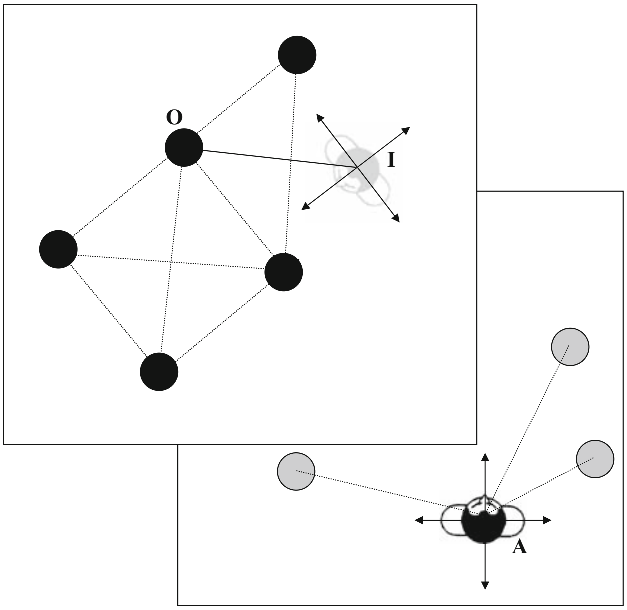

Fig. 2 A model describing spatial reasoning about a non-immediate environment. *Black circles* represent objects in the remote environment while *grey circles* objects in the immediate environment. The sensorimotor representation is disengaged from the object-to-object representation. No spatial relation exists between the actual perspective *A* and object *O* as the two are coded in distinct representations

responses (e.g., Fitts and Deininger 1954). In a typical S–R trial, a simple stimulus is presented either to the left or to the right of fixation and the participant is instructed to report its location by pressing one of two possible keys. S–R compatibility refers to the finding that performance is faster when the two display locations are paired with ipsilateral than contralateral response keys. A similar finding is observed even when the stimulus display location is irrelevant to the task. This finding is known in the literature as the Simon effect (Simon 1969). Both S–R compatibility and the Simon effect are believed to be response selection phenomena with performance facilitated or impaired depending on the congruence of two spatial codes, one for the location of the stimulus and one for the location of the response.

The majority of models formulated over the years to account for S–R compatibility and the related Simon effect (e.g., De Jong et al. 1994; Kornblum et al. 1990; Zorzi and Umiltà 1995) posit that stimulus presentation generates a spatial code which in turn automatically activates a response on the basis of pre-existing associations from long-term memory (but see Ansorge and Wühr 2004 for a somewhat different account). These long-term spatial links between locations and responses may result from overlearned compatible S–R parings in daily life (e.g., occulomotor responses to visual and auditory stimulation, reaching and grasping actions towards objects; see Umiltà and Zorzi 1997). As these models suggest, tasks that employ compatible S–R pairings exhibit enhanced performance while those that employ alternative pairings (e.g., pressing a right key for a stimulus presented on the left) suffer from interference. In fact, these models posit that there exist two separate routes that link perception to action (e.g., Eimer et al. 1995; De Jong et al. 1994; Zorzi and Umiltà 1995). The *indirect route* links stimuli to responses in an arbitrary manner on the basis of task instructions. The *direct route*, which is more relevant to our discussion, links stimuli to responses on the basis of long-term associations allowing for the automatic activation of responses. There is ample evidence in the literature to support this claim. For example, evidence from studies using electrophysicaological recordings suggests that "incorrect" motor responses are initially activated but are subsequently suppressed in both human (Coles et al. 1985; Gratton et al. 1988) and primate populations (e.g., Georgopoulos et al. 1989). Importantly, S–R compatibility effects have been shown to exist even for stimuli that are not visually present at the time of the response but are instead maintained in memory (e.g., Bächtold et al. 1998; Hommel 2002; Tlauka and McKenna 1998).

It is our opinion that S–R compatibility findings can shed some light on how people solve more typical spatial cognition tasks, especially tasks requiring spatial updating. First, it should be pointed out that stimuli and responses used in spatial updating studies exhibit substantial dimensional overlap; that is, the typical stimulus and response sets in spatial updating experiments have a common property: spatial location. Stimuli occupy spatial locations and responses are directed to spatial locations. Common stimuli are objects located in space (Loomis et al. 2002), points on paths (Waller et al. 2002), and so on, while responses include among others, pointing with the arm or a pointer (e.g., Rieser et al. 1986), turning the body toward the direction of the target (Avraamides et al. 2004a, b; Klatzky et al. 1998), walking to targets (Loomis et al. 2002; Riecke et al. 2002) and using verbal labels to locate objects (e.g., Wraga 2003). Second, the elements of the two sets are homomorphically paired; that is, stimuli and responses are arranged in spatial correspondence. For example, an object with an egocentric bearing of 30° requires a pointing response of the same bearing. According to Kornblum et al. (1990), when there is dimensional overlap between the stimulus and response sets with their elements being homomorphically paired, stimulus presentation will automatically activate the corresponding response. For example, presenting a stimulus on the left part of a computer screen or a left-pointing arrow in the center of the screen will automatically increase activation for a response that requires pressing a key that is also located to the left of the observer. If indeed pressing the left key is the correct response then the trial is said to be congruent and the response benefits from the pairing. If, however, a participant is instructed to respond to a left arrow by pressing a key located on the right then the trial will be incongruent and suffer a cost (Schwartz et al. 1977). Presumably, this cost occurs due to the fact that the instructed S–R pairings are incompatible with the well-learned S–R links that exist in long-term memory (Tagliabue et al. 2000). Of course, in cases where the stimulus and response have no dimensional overlap, there will be neither a benefit nor a cost (Kornblum et al. 1990).

Figure 3 presents an information-processing model to account for the primary findings on spatial updating in terms of facilitation and interference, drawing on the S–R compatibility and Simon effect literatures. The model adopts the logic of dual-route models of S–R compatibility. According to the model when a participant is instructed to execute a spatial response towards a stimulus occupying a specific location in space, the location of the stimulus automatically activates the homomorphic element in the response set.

To illustrate how the model works, imagine a typical spatial updating task. First, the participant is allowed to study and encode in memory the locations of a number of objects placed in his/her immediate environment. Based on the model described in "A model of spatial memory and

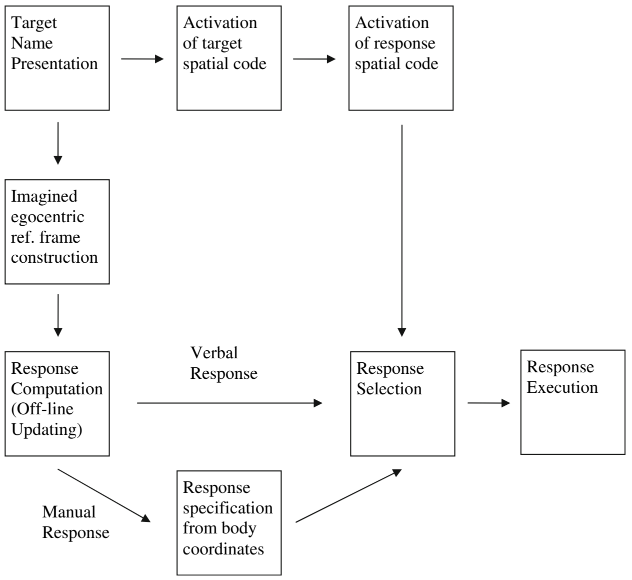

Fig. 3 An information-processing model of sensorimotor facilitation/interference. One route of the model is involved in automatically activating egocentric responses. Another route describes the deliberate computations needed to compute the correct response for incongruent trials. Interference in incongruent trials is believed to occur at the response selection stage

action", the object locations are represented in two systems: an allocentric long-term memory system coding object-to-object relations and a sensorimotor egocentric system (Fig. 1). During the testing phase the participant is presented either visually or auditorily with the name of one of the objects and is asked to point towards its remembered location from a perspective specified by the experimenter. Note that the response set and the sensorimotor representation of the objects are both egocentrically organized. Now, lets consider three different types of possible trials.

In *learning-standpoint* trials the participant is asked to locate a target-object while standing in the same position and orientation s/he occupied during learning (e.g., "Point to O from position A" in Fig. 1). Based on the S–R compatibility literature we argue that over-learned links connecting the spatial codes of egocentric locations and responses already exist in memory. According to the model, presenting the name of the target-object automatically generates a spatial code about its egocentric location. This spatial code in turn activates the corresponding egocentric response. Responses from the learning standpoint are always congruent, as both the stimulus and response sets are defined in aligned egocentric reference frames. Therefore, the activated response will always be valid and can be selected and executed very fast. In S–R compatibility terms these trials represent compatible pairings between stimuli and response locations.

In *novel-imagined orientation* trials the participant remains at the same position and orientation occupied during learning but is instructed to point to a target-object from a new imagined perspective (e.g., in Fig. 1, "Imagine perspective I. Point to O"). Like learning-standpoint trials, the identity of the target activates an egocentric spatial code that in turn primes an egocentric response toward that location. In this case, however, this automatically activated response is invalid and must be inhibited. Instead, the participant must compute the correct response in a deliberate and effortful manner (Rieser 1989). First, s/he needs to establish a cognitive egocentric reference frame at the instructed position and orientation (Presson and Montello 1994; Sholl 2001) as indicated by position I in Fig. 1. Then s/he must compute a response vector using that reference frame. Perhaps this computation takes place using an off-line updating process (Amorim et al. 1997; Hodgson and Waller 2006). One form of off-line updating that could be used is that of mentally simulating movement in space and deliberating observing its consequence on imagined egocentric locations. While computing the correct response the participant continuously experiences interference from the automatic activation of the incorrect response. The longer latencies commonly associated with imagined rotation reflect, in part, the time needed to deliberately compute a correct response while suppressing interference. It is also likely that the efficiency with which this computation can be executed is dependent on the availability of working memory resources and the person's capacity to suppress distracting information. After the appropriate response vector is determined it must then be executed from the reference frame governing the response medium entailed by the task. Manual tasks, such as pointing or turning to face an object, are organized based on a sensorimotor reference frame oriented with the body, which in this case is misaligned with the imagined egocentric reference frame used to compute the response vector. Therefore, the participant must effortfully transform the computed response vector—perhaps through a mental rotation process—into egocentric coordinates before it can be executed. Based on this account, responding with linguistic deictic terms such as "front", "left", etc. from imagined orientations should be somewhat easier than manual responding since no transformation to egocentric coordinates is needed after the response is computed. This prediction is supported by empirical findings (e.g., Avraamides et al. 2007; Wang 2004; Wraga 2003). Note, however, that effects due to the spatial compatibility of stimulus and response locations have also been reported with verbal responses (Wühr 2006). Therefore, the model predicts that performance in novel-imagined orientation trials would still be inferior to performance with learning-orientation trials even when responding verbally.

In the *novel-physical orientation* trials the participant is instructed to point to a target-object after physically locomoting to a new orientation (or position and orientation). A great body of literature on spatial updating suggests that the proprioceptive and vestibular information that accompany physical movement enable moving observers to update dynamically the egocentric locations of objects (e.g., Rieser et al. 1986). If this is the case, then performance after physical locomotion should be identical to that from novel-learning standpoint trials. When the participant is presented with target name, the updated egocentric spatial code is activated and a response towards that location is primed. Therefore, trials of this type are also congruent and thus elicit fast latencies.

The model presented in Fig. 3 explains the sensorimotor alignment effect obtained in spatial updating studies in terms of facilitation and interference caused by the automatic activation of spatial codes. Two things are also worth noting. First, according to the model, facilitation and interference due to S–R compatibility should be expected only when reasoning about immediate environments. This is because the facilitation and interference occurs with respect to the sensorimotor egocentric representation, which only represents objects within the immediate environment. Objects from a remote environment cannot produce the same facilitation and interference because they are not represented in the sensorimotor system. Second, we believe the sensorimotor interference account to be compatible with traditional spatial updating accounts emphasizing the importance of idiothetic information (see also May 2004). In this model, sensorimotor facilitation and interference are regarded as consequences of egocentric updating success and failure, respectively. Our conjecture is that if people had been able to update egocentric locations in an on-line manner even during imagined movements, all imagined perspectives would be congruent and no sensorimotor interference would arise (as in the case of novel-physical orientation trials).

The model we present can account for the common finding of superior performance when localizing a target from either the learning or a novel standpoint adopted through physical movement, compared to the inferior performance from a novel standpoint adopted through imaginary movement. To do so, the model combines May's (1996, 2004) sensorimotor interference theory with traditional accounts that emphasize the importance of idiothetic cues for spatial updating. By relying heavily on findings and models from the S–R compatibility literature, the model provides an explicit account of how interference and facilitation effects (e.g., May 1996; Waller et al. 2002) are manifested in spatial cognition studies.

The dual-system model presented here can also account for additional findings reported in the spatial cognition literature. For example, a number of studies report an overall performance benefit of disorientation on imagined perspective taking (e.g., May 1996; Mou et al. 2006; Waller and Hodgson 2006; Waller et al. 2002). A closer examination of this finding reveals that performance after disorientation, compared to performance when remaining oriented to the environment, is diminished for imagined perspectives coinciding with participant's physical perspective and is enhanced for perspectives misaligned with the physical perspective (May 1996; Waller et al. 2002). It seems that disorientation reduces both the facilitation for congruent trials and the inhibition for incongruent trials caused by the automatic activation of sensorimotor codes. Similar to the argument made by Waller and Hodgson (2006), participants switch from a sensorimotor representation to a long-term representation after disorientation. One reason for why this happens is that participants lose track of how their sensorimotor egocentric representation is oriented relative to the allocentric representation stored in memory. As a result, they either disregard their sensorimotor representation or they align the two representations by assuming a subjective orientation heading parallel to the preferred orientation of the stored representation. Support for the latter possibility is provided by Mou et al. (2006). In terms of the model presented in Fig. 1, disorientation relaxes the influence of the sensorimotor egocentric system by impairing awareness of one's allocentric heading, which allows participants to assume any subjective heading with ease.

Summary and conclusions

In the field of perception two seemingly contrasting theoretical approaches have flourished. On one hand, Gibson's ecological approach has claimed that tasks such as locomoting, reaching, grasping and ball-catching can be carried out by picking up visual information directly from the environment. On the other hand, the constructivist-indirect approach has focused on perceptual tasks that require cognitive mediation (i.e., going beyond the processing of information available to our senses), such as the various types of constancies (e.g., size constancy, shape constancy). Although the two approaches may seem incompatible, it is possible that both are valid accounts of different aspects of perception (Norman 2002).

Adopting the same logic, we have attempted to review evidence that spatial/egocentric updating and spatial memory represent a similar dichotomy between on-line/sensorimotor and off-line/representational aspects of spatial cognition. Tasks such as moving through the environment without vision, grasping objects, and pointing to targets in the immediate surroundings are tasks that seem to depend primarily on dorsal representations. These representations are short-lived, organized around sensorimotor egocentric reference frames, and are typically not available to conscious awareness. In contrast, tasks such as reasoning about a non-immediate environment seem to rely more on ventral representations. These representations maintain object-to-object locations in long-term memory, and are readily available to conscious awareness.

We have reviewed the main findings from two areas of research within spatial cognition, namely spatial updating and spatial memory, and we have considered the postulates of the recent theoretical accounts, which attempt to unify these findings. In an attempt to offer an account that goes into greater detail in terms of the mechanisms it involves, we have incorporated May's (1996, 2004) theory of sensorimotor interference into a two-system theory of spatial memory. The two-system theory we have chosen represents a hybrid between Sholl's (2001) and Mou et al.'s (2004) models, formulated in a way that can explain the process of reasoning about immediate and distal environments. This theory is compatible with the account proposed by Waller and Hodgson (2006) and it contains elements (e.g., a dynamic egocentric system) from the model proposed by Wang and Spelke (2000). In the context of this theory, we have laid out in detail how sensorimotor influence is manifested in spatial reasoning under various situations. To do so, we have consulted empirical evidence and theories from the field of S–R compatibility.

In closing, we should point out that although we have based our theorizing on empirical findings, in some cases we have resorted to choices that are nothing more than "best guesses". Therefore, we regard the outcome of our endeavor as a working hypothesis that will hopefully stimulate further research in spatial cognition. For example, one issue that needs to be examined is whether sensorimotor interference is an "all-or-none" phenomenon (i.e., either exists or not). Throughout this paper we have assumed that this is so. However, empirical results show that latencies increase with greater ODD (May 2004), suggesting that interference varies. Future research could address whether this empirical finding reflects indeed the presence of interference at various degrees or whether it can be accounted otherwise (e.g., strategies involved in off-line updating).

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