THE REPRESENTATIONAL FOUNDATIONS OF UPDATING OBJECT LOCATIONS

By

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CHAPTER I

INTRODUCTION

A central component of successful navigation is the ability to stay oriented with respect to various aspects of the environment as we move around (Golledge, 1999). This ability to compensate for the changes in the relationship between the observer and elements of the environment is commonly referred to as *spatial updating*. The representational basis of and the mental processes involved in spatial updating are the object of an ongoing debate in current research on spatial cognition (e.g., May & Klatzky, 2000; Rieser, 1989; Waller, Montello, Richardson, & Hegarty, 2002).

The foundation of any spatial representation is a spatial reference system. Because the location of an object is inherently relative, it needs to be specified with respect to a particular frame of reference (Klatzky, 1998). There are various ways for classifying spatial reference systems (see Levinson, 1996, for an overview), but for the purpose of studying spatial cognition, a distinction between egocentric and allocentric reference systems has proven useful. In *egocentric* reference systems, locations are specified with respect to one's own body or part of one's body (e.g., in retina, arm, or trunk coordinates). In *allocentric* reference systems, spatial relations are specified independently of the observer. An allocentric reference system can be defined, for instance, by an individual object, by a layout of objects, by cardinal directions, or by any geometrical feature of the environment.

Even though it is generally accepted that human navigation must involve both egocentric and allocentric reference systems, an ongoing debate exists about the relative importance of each system (e.g., Burgess, Spiers, & Paleologou, 2004). A strong proponent of egocentric representations are Wang and colleagues. In Wang and Spelke's (2000, 2002) theory, the primary subsystem for guiding navigation is the dynamic egocentric system. In this subsystem, the locations of objects in the surrounding environment are represented in the form of egocentric vectors. Individual objects are represented independently of each other and independently of other features in the environment. As a person moves, the individual self-to-object relations are dynamically updated. This primary subsystem is complemented by two other subsystems. The second subsystem, in contrast to the dynamic egocentric subsystem, stores information relative to allocentric frames of reference. This subsystem, however, does not represent the locations of objects. Instead, information about the geometric shape of the environment (e.g., walls of a room or other geometrical features of the environment) is stored for the purpose of reorientation in case the dynamic egocentric system is disrupted. The third subsystem stores the appearance of familiar landmarks and places in the form of view-dependent representations and serves primarily for place recognition. Like the dynamic egocentric system, this system represents object locations with respect to an egocentric reference frame, but the views stored in this system are static and are therefore not updated.

Whereas egocentric representations are considered the primary foundation of human navigation in Wang and Spelke's (2000, 2002) model, McNamara and colleagues emphasize the importance of allocentric representations over egocentric representations. Their model (e.g., McNamara, 2003; Mou, McNamara, Rump, & Xiao, 2006; Mou, McNamara, Valiquette, & Rump, 2004) proposes an egocentric subsystem that is similar to the dynamic egocentric system in Wang and Spelke's (2000, 2002) model in that object locations are represented in terms of dynamically updated self-to-object spatial relations.

In contrast to Wang and Spelke's model, these representations are considered to be very transient and to decay relatively rapidly in the absence of perceptual support. Through deliberate rehearsal, self-to-object relations in this system can be maintained even in the absence of perceptual support, but it is proposed that such a process is limited to a very small number of self-to-object relations. The primary role of this system is to guide locomotion through and interaction with the immediate surroundings when vision is available.

The main subsystem in McNamara and colleagues' (e.g., Mou et al., 2004) model for the purpose of navigation is the environmental subsystem. This subsystem holds enduring representations of familiar environments that are specified with respect to allocentric reference frames. The locations of objects are represented with respect to one or a small number of typically orthogonal reference directions that are intrinsic to the to-be-represented environment. Accessing a spatial representation from an orientation that corresponds to an employed reference direction is efficient because interobject spatial relations are explicitly represented with respect to this direction and can therefore be directly retrieved. When the representation is accessed from any other orientation, spatial relations cannot be simply retrieved but instead need to be inferred, which is assumed to produce costs in terms of latency and accuracy (e.g., McNamara, Rump, & Werner, 2003).

Different experimental paradigms have been used to investigate the extent to which humans rely on dynamic egocentric representations or on enduring allocentric representations when updating the locations of multiple objects. Preliminary support for the hypothesis that updating is based on egocentric representations came from experiments that showed decreases in the consistency of pointing to a configuration of objects after disorientation (e.g., Wang & Spelke, 2000). The underlying logic in these studies was that if object locations were stored in the form of independent, individually updated self-to-object spatial relations, then disruptions of the updating process, such as those caused by disorientation, would affect the individual self-to-object spatial relations differently. As a consequence, not only would disorientation result in a lack of knowledge regarding the actual facing direction (which would result in all reported object directions being offset by a certain amount, determined by the discrepancy between the actual facing direction and the assumed one), but it would also result in the directions of the objects with respect to each other being reported with less accuracy, because the error added to each self-to-object direction would not be identical. If, in contrast, object locations were represented and updated within an enduring allocentric system, then disorientation should only produce a constant offset in all pointing responses and not impair the configurational knowledge of the objects. The assumption is that with an allocentric system, disorientation should only affect the knowledge of the position of the person with respect to the representation, but not affect the fidelity of the representation as a whole.

Wang and Spelke (2000) observed increases in configuration error after disorientation, as predicted by the egocentric updating hypothesis, but these increases were rather modest (typically in the order of 5° to 10°). In other words, participants still demonstrated relatively accurate configurational knowledge even after a complete breakdown of the egocentric system due to disorientation. This finding has recently led Waller and Hodgson (2006) to suggest that the observed increase in configuration error should not be attributed to participants relying on egocentric representations that are degraded by disorientation, but instead to participants having to switch from an accurate but transient to a less accurate but enduring representation after disorientation.

Further support for this switching notion came from an experiment in which Waller and Hodgson (2006) investigated changes in configuration error as a function of turning angle, without the use of disorientation. In this experiment, participants studied layouts of objects from a certain perspective and then had to close their eyes and point to the objects after various amounts of rotation. The results showed that configuration error was comparable for smaller turning angles (0°, 45°, & 90°) and then increased abruptly for 135° rotations. This finding led Waller and Hodgson to suggest that updating within the precise but transient system can be done in the absence of perceptual support for turning angles up to between 90° and 135°, and that for larger turning angles, the less precise but enduring system needs to be recruited. Even though Waller and Hodgson avoided labeling their proposed systems as egocentric and allocentric, their two systems strongly resemble the transient egocentric and the enduring allocentric subsystems that many contemporary theories of spatial memory propose (e.g., Amorim, Glasauer, Corpinot, & Berthoz, 1997; Mou et al., 2004; Sholl & Nolin, 1997).

It is important to note that, as described above, the assumption is commonly made that reliance on a given enduring allocentric representation produces a constant level of configuration error that is independent of the particular retrieval conditions (e.g., whether disoriented or not, the amount of movement that preceded retrieval, etc.). One goal of the experiments proposed in this paper was to test this assumption and to investigate whether performance on updating the locations of multiple objects may be best explained by sole reliance on allocentric representations that vary in their degree of fidelity, depending on the particular circumstances of retrieval. The following section describes two pilot experiments that lend preliminary support to the notion of the primacy of allocentric representations in spatial updating.

CHAPTER II

PILOT EXPERIMENTS

The experiments presented in this section were partially motivated by Waller and Hodgson's (2006) claim that spatial updating is based on precise but transient representations for small rotation angles (i.e., 90° and smaller) and on less precise but enduring representations for large rotation angles (i.e., 135° and greater). One potential limitation of their study was that they did not actually test any large rotation angles other than 135°. Specifically, the problem was that 135° was not only the largest rotation angle, but also the rotation angle that resulted in a facing direction that was the most misaligned with the original 0° direction. Studies of spatial memory in which participants were tested at a remote location (and were therefore restricted to recruiting enduring representations) often showed particularly poor performance for headings that were 135° or 225° discrepant from the original study orientation (e.g., Mou & McNamara, 2002; Shelton & McNamara, 2001). In other words, performance on the 135° rotation would have also been expected to be the worst, even if participants in Waller and Hodgson's (2006) experiment had, in all rotation conditions, solely relied on allocentric representations that were specified relative to a reference system aligned with the 0° direction. All experiments described in this paper avoided this ambiguity by using rotation angles for which the hypothesis of a switch between two memory systems and the sole reliance on allocentric representations generated substantially different predictions.

The goal of these experiments was to contrast three different hypotheses on spatial updating. First, if updating is exclusively based on dynamically updated egocentric representations as Wang and Spelke (Wang, 1999; Wang & Spelke, 2000) have suggested, then configuration error should either be unaffected by rotation angle (if updating is efficient) or it should increase as a function of rotation angle. Second, if updating is based on precise but transient representations for small rotation angles and on less precise but enduring representations for larger rotation angles as Waller and Hodgson (2006) have suggested, then configuration error should be low for rotations up to a certain amount and then increase abruptly. Third, if updating is based on enduring allocentric representations as McNamara and colleagues (e.g., Mou et al., 2004) have suggested, then performance should not be determined by the amount of rotation, but instead by whether the resulting facing direction is aligned with salient environmental features and thereby likely to correspond to a reference direction in the representation.

Pilot Experiment 1

In Pilot Experiment 1, participants studied object locations from a position that was aligned with the walls of the surrounding rectangular room, which provided a salient reference frame for organizing the local environment. It was assumed that these study conditions would encourage participants to represent objects relative to the four reference directions that corresponded to the four walls of the room (e.g., Valiquette, McNamara, & Smith, 2003).

Method

Participants. Twenty-four students and members of the Nashville community (12 women, 12 men) participated in the experiment in return for class credit or monetary compensation.

Materials and design. Participants studied layouts of six objects from the center of each layout while facing a direction (0°) that was aligned with the long axis of the surrounding rectangular room (see Figure 1). Marked on the floor around the study position of the participant were four colored lines that indicated the four different directions participants had to rotate to during testing: 0°, 90°, 135°, and 270°. Colored lines were used to communicate these directions instead of a second set of objects, because they were visually very salient and clearly distinct from the objects that formed the to-be-represented layout. Responses were recorded using a wireless joystick that was

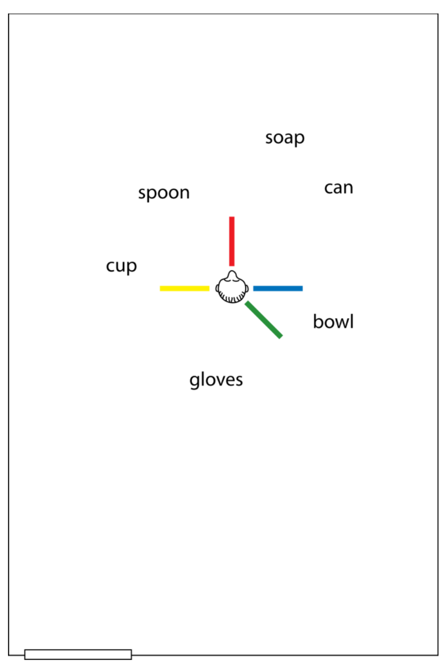

Figure 1. Sample object layout used in Pilot Experiment 1. The participant is surrounded by the objects and is facing the 0° study direction. The four colored lines on the floor indicate the directions that the participant has to turn to before being tested.

mounted on a wooden platform, which was affixed to participants through shoulder and waist straps.

Procedure. Before entering the study room, participants were briefed on the general procedure of the experiment and familiarized with the use of the wireless joystick. They were then blindfolded and led to the center of the object layout, facing the 0° heading. After removing the blindfold, the experimenter pointed to and named each of the objects to establish a common terminology. Participants then studied the locations of the objects and the colored lines for 30 seconds. While studying, participants were allowed to look around freely by turning their heads, but they were not allowed to turn their bodies away from the 0° learning direction. Participants were then asked to close their eyes and to point to the objects and the colored lines as they were named by the experimenter. This procedure was repeated until participants were able to point promptly and reliably to the objects and lines and at least three times.

After studying, participants were briefed on the testing procedures. For each of the four rotation angle conditions, participants were asked to don a blindfold and to turn clockwise to the corresponding colored line while keeping track of the locations of the objects with respect to their bodies. Half of the participants (those in the correction condition) were corrected by the experimenter if they overturned or underturned by more than a small amount, the other half (those in the no-correction condition) were tested at whatever direction they wound up in. This correction manipulation was included because it was not clear if correcting participants' facing direction, and thereby reducing insecurities about their heading but also increasing the delay between loss of perceptual support and the beginning of testing, would benefit or hinder the usage of egocentric representations. By including both a correction and a no-correction condition, the likelihood of observing results in support of egocentric representation was increased.

Participants then pointed to each object twice using a joystick in a randomized order that was announced by the testing computer. No feedback was provided to participants about their performance. After having completed all twelve trials for a given rotation angle condition, participants turned back to the 0° direction, lifted the blindfold, and were allowed to refresh their memories of the objects, before the next colored line they had to turn to was announced.

The primary measures of interest were configuration error and response time. When participants repeatedly point to various objects from a stationary position, their pointing errors can be partitioned into three logically separate components: heading error, defined as the mean of the means of the signed pointing error per target object; pointing variability, defined as the square root of the mean of the variances of the signed pointing error per target object; and configuration error, defined as the standard deviation of the means of the signed pointing error per target object.

Heading error represents the common offset of all pointing responses. If a participant, for instance, consistently localized objects 20° further clockwise than they actually were with respect to his or her current heading, then his or her heading error would be 20°. Heading error can be thought of as the difference between a participant's actual heading and the heading the participant adopted in imagination.

Pointing variability represents the reliability of the individual pointing responses. Pointing variability increases when multiple pointing responses to the same object deviate from another. Pointing variability is often considered an indicator of the imprecision of pointing judgments.

Configuration error can be understood as a measure of a participant's (in-)ability to localize the objects correctly with respect to each other. If a participant, for instance, consistently localized an object closer to another object than it really was, then this would increase his or her configuration error. Configuration error is often considered an indicator of the quality of the underlying representation of the object locations. The advantage of using configuration error as the primary dependent measure instead of the computationally simpler absolute pointing error is that, in contrast to the latter, configuration error provides a measure of the quality of the underlying representation that does not contain the error components that are due to participants' insecurities about their facing direction and those due to variability in their pointing responses.

The primary independent variables were correction (correction and no-correction after participants had turned to a colored line) and rotation angle (0°, 90°, 135°, and 270°). Correction was varied between participants and rotation angle was varied within participants. To obtain more data and to increase the generalizability of the results, participants studied and were tested on four different randomly generated object layouts. To minimize interference between the representations of the different layouts, each layout contained objects from a different theme (kitchen objects, fruits, animal models, and toys). Participants were tested on all four rotation angle conditions for each of the four layouts. With 12 trials per rotation angle per layout, the total number of trials was 192. The total duration of the experiment was typically on the order of 70 minutes.

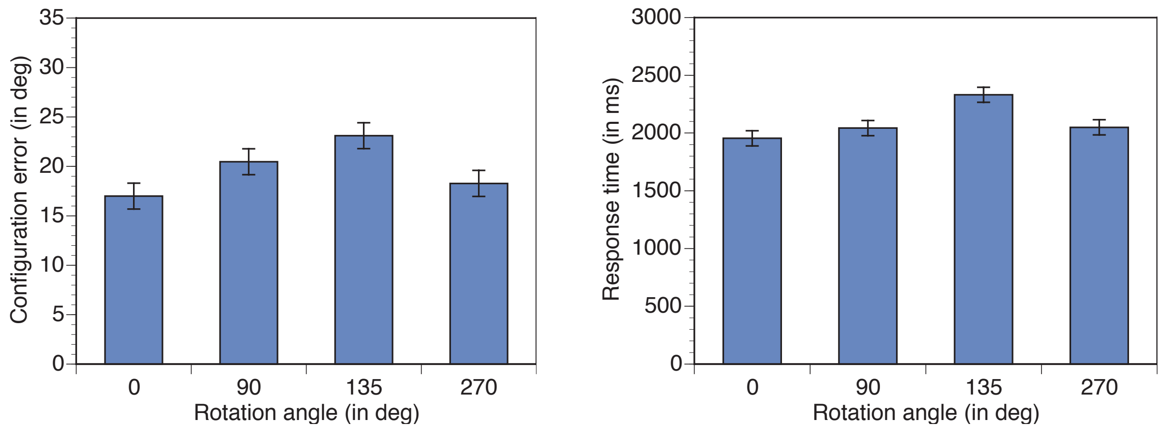

Figure 2. Configuration error (A) and response time (B) as a function of rotation angle in Pilot Experiment 1. Error bars are confidence intervals corresponding to ± 1 standard error, as estimated from the ANOVA.

Results and Discussion

The data were analyzed using a 2 (correction) x 2 (gender) x 4 (rotation angle) x 4 (layout) mixed-model ANOVA, with correction and gender as between factors and rotation angle and layout as within factors.

The main effect of rotation angle was significant for configuration error, $F(3, 60) = 8.31$, $p < .001$, $MSE = 82.93$. As depicted in Figure 2a, configuration error increased from 0° rotations to 90° rotations, $F(1, 60) = 7.01$, $p < .05$, $MSE = 82.93$, and from 90° rotations to 135° rotations, $F(1, 60) = 4.01$, $p < .05$, $MSE = 82.93$, as would be predicted by participants relying on dynamically updated egocentric representations. Configuration error was, however, significantly lower for 270° rotations than for 135° rotations, $F(1, 60) = 13.49$, $p < .001$, $MSE = 82.93$, which is irreconcilable with the both the hypothesis that updating is based on dynamically updated egocentric representations and the hypothesis of a switch from precise but transient to less precise but enduring representations for larger rotation angles. Instead, the results support the notion that participants relied on allocentric representations that were specified relative to the 0° reference direction, and to some extent, to the 90° and 270° reference directions.

The only other significant effect in the configuration error data was an interaction between rotation angle and layout, $F(9, 180) = 2.18$, $p < .05$, $MSE = 79.54$. Visual inspection revealed that this interaction was largely caused by the third layout showing only very small effects of rotation angle. When conducted without the data from the third layout, the rotation angle by layout interaction was no longer significant in the ANOVA, $F(6, 120) = 1.76$, $p = .11$, $MSE = 92.12$.

The results for response time as a function of rotation angle are depicted in Figure 2b. The main effect of rotation angle was significant, $F(3, 60) = 12.53$, $p < .001$, $MSE = 0.21$. Participants responded equally fast after 0°, 90°, and 270° rotations, Fs$(1, 60) \leq 2.11$, ps $\geq .15$, $MSE = 0.21$ and slower after 135° rotations than after all other rotations, Fs$(1, 60) \geq 18.57$, ps $< .001$, $MSE = 0.21$. No other effects were significant in the response time data.

For both configuration error and response time, performance was better after 270° rotations than after 135° rotations. This finding is in stark contrast to the hypothesis that dynamic egocentric representations are the basis of spatial updating. It is also not compatible with the hypothesis of a switch from precise but transient to less precise enduring representations for larger rotation angles. Instead, the results are in agreement with the notion that participants relied on allocentric representations that were specified relative to reference directions aligned with the walls of the surrounding room.

Pilot Experiment 2

Pilot Experiment 1 established that allocentric representations play a fundamental role in the updating of multiple object locations. The goal of the second pilot experiment was to investigate the importance of alignment with the dominant geometric organization of the environment (i.e., the walls of the surrounding room) for the selection of allocentric reference directions. More specifically, the goal of Pilot Experiment 2 was to investigate the extent to which the performance advantage for the tested directions of 90° and 270° relative to 135° in Pilot Experiment 1 was indeed due to the fact that the former directions were aligned with the walls of the surrounding room and therefore more likely to be selected as reference directions. An alternative explanation would be that the observed advantage for 90° and 270° was due to their orthogonal relation to the learning orientation of 0°, independent of the features of the surrounding environment.

To test between these two possibilities, both the learning orientation and all the tested headings were rotated by 60° so that they were misaligned with the walls of the surrounding room. To further decontextualize the objects from the global structure of the room, they were placed on a large round mat in the center of which participants stood during the experiment.

The logic of this experiment was as follows. If alignment with the walls of the room were an important factor for the selection of reference directions, then the performance advantage of 90° and 270° over 135° should largely be eliminated in Pilot Experiment 2. If, on the other hand, 90° and 270° were primarily benefited in Pilot Experiment 1 because of their orthogonal relation to the learning orientation, then rotating all directions, so that they would be misaligned with the walls of the surrounding room should have little impact on the performance advantage of 90° and 270° over 135°.

Method

Participants. Twenty-four students and members of the Nashville community (14 women, 10 men) participated in the experiment in return for class credit or monetary compensation.

Materials, design, and procedure. The materials, design, and procedure of Pilot Experiment 2 were similar to those of the first pilot experiment with the following differences. Participants stood in the center of a round mat that had a diameter of approximately 3 meters and on which the objects were placed. Participants still studied the objects from a 0° direction and were tested after clockwise rotations of 0°, 90°, 135°, and 270°; the 0° direction, however, was no longer aligned with the long axis of the surrounding rectangular room. Instead, it was rotated clockwise by 60° relative to the 0° direction in Pilot Experiment 1, resulting in all tested directions being misaligned with

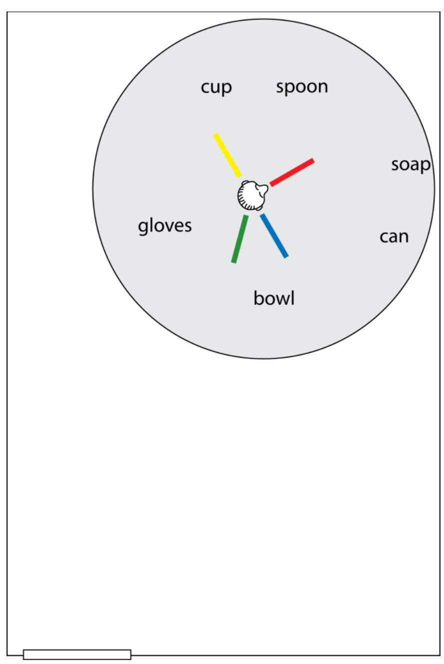

Figure 3. Sample object layout used in Pilot Experiment 2. The objects were placed on a round mat. The object layouts, the learning direction and the tested headings were rotated clockwise by 60° relative to Pilot Experiment 1.

the walls of the room (see Figure 3).

Participants studied and were tested on the same four layouts using the same trials that were used in Pilot Experiment 1. Because the correction manipulation in Pilot Experiment 1 did not produce a significant effect, all participants were tested under no-correction conditions (i.e., the experimenter did not correct their facing direction if they did not turn exactly to the appropriate colored line).

Results and Discussion

The data were analyzed using a 2 (gender) x 4 (rotation angle) x 4 (layout) mixed-model ANOVA, with gender as a between factor and rotation angle and layout as within factors.

For configuration error, the main effect of rotation angle, though approaching significance, was not significant, $F(3, 66) = 2.28$, $p = .09$, $MSE = 203.83$. Figure 4a depicts configuration error as a function of rotation angle. There were no significant differences between the 90°, 135°, and 270° rotations, $Fs(1, 66) \leq 3.30$, $ps \geq .07$, $MSE = 203.83$. Configuration error was lower for 0°, however, than for 90° and 135°, $Fs(1, 66) \geq 4.29$, $ps < .05$, $MSE = 203.83$. None of the other main effects or interactions were significant.

Response time as a function of rotation angle is shown in Figure 4b. The main effect of rotation angle was significant, $F(3, 66) = 24.38$, $p < .001$, $MSE = 0.13$. Response times did not differ between 90° and 270° rotations, $F(1, 66) = 1.45$, $p = .29$, $MSE = 0.13$, but all other differences were significant, $Fs(1, 66) \geq 10.96$, $ps < .01$, $MSE = 0.13$. No other effects were significant.

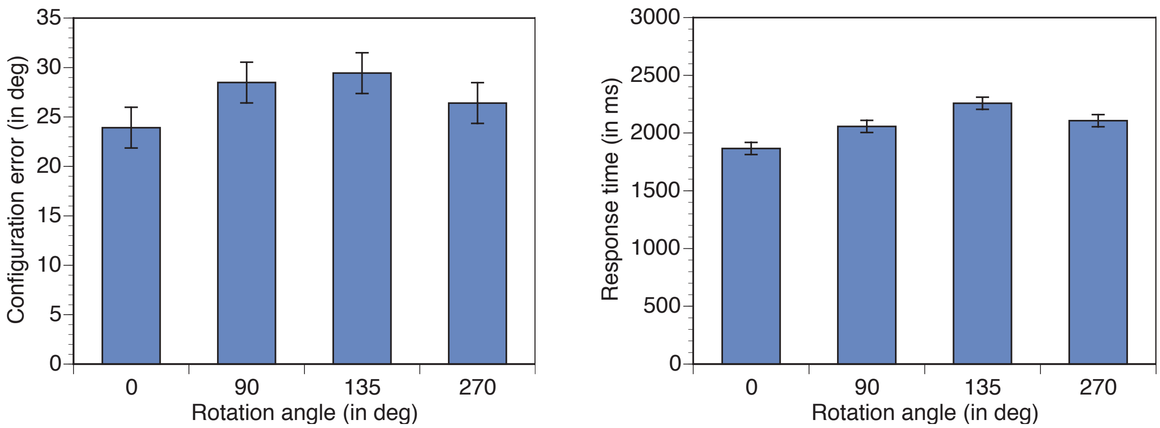

Figure 4. Configuration error (A) and response time (B) as a function of rotation angle in Pilot Experiment 2. Error bars are confidence intervals corresponding to ± 1 standard error, as estimated from the ANOVA.

In contrast to Pilot Experiment 1, configuration error was not lower for 90° and 270° rotations than for 135° rotations, which suggests that alignment with the walls of the room is an important factor for the selection of reference directions. The importance of alignment with dominant geometric features is further illustrated by the overall increase in configuration error from Pilot Experiment 1 to Pilot Experiment 2 (19.71° vs. 24.02°), though caution is always indicated when making such cross-experimental comparisons. When comparing the individual rotation angles across experiments, configuration error increased from Pilot Experiment 1 to Pilot Experiment 2 for the rotation angles of 0°, 90°, and 270°, $ts(46) \geq 2.04$, $ps < .05$, $SE = 2.01$, but not for the rotation angle of 135°, $t(46) = 1.50$, $p = .14$, $SE = 2.01$. In other words, performance on the headings of 0°, 90°, and 270° was worse in Pilot Experiment 2, in which those headings were no longer aligned with the walls of the room, than in Pilot Experiment 1, in which they were aligned with the walls of the room, but no such performance difference was apparent for the heading of 135° that was misaligned with the walls in both experiments.

The response time data paint a somewhat different picture. In contrast to the results for configuration error, there was some benefit apparent in response time for 90° and 270° rotations over 135° rotations, even though, unlike in Pilot Experiment 1, response times were considerably higher for 90° and 270° than for 0° rotations.

Overall, these results suggest that alignment with the dominant geometric features of the environment is an important factor for the selection of reference directions. The response time data, however, suggest that directions can also profit from orthogonality relations to the learning orientation, even when they are not aligned with dominant geometric features of the environment. In the remaining experiments in this paper, alignment with the dominant geometric features of the environment and orthogonality relations to the learning orientation will be perfectly confounded like they were in Pilot Experiment 1. For the sake of simplicity, headings will only be described as being aligned or misaligned with the dominant geometric features of the environment, even though they are also orthogonal or not with respect to the learning orientation.

CHAPTER III

MAIN EXPERIMENTS

The central finding of the pilot experiments was that configuration error neither increased monotonically with rotation angle, as the dynamic egocentric updating hypothesis (e.g., Wang & Spelke, 2000) predicted, nor did it follow a simple step function, as Waller & Hodgson's (2006) hypothesis of a switch from precise but transient to less precise but enduring representations for larger rotation angles predicted. Instead of having been determined by the actual amount of rotation, performance was determined by the particular heading at which participants were tested and the relationship between that heading and both the learning perspective and salient environmental features. These results support the hypothesis that updating multiple object locations in the absence of perceptual support is done based on allocentric representations.

These conclusions, however, are seemingly at odds with the results of spatial updating experiments that employed disorientation as a manipulation (e.g., Wang & Spelke, 2000). As described earlier, the underlying assumption in those experiments was that disorientation would only eliminate participants' knowledge about their actual position with respect to an allocentric representation, but not impair the fidelity of the allocentric representation as a whole. Hence, the finding that configuration error increased after disorientation was considered conclusive evidence for the prevalence of dynamic egocentric representations in spatial updating. The results of the pilot experiments described earlier, however, indicated that the fidelity of an allocentric representation can be affected, for instance, by the particular heading adopted. Therefore, the assumption that the fidelity of allocentric representations is constant and not affected by disorientation needs to be reconsidered.

One limitation of those studies that investigated the effect of disorientation on configuration error was that they did not provide direct means for drawing inferences about the representation types used before and after disorientation. Consider, for instance, the results of Mou, McNamara, Rump, and Xiao (2006). Across a series of experiments, the authors showed that configuration error did not increase after disorientation when participants had learned an object layout with salient intrinsic axes while standing at the periphery of the layout. An increase in configuration error was, however, observed after disorientation when participants had learned an object layout without salient intrinsic axes while standing amidst the objects.

The explanation offered by the authors was that participants who studied the layout with salient intrinsic axes were able to form allocentric representations of high fidelity, on which they could rely for both pre- and post-disorientation testing. Hence, configuration error did not increase after disorientation. Participants who studied the layout without salient axes, in contrast, were only able to form allocentric representations of lower fidelity. When these participants were tested before disorientation, they would rely on transient egocentric representations that were of higher precision than the low fidelity allocentric representations they had formed. After disorientation, the transient egocentric representations were no longer available and these participants had to rely on the low fidelity allocentric representations, which resulted in an increase in configuration error.

A limitation of those experiments is that they did not provide any direct evidence concerning the types of representations used before and after disorientation. Whereas the dependence of the increase in configuration error on layout type is difficult to reconcile with the notion that egocentric representations are used both before and after disorientation (as Wang & Spelke, 2000, originally proposed), the interpretation of the pre-disorientation performance is more ambiguous. An alternate explanation would be that even participants who learned the layout with salient intrinsic axes relied on egocentric representations before they were disoriented, and these egocentric representations happened to be roughly of the same precision as the high fidelity allocentric representations they relied on after disorientation. Another possibility would be that even participants who studied the layout without salient intrinsic axes relied on their allocentric representations before disorientation. For this explanation to work, one would need to make the assumption that the allocentric representations of the layout without salient intrinsic axes were more negatively affected by disorientation than the allocentric representations of the layout with salient intrinsic axes were.

The results of the earlier described pilot experiments lend support to this latter possibility, that participants in both conditions relied on allocentric representations even when they were still oriented. This would suggest that people generally rely on allocentric representations for updating multiple object locations and that the observed selective performance impairments caused by disorientation are due to some allocentric representations being more vulnerable to disorientation than others. Another possibility, however, is that for unknown methodological reasons, the studies involving disorientation encouraged participants to rely on dynamic egocentric representations, whereas the pilot experiments did not. In this case, it could still be argued that that performance impairments caused by disorientation are due to participants switching from higher precision egocentric representations to lower precision allocentric representations.

The goal of Experiment 1 was to test between these possibilities by incorporating the systematic heading manipulation of the pilot experiments into a disorientation paradigm.

Experiment 1

Previous disorientation studies either did not control for the tested heading at all (Waller & Hodgson, 2006, Experiments 1-2; Wang & Spelke, 2000) or kept the tested heading constant between the oriented and the disoriented condition (Mou et al., 2006). As the pilot experiments illustrated, systematically manipulating rotation angle (and thereby the tested heading) can be an effective tool for making inferences about the types of representations used: Whereas reliance on dynamic egocentric representations predicts configuration error to increase as a function of rotation angle, reliance on allocentric representations predicts performance to be determined by whether or not a tested heading is aligned with a reference direction of the representation.

The goal of Experiment 1 was to systematically vary the headings at which participants were tested, in both an oriented and a disoriented condition. In the oriented condition, participants rotated 0°, 135°, or 270° relative to the learning heading after donning a blindfold. In the disorientation condition, participants were tested at the same three headings after having been disoriented through a series of large left and right turns while blindfolded and while wearing headphones that blocked orienting auditorial cues.

The first question of interest concerned the type of representation participants relied on in the oriented condition. If they recruited dynamic egocentric representations for the pointing task, configuration error would be lower for 135° than for 270°, because less error would accumulate during the shorter 135° rotation than during the longer 270°

rotation. If, in contrast, participants located objects based on allocentric representations that were, at least to some extent, specified with respect to the 90°-270° axis, then configuration error would be lower for 270° than for 135°, because participants would be able to directly retrieve object locations relative to the reference direction of 270°, but they would have to go through a costly and error prone inference process in order to retrieve object locations relative to 135°. Based on the results of the pilot experiments, it was expected that the data would support the usage of allocentric representations.

The second question of interest was whether or not configuration error would increase after disorientation. If participants relied on allocentric representations when oriented (i.e., performance was better for 270° than for 135°) and configuration error increased after disorientation, then this would directly challenge the established interpretation that participants in previous disorientation studies relied on egocentric representations when oriented and that observed increases in configuration error were a consequence of participants no longer being able to rely on precise egocentric representations after disorientation. In other words, in light of this finding, the claim of previous disorientation studies that any observed increases in configuration error after disorientation would indicate the usage of egocentric representation would no longer be tenable.

If participants relied on allocentric representations when oriented (i.e., performance was better for 270° than for 135°) and configuration error did not increase after disorientation then it would not be possible to draw such strong conclusions about the interpretations of previous disorientation studies. Such an outcome would neither support nor disconfirm the notion that participants in previous disorientation studies relied on egocentric representations when they were oriented. It would, however, cast further doubt on the hypothesis that egocentric representations are commonly relied on for updating the locations of multiple objects.

One potential problem with the above considerations and the reasoning involved in previous disorientation studies is that it is assumed that in any given situation only one type of representation is relied on. The picture becomes considerably more complex if we allow for the possibility that one type of representation is used predominantly, but performance is somewhat augmented by the other type of representation. A specific example of such a case would be if participants primarily relied on allocentric representations, but also always tracked one or two objects using their egocentric system. On the majority of trials in the oriented condition, participants would then rely on their allocentric representations, which in turn would produce an overall performance pattern across the different headings that was supportive of allocentric representation. On the few trials in the oriented condition that involved the objects they tracked using their egocentric system, they would, however, localize the target object based on a, supposedly higher precision, egocentric representation. Since, by conjecture, dynamic egocentric representations are not available after disorientation, an increase in configuration error after disorientation could be, at least in part, due to such a residual use of egocentric representations, even though the overall performance pattern in the oriented condition indicated a reliance on allocentric representations.

To assess whether performance in the oriented condition was augmented through the residual use of egocentric representations, participants either turned directly or indirectly to the tested headings. In the direct case, participants either stayed at 0°, or turned 135° or 270° clockwise. In the indirect case, participants first turned 90° counterclockwise before they turned clockwise to the tested heading. This preceding 90°

counterclockwise turn increased the amount of rotation required to reach each tested heading in the indirect turn condition by 180°. This additional movement would have negatively effected residual dynamic egocentric representations, but not allocentric representations. The comparison of direct turns and indirect turns for each tested heading therefore allowed for assessing whether residual egocentric representations played a significant augmentative role in the updating performance of oriented participants.

Method

Participants. Twenty-four students and members of the Nashville community (14 women, 10 men) participated in the experiment in return for class credit or monetary compensation.

Materials and design. A randomly generated layout of six objects was used. The tested headings were marked on the floor by three colored lines. Responses were recorded using a wireless joystick that was mounted on a wooden platform, which was affixed to participants through shoulder and waist straps. Participants were wearing active noise cancellation headphones that were used to present the trial information as well as a masking sound to eliminate potential orienting auditorial cues in the disorientation condition. The headphone cable ran through a hook in the ceiling to prevent it from interfering with participants' turning movements.

The primary independent variables were tested heading (0°, 135°, & 270°) and turning mode (oriented direct turn, oriented indirect turn, & disorientation). Both variables were varied within participants. The order of the resulting nine factor combinations was balanced across participants. Participants pointed to each of the six objects three times per factor combination, resulting in 162 trials total. The dependent measures were configuration error and response latency.

Procedure. The procedures for studying the object layout were similar to those of Pilot Experiment 1. Participants were tested on nine blocks of trials that were formed by the combination of the three tested headings and the three turning modes. At the beginning of each block, participants were told at which line and under which turning condition they would be tested and encouraged to look at the objects to refresh their memories of the layout. When they were ready, they donned the blindfold and turned to the appropriate tested heading in a manner depending on the turning mode of the block. In the oriented direct turn condition, participants either stayed at 0° or turned 135° or 270° clockwise. In the oriented indirect turn condition, participants turned 90° counterclockwise before they turned clockwise to the appropriate tested heading. In the disorientation condition, participants were turned by the experimenter in a series of large alternating turns before they were turned to face the appropriate tested heading and told again the colored line they were now facing.

Once participants had arrived at the tested heading, they were able to start the presentation of the trials by pressing a joystick button. For each trial, participants were presented with an individual object name and then pointed in the direction of that object using the joystick. One and a half seconds after they had returned the joystick to the center position, the next object name was presented. After they had pointed to all objects three times in the order announced by the computer, they returned to the 0° direction, lifted their blindfold, and were allowed to look at the objects again. When they were ready, they were told the turning mode and the tested heading for the next block. The duration of the experiment was typically ca. 60 minutes.

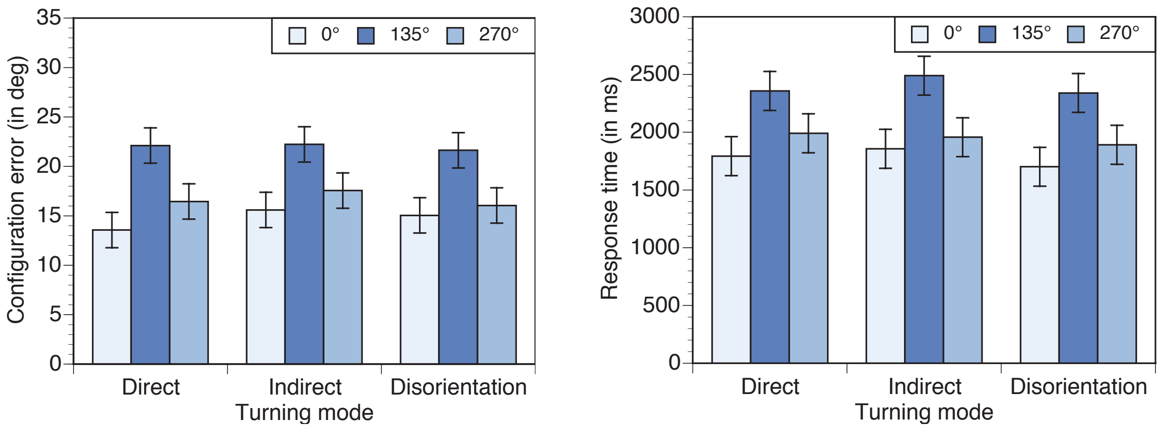

Figure 5. Configuration error (A) and response time (B) as a function of tested heading and turning mode in Experiment 1. Error bars are confidence intervals corresponding to ± 1 standard error, as estimated from the error term for the tested heading by turning mode interaction in the ANOVA.

Results and Discussion

The data were analyzed using a 2 (gender) x 3 (tested heading) x 3 (turning mode) mixed-model ANOVA, with gender as a between factor and turning mode and tested heading as within factors.

Configuration error as a function of turning mode and tested heading is depicted in Figure 5a. The main effect of tested heading was significant, $F(2, 44) = 16.25$, $p < .001$, $MSE = 60.87$. Configuration error did not differ between the tested headings of 0° and 270°, $F(1, 44) = 2.25$, $p = .14$, $MSE = 60.87$, but was lower for those two headings than for the tested heading of 135°, Fs$(1, 44) \geq 16.64$, ps $< .001$, $MSE = 60.87$. Neither the main effect of turning mode was significant, $F(2, 44) = 1.15$, $p = .33$, $MSE = 34.99$, nor the tested heading by turning mode interaction, F(4, 88) < 1, $MSE = 38.31$. None of the other effects were significant.

As shown in Figure 5b, the results for response time were virtually identical with the ones for configuration error. The main effect of tested heading was significant, $F(2, 44) = 14.45$, $p < .001$, $MSE = 0.55$. Participants performed equally fast on the tested headings of 0° and 270°, $F(1, 44) = 1.73$, $p = .20$, $MSE = 0.55$, but slower on the tested heading of 135° than on the former two, $Fs(1, 44) \geq 13.16$, $ps < .001$, $MSE = 0.55$. As for configuration error, neither the main effect of turning mode was significant, $F(2, 44) = 1.26$, $p = .29$, $MSE = 0.23$, nor the tested heading by turning mode interaction, $F(4, 88) < 1$, $MSE = .34$. None of the other effects were significant.

As anticipated, the results for the two oriented turn conditions of Experiment 1 replicated the results of the pilot experiments. Both in terms of accuracy and in terms of response time, participants performed better on the tested heading of 270°, which was associated with a larger rotation angle but aligned with the dominant geometric features of the environment, than on the tested heading of 135°, which was associated with a smaller turning angle but misaligned with those features. The same pattern was observed in the disorientation condition. These findings indicate that participants relied on allocentric representations in all three turning mode conditions of the experiment. If residual egocentric representations were used in addition to allocentric representations, their impact was not large enough to provide the oriented direct turn condition with a visible advantage over the oriented indirect turn and the disorientation condition.

Unlike in several other disorientation studies, no increase in configuration error was observed after disorientation in Experiment 1. Possible reasons for this failure to replicate and comparisons with other studies that have either found or not found an increase in configuration error after disorientation will be presented in the General Discussion. Because no increase in configuration error was observed in Experiment 1, no strong conclusions can be drawn about whether the observed increase in configuration error after disorientation in earlier studies was in fact due to participants having relied on precise dynamic egocentric representations when oriented but not when disoriented, as claimed by those studies. However, the fact that participants in Experiment 1, like those in the pilot experiments, seemed to have universally relied on allocentric representations calls further into question the notion that egocentric representations are a crucial factor for updating the locations of multiple objects.

Experiment 2

The general goal of Experiment 2 was to identify the limitations of dynamic egocentric representations. Many prominent contemporary theories of spatial memory propose the existence of a dynamic egocentric system for updating the locations of objects in vicinity of the observer (e.g., Mou et al., 2004; Sholl, 2000; Wang, 1999) and there is abundant evidence for the importance of egocentric reference frames for interactions with the immediate environment in both humans and other primates (e.g., Galati et al., 2000; Milner & Goodale, 1995; Soechting & Flanders, 1992; Woodin & Allport, 1998). The fact that the results of Experiment 1, like those of the pilot experiments, indicated a reliance on allocentric representations does not necessarily cast doubt on the existence of a dynamic egocentric system, but it suggests that the experimental task went beyond the limitations of this system.

There are a number of ways in which the dynamic egocentric system may be limited. Relevant variables include, but are not limited to, the number of simultaneously tracked objects, the delay between the loss of perceptual support and retrieval of an object's location, and the amount of movement that has occurred since the loss of perceptual support. The goal of Experiment 2 was to primarily focus on limitations of the egocentric subsystem in terms of the number of objects that can be tracked simultaneously. Potential temporal limitations were also considered, which is why

Experiment 2 employed a testing method that minimized the delay between the loss of perceptual support and the retrieval of each object's location.

It is important to note that Experiment 2 is not the first study that has tried to shed light on capacity limitations of spatial updating. Systematic manipulations regarding the number of to-be-tracked objects were also employed in the studies of Hodgson and Waller (2006) and Wang et al. (2006). The results of these studies were not conclusive, however. Hodgson and Waller (2006) varied the number of to-be-tracked objects between one and fifteen and expected to find a sudden decrease in performance once the capacity limit was reached. Contrary to their initial expectation, accuracy was not affected and response time gradually increased as a function of the number of to-be-tracked objects. The interpretation offered by the authors was that this gradual increase in response time was to be attributed to processing costs associated with selecting from a larger set of target objects and not to capacity limitations of spatial updating.

Wang et al. (2006) only varied the number of to-be-tracked objects between one and three. They found an increase in both error and response time as a function of the number of to-be-tracked objects, which mainly occurred between one and two tracked objects. Wang et al. argued that these findings supported the hypothesis that spatial updating is based on dynamic egocentric representations, because, according to their assumptions, the number of to-be-tracked objects should not affect performance when updating is based on enduring allocentric representations. Whether or not this assumption is tenable, however, may be subject to debate.

One potential limitation of Hodgson and Waller's (2006) and Wang et al.'s (2006) studies was that both only tested for changes in the overall level of performance, but did not take any measures that would allow for making direct inferences regarding the representational system used. In Hodgson and Waller's (2006) study, it is conceivable that participants relied on dynamic egocentric representations for smaller set sizes and on allocentric representations for larger set sizes. If those two types of representations had been roughly of the same fidelity, the switch from one representation type to the other would have remained undetected. In Wang et al.'s (2006) study, it is possible that participants used dynamic egocentric representations for all set sizes, as the authors have claimed, and that the quality of the egocentric updating process suffered, as more objects had to be tracked. It is however equally possible that participants, for instance, only recruited the dynamic egocentric system when tracking a single object, and that the drop in performance from one tracked object to two tracked objects resulted from a switch to allocentric representations of lesser fidelity.

Experiment 2 aimed to avoid such interpretational ambiguities by employing the same systematic heading manipulation that was used in the previous experiments described in this paper. As stated above, the main goal of this experiment was to identify limitations in the number of simultaneously tracked objects in the egocentric subsystem, while minimizing the delay between the loss of perceptual support and the retrieval of an object's location. The amount of rotation was also varied, but, as in Experiment 1, the performance for different rotation angles was used to determine whether participants predominantly relied on allocentric or dynamic egocentric representations. Hence, the ability of Experiment 2 to shed light on potential limitations of the dynamic egocentric system in terms of the amount of movement done after the loss of perceptual support is limited.

In order to minimize the delay between the loss of perceptual support (i.e., participants closing their eyes) and the retrieval of an object's location, participants in

Experiment 2 were only tested on a single object after each rotation, unlike participants in Experiment 1, who pointed to each of the objects three times after each rotation. This single object testing was considerably more time-consuming and taxing on the participants because of the large number of rotations they had to perform, but minimizing the delay between loss of perceptual support and retrieval of an object's location was essential for maximizing the probability of participants relying on dynamic egocentric representations for the task.

The first independent variable was the number of tracked objects, which was either one, three, or all six of the objects of the studied layout. The maximum number of six to-be-tracked objects was chosen in order to enable direct comparisons with the results of the pilot experiments and Experiment 1, in which participants did not show evidence for a reliance on egocentric representations when testing was blocked. One to-be-tracked object was included because it represents the smallest possible capacity of the egocentric system. Three to-be-tracked objects was included because it lies roughly in the middle of the other two values. Participants were told at the beginning of each trial which objects they had to keep track of, and after the rotation they were presented with the particular object that they had to point to.

The second independent variable was tested heading, which equaled amount of rotation. As in the oriented direct turn condition of Experiment 1, participants either rotated 0°, 135°, or 270° clockwise. The comparison of performance for the tested headings of 135° and 270° was used again to determine whether participants relied on allocentric or dynamic egocentric representations. Both independent variables were manipulated within participants and were varied on a trial-by-trial basis. Because participants were tested only on a single object after each rotation, configuration error could no longer be extracted from overall pointing error. Therefore, absolute pointing error was used instead of configuration error together with response latency as the dependent measure.

Method

Participants. Twenty-two students and members of the Nashville community (13 women, 9 men) participated in the experiment in return for class credit or monetary compensation.

Materials and design. The same randomly generated layout of six objects was used that was used in Experiment 1. Since Experiment 2 did not involve a disorientation procedure that required the elimination of orienting auditorial cues, participants did not wear headphones. Instead, the trials were presented to them through the speakers of the testing computer.

The primary independent variables were tested heading (0°, 135°, & 270°) and number of tracked objects (1, 3, & 6). Both variables were varied within participants. For each of the resulting nine factor combinations, participants pointed to each of the six objects once. The resulting 54 trials were presented in randomized order. For the trials in the three tracked objects condition, two objects were randomly selected in addition to the actual target object to serve as the tracked objects for a given trial.

Procedure. The procedure of Experiment 2 was very similar to the procedure of the oriented direct turn condition of Experiment 1. The main difference was that, at the beginning of each trial when participants were still allowed to look around and refresh their memories of the layout, they were provided with one or three objects to track or told that they were supposed to track all six objects. They then closed their eyes (instead of donning a blindfold, because using a blindfold would have been too cumbersome given the single object testing) and were told to which colored line to turn. After they had turned to the appropriate colored line, they were presented with the target object for that particular trial. Participants pointed to the target object and then returned to the 0° orientation, where they opened their eyes in anticipation of the next trial. The total duration of the experiment was typically on the order of 45 minutes.

Results and Discussion

The data were analyzed using a 2 (gender) x 3 (tested heading) x 3 (number of tracked objects) mixed-model ANOVA, with gender as a between factor and tested heading and number of tracked objects as within factors.

Figure 6a depicts absolute pointing error as a function of tested heading and number of tracked objects. The main effect of tested heading was significant, $F(2, 40) = 48.87$, $p < .001$, $MSE = 52.57$. Absolute pointing error did not differ between the tested headings of 0° and 270°, $F(1, 40) < 1$, $MSE = 52.57$, but was lower for those two headings than for the tested heading of 135°, Fs(1, 40) ≥ 63.60, ps < .001, MSE = 52.57. The main effect of number of tracked objects was not significant, $F(2, 40) < 1$, MSE = 37.92, and neither was the tested heading by number of tracked objects interaction, $F(4, 80) < 1$, $MSE = 34.47$. No other effects were significant.

The results for response time are shown in Figure 6b. The main effect of tested heading was significant, $F(2, 40) = 4.93$, $p < .05$, $MSE = 0.19$. Response times did not differ between the tested headings of 0° and 270°, $F(1, 40) = 2.30$, $p = .14$, $MSE = 0.19$,

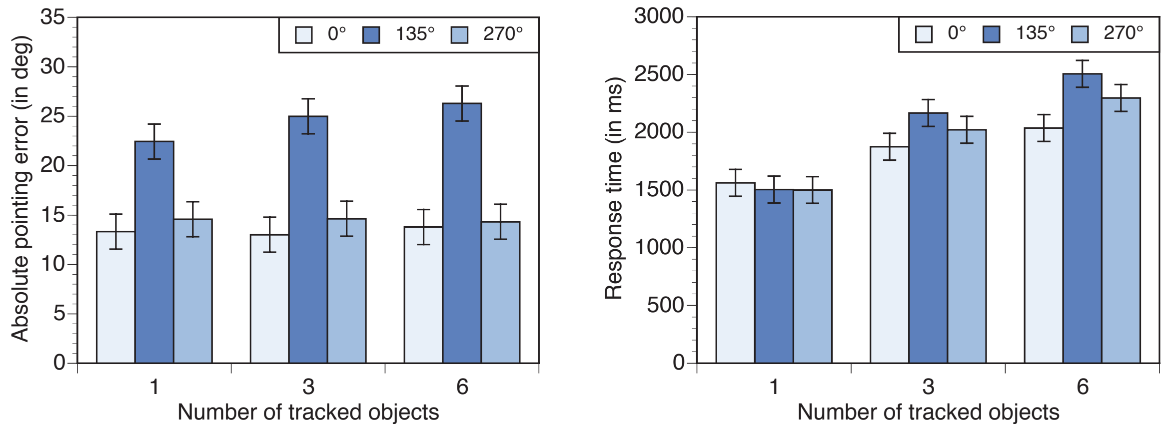

Figure 6. Absolute pointing error (A) and response time (B) as a function of tested heading and number of tracked objects in Experiment 2. Error bars are confidence intervals corresponding to ± 1 standard error, as estimated from the error term for the tested heading by number of tracked objects interaction in the ANOVA.

or between 135° and 270°, $F(1, 40) = 2.50$, $p = .12$, $MSE = 0.19$, but response times were lower for the heading of 0° than for the heading of 135°, $F(1, 40) = 9.60$, $p < .01$, $MSE = 0.19$. In contrast to the results for absolute pointing error, the main effect of number of tracked objects was significant for response time, $F(2, 40) = 38.32$, $p < .001$, $MSE = 0.25$. Participants responded faster for one tracked object than for three tracked objects, $F(1, 40) = 33.38$, $p < .001$, $MSE = 0.25$, and faster for three tracked objects than for six tracked objects, $F(1, 40) = 8.97$, $p < .01$, $MSE = 0.25$.

The tested heading by number of tracked objects interaction was also significant for response time, $F(4, 80) = 2.49$, $p < .05$, $MSE = 0.15$. As can be seen in Figure 6b, the three tested headings did not differ for one tracked object, $Fs(1, 80) < 1$, $MSE = 0.15$. For three tracked objects, response time was lower for 0° than for 135°, $Fs(1, 80) = 6.35$, $p < .05$, $MSE = 0.15$, but no other differences were significant, $Fs(1, 80) \leq 1.60$, $ps \geq .21$, $MSE = 0.15$. For six tracked objects, response time was lower for 0° than for 135° and 270°, $Fs(1, 80) \geq 5.02$, $ps < .05$, $MSE = 0.15$, and there was a tendency for responses to be faster for 270° than for 135°, $F(1, 80) = 3.26$, $p = .07$, $MSE = 0.15$.

In absolute pointing error, the pattern for tested heading was virtually identical with the patterns of the previous experiments. Participants were very accurate when they were tested at the 0° and 270° headings and they performed considerably worse when they were tested at the 135° heading, indicating that they relied on allocentric representations for the task. This even held true when participants were only tracking a single object. To emphasize this point further, even when participants only had to track a single object and the delay between loss of perceptual support (i.e., participants closing their eyes) and them pointing to the target object was minimized because of the single trail testing in Experiment 2, there was still no evidence for the usage of dynamic egocentric representations.

No effect of number of tracked objects was evident in pointing error. Neither did participants point more accurately when they only had to track a single object or three out of the six objects, nor was the pattern for tested heading affected by the number of tracked objects. One obvious explanation for these findings could be that participants simply ignored the instructions to track the pre-announced object(s) while they turned and then retrieved the direction of the target object when that object was announced.

The results for response time, however, strongly argue against this possibility. In response time, participants clearly profited considerably when they only had to track a subset of the objects, and in particular, when they only had to track a single object. Furthermore, when participants only had to track a single object, the function for tested heading became completely flat and responses at the 135° heading were as fast as those at the 0° and 270° headings. These results suggest that participants did indeed follow instructions to track the announced object, which enabled them to point from the 135°

heading without the latency cost that has been consistently observed for this heading in the earlier experiments in this paper.

If participants did indeed follow instructions regarding the tracking of objects, why was no such effect present in the pointing error results? As shown by the pointing error data, participants were relying on allocentric representations to perform the task. Therefore, the tracking of individual objects that the instructions required participants to do would have been done with respect to these allocentric representations. The fact that participants were able to point faster but not more accurately when provided with a smaller number of objects to track and in particular, when only tracking a single object, suggests that allocentric tracking involves highlighting objects within allocentric representations, so their locations can be accessed faster, but it also suggests that allocentric tracking does not affect the fidelity of the representation itself. Therefore, participants were able to point to objects faster, but they were not able to report object directions more accurately from the 135° heading that did not correspond to a reference axis in their representation.

One question that has not been addressed so far concerns the capacity of allocentric tracking. Whereas for one tracked object, there were no differences in response time between the three tested headings; for three tracked objects, response times of the headings diverged and were significantly lower for 0° than for 135°. This finding suggests that participants were able to track a single object but not three objects simultaneously. When asked to track three objects, participants were apparently only able to track a subset of those three objects. Hence, on some trials, participants had to point to an object that they had not tracked successfully. On these trials, response time would have been affected by tested heading, as it had been in the previous experiments in this paper. Because the response times for three tracked objects were a composite of successfully tracked and not successfully tracked target objects, they exhibited a significant, yet attenuated, effect of tested heading. These considerations suggest that the capacity limit of allocentric tracking is one or possibly two objects.

Experiment 3

One central component of all previous experiments described in this paper was the manipulation of tested heading, which was used to make inferences about the representations on which participants relied. The key comparison was always between performance on the 135° heading, which was associated with a smaller rotation angle but was not aligned with the dominant geometric organization of the environment, and performance on the 270° heading, which was associated with a greater rotation angle but was aligned with the dominant geometric organization of the environment. Both the hypothesis of dynamic egocentric updating (e.g., Wang & Spelke, 2000) and the hypothesis of a switch from precise but transient to less precise but enduring representations (Waller & Hodgson, 2006) predicted that performance on 135° would be better or at least not worse than performance on 270°. The hypothesis of allocentric updating, in contrast, predicted that performance on 270° would be better than performance on 135°.

When only considering the above three hypotheses, the tested heading manipulation employed in the previous experiments described in this paper can be considered an effective tool for answering questions about the nature of spatial updating. There was, however, another dimension in which the 135° and the 270° headings differed, in addition to their associated rotation angles and the question of whether or not they were aligned with the dominant geometric features of the environment. This additional factor was the amount of disparity between the tested headings and the 0° learning orientation. None of the above three hypotheses consider this variable relevant, but it is not unconceivable that this variable could affect task performance. In the area of object recognition, for instance, the disparity between a tested orientation and the learning orientation has been shown to be an important determinant of recognition speed and accuracy (e.g., Bülthoff & Edelman, 1992; Tarr, 1995).

One prominent class of models, the so called image-based recognition models, has been proposed to explain this finding (Tarr & Bülthoff, 1998). At the core, these models contain a matching mechanism where the currently perceived visual image of an object or, more typically, features of that image are compared to stored images or feature sets of familiar objects. Because these images or feature sets are stored in a viewpoint dependent manner, matching a perceived object with its memory representation becomes more difficult and error-prone, the greater the disparity between the orientation of the perceived object and the orientation of its memory representation.

In the area of spatial memory, Wang and Spelke (2000, 2002) have proposed a memory subsystem that bears some resemblance to image-based object recognition models. As discussed in the introduction of this paper, the third subsystem in Wang and Spelke's theory stores the appearance of familiar landmarks and places in the form of static view-dependent snapshots. The theory posits that this subsystem's main responsibility is to aid in place recognition, but in principle, a system of stored egocentric views like this one could also be used for remembering the locations of objects. Because these stored views are viewpoint-dependent, some additional process would be needed for retrieving object locations relative to a novel orientation. Such a process would either introduce a constant performance cost, regardless of the particular novel orientation, or, more likely, would introduce a processing cost that was determined by the disparity between the familiar orientation and the novel orientation, as it is the case with a mental rotation like processes (e.g., Easton & Sholl, 1995).

In all experiments described in this paper, participants never visually experienced any view other than the one from the 0° learning orientation. Therefore, their performance would have been determined by the disparity between the particular tested heading and the 0° learning orientation if they had relied on a memory system of stored views. Since the disparity between the 135° heading and the 0° learning orientation is 135° and the disparity between the 270° heading and the 0° learning orientation is only 90°, it is entirely possible that the consistently observed performance advantage for 270° over 135° was not due to 270° being aligned with the walls of the room and 135° not, but instead due to 270° being less disparate from 0° than 135° was.

The goal of Experiment 3 was to determine if the results of the previous experiments in this paper could indeed simply be explained by differences in disparity between the tested headings and the 0° learning orientation, or if they were genuinely indicative of the usage of allocentric representations as originally claimed. The tested headings used in Experiment 3 were 0°, 70°, and 270°. Like the previously used 135° heading, the 70° heading was associated with a smaller rotation angle than the 270° heading, and unlike the 270° heading, it was not aligned with the dominant geometric organization of the environment. In contrast to the 135° heading, however, the 70° heading was less disparate from the 0° learning orientation than the 270° heading was.

Hence, the allocentric updating hypothesis and the stored egocentric views hypothesis made opposite predictions regarding the relative performance on the headings of 70° and 270°. The allocentric updating hypothesis predicted that performance should be better on 270° than on 70°, because the former heading was aligned with the dominant geometric organization and the latter was not. The stored egocentric views hypothesis predicted that performance should be better on 70° than on 270°, because the disparity between the former heading and the learning orientation was only 70°, whereas the disparity between the latter and the 0° learning orientation was 90°.

Apart from using the 70° heading instead of the 135° one, Experiment 3 was very similar to the oriented direct turn condition of Experiment 1.

Method

Participants. Thirteen students and members of the Nashville community (6 women, 7 men) participated in the experiment in return for class credit or monetary compensation.

Materials, design, and procedure. The materials, design, and procedure of Experiment 3 were very similar to those of the oriented direct turn condition in Experiment 1. Participants studied the same randomly generated layout that was used in Experiments 1 and 2. Since Experiment 3 did not involve a disorientation procedure that required the elimination of orienting auditorial cues, participants did not wear headphones and the trials were presented to them through the speakers of the testing computer.

The primary independent variable was tested heading (0°, 70°, & 270°), which was varied within participants. As in Experiment 1, testing was blocked. Participants were tested twice on each heading, resulting in six blocks of trials. For each block, participants turned clockwise to the appropriate heading and pointed to each of the six objects three times in random order. The total number of trials was 108 and the experiment took an average of about 40 minutes. Because testing was blocked, configuration error could again be used as the primary dependent measure in addition to response time.

Results and Discussion

The data were analyzed using a 2 (gender) x 3 (tested heading) mixed-model ANOVA, with gender as a between factor and tested heading as a within factor. Figure 7a depicts configuration error as a function of tested heading. The main effect of tested heading was significant, $F(2, 22) = 9.03$, $p < .01$, $MSE = 14.22$. Configuration error did not differ between the headings of 0° and 270°, $F(1, 22) = 2.49$, $p = .13$, $MSE = 14.22$, but was lower for those two headings than for the heading of 70°, $Fs(1, 22) \geq 6.90$, $p < .05$, $MSE = 14.22$.

Response time as a function of tested heading is plotted in Figure 7b. The main effect of heading was significant, $F(2, 22) = 6.00$, $p < .01$, $MSE = 0.036$. Response time did not differ between the headings of 0° and 270°, $F(1, 22) = 1.85$, $p = .19$, $MSE = 0.036$, but was lower for those two headings than for the heading of 70°, $Fs(1, 22) \geq 5.02$, ps $< .05$, $MSE = 0.036$.

The results for configuration error and response time were virtually identical. For both measures, participants performed significantly better on the 270° heading, which was aligned with the dominant geometric organization of the environment but more disparate from the learning orientation, than on the 70° heading, which was misaligned

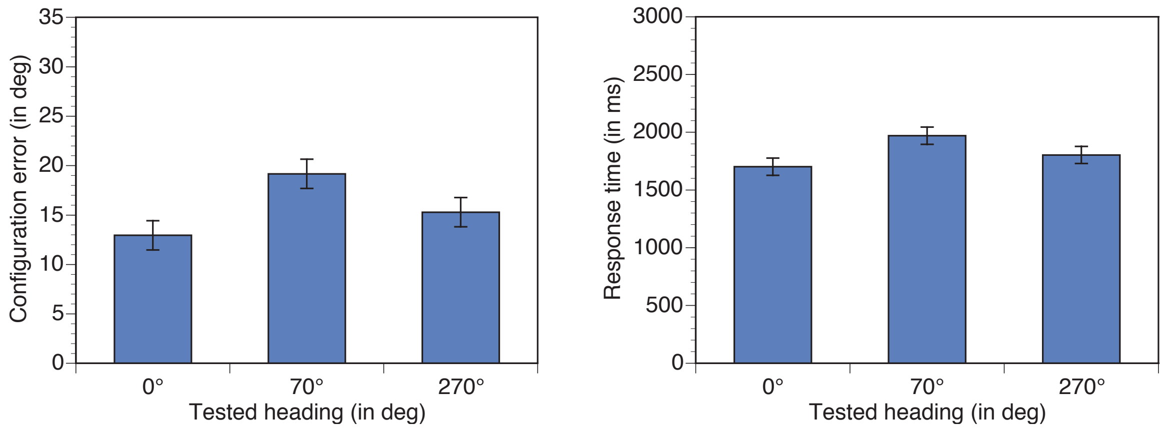

Figure 7. Configuration error (A) and response time (B) as a function of tested heading in Experiment 3. Error bars are confidence intervals corresponding to ± 1 standard error, as estimated from the ANOVA.

with the dominant geometric organization of the environment but less disparate from the learning orientation. These results are not compatible with the notion that participants relied on static egocentric views to locate the objects. Instead, they support the hypothesis that participants recruited allocentric representations in which the dominant environmental axes were used as reference axes in the representations.

CHAPTER IV

GENERAL DISCUSSION

The overarching goal of the experiments presented in this paper was to investigate the relative importance of dynamic egocentric representations and enduring allocentric representations for updating the locations of multiple objects in the absence of perceptual support. In this context, three prominent hypotheses on spatial updating were contrasted. The first one was that spatial updating is generally based on dynamically updated egocentric representations (Wang & Spelke, 2000). The second hypothesis was that precise but transient representations are used when a person is oriented and did not rotate more than a small angle after the loss of perceptual support, and that less precise but enduring representations are used when the person is disoriented or has rotated a larger angle after the loss of perceptual support (Waller & Hodgson, 2006). The third hypothesis was that spatial updating is primarily based on enduring allocentric representations that are specified with respect to reference directions that are intrinsic to the represented environment (Mou et al., 2004).

The first pilot experiment contrasted these three hypotheses on spatial updating through the use of a systematic manipulation of rotation angle and thereby tested heading. Participants studied random layouts of objects from a 0° orientation, which was aligned with the walls of the surrounding room and then had to point to the objects after rotations of 0°, 90°, 135°, and 270°. The results showed that performance neither decreased with increasing rotation angle, as the dynamic egocentric updating hypothesis predicted (Wang & Spelke, 2000), nor did it follow a simple step function, as Waller and

Hodgson's (2006) hypothesis of a switch from precise but transient to less precise but enduring representations for larger rotation angles predicted. Instead, performance was good for the tested headings of 0°, 90°, and 270°, which were aligned with the walls of the surrounding room, and performance was worse for the 135° heading, which was misaligned with the walls. In other words, performance was determined by whether a particular heading was aligned with the dominant geometric organization of the environment, as predicted by the hypothesis that updating is based on allocentric representations that employ salient environmental axes as reference directions.

The second pilot experiment examined whether the benefited headings in the first pilot experiment were indeed benefited because they were aligned with the dominant geometric features of the environment, or whether they were benefited simply by being orthogonal to the learning orientation. This was accomplished by using the same tested headings as in the first pilot experiment, but rotating both the tested headings and the learning orientation by 60° so that none of them would remain aligned with the walls of the room. The results showed that configuration error was no longer lower for the headings of 90° and 270º than for the heading of 135°, when the headings of 90° and 270° were not aligned with the walls of the room. This finding supported the hypothesis that alignment with the dominant features of the environment is an important factor for performance on a particular heading, because it increases the likelihood that that direction is selected as a reference direction in the representation. The results for response time, however, only partially supported this conclusion. Response time did increase for the 90° and 270° headings relative to the 0° heading, but it was still lower for the former two headings than for the 135° heading, even though they were no longer aligned with the dominant geometric organization of the environment. These results suggest that, in addition to alignment with environmental features, orthogonality to the learning view is also a relevant factor.

It is important to note that the process of selecting reference directions is not yet fully understood. A number of variables have been shown to be important for increasing the saliency of intrinsic directions, and thereby making them more likely to be selected as reference directions, including actually experiencing a direction, the prominence of environmental axes, the layout and grouping of objects in the environment, and emphasizing intrinsic axes via instructions (Mou & McNamara, 2002; Valiquette, McNamara, & Mullen, in preparation). Typically, experiencing a direction is the most dominant cue, but this cue can be overshadowed if the combination of other opposing cues is strong enough (Mou & McNamara, 2002). Clearly, more work is required to better understand the relative importance of these cues and the interactions between them.

The primary support for the usage of egocentric representations in spatial updating comes from studies that observed an increase in configuration error after disorientation (e.g., Waller & Hodgson, 2006; Wang & Spelke, 2000). As explained earlier, at the core of these studies is the assumption that the fidelity of allocentric representations could not be affected by disorientation, and therefore, participants could not have relied on allocentric representations both when oriented and disoriented. Instead, it is argued, participants must have relied on precise egocentric representations when oriented, and then they must have either switched to less precise allocentric representations after disorientation, or those egocentric representations must have been degraded by the disorientation. A fundamental limitation of these studies was that they did not provide any direct means for making inferences about the type of representation used. Instead, the validity of their conclusions rested entirely on the assumption that the fidelity of allocentric representations could not be affected by disorientation.

The central goal of Experiment 1 was to address this shortcoming by incorporating the systematic tested heading manipulation of the pilot experiments into a disorientation paradigm. Using the same logic as in the pilot experiments, it was possible to draw inferences about whether participants relied on dynamic egocentric representations or allocentric representations in the different turning mode conditions of the experiment, by comparing the performance for the headings of 135° and 270°. The results indicated that participants relied on allocentric representations in both oriented turn conditions, which replicated the results of the pilot experiments. Performance was not better in the oriented direct turn condition than in the oriented indirect turn condition, which suggested that performance was not significantly augmented through the use of residual dynamic egocentric representations.

As anticipated, the results for the disorientation condition also indicated that participants relied on allocentric representations. In contrast to several previous disorientation studies, however, no increase in configuration error after disorientation was observed. Had an increase in configuration error been observed, the claim that the observed increase in configuration error was caused by participants using dynamic egocentric representations when oriented, and then relying on either degraded egocentric representations or lower precision allocentric representations after disorientation, would have been contradicted. Since configuration error did not increase after disorientation in Experiment 1, no such strong conclusions can be drawn about the results and interpretations of those disorientation studies that are cited as evidence for the importance of dynamic egocentric representations in spatial updating.

The results of the experiments discussed so far in this paper cast doubt, though, on the notion that dynamic egocentric representations are typically relied on for spatial updating. Neither in the pilot experiments nor in Experiment 1 did participants primarily rely on dynamic egocentric representations. Furthermore, the comparison between the oriented direct and the oriented indirect turn conditions in Experiment 1 suggested that not even residual egocentric representations played a role.

An open question remains why no increase in configuration error after disorientation was observed in Experiment 1. A number of studies have observed such an increase (e.g., Mou et al., 2006, Experiment 4; Waller & Hodgson, 2006, Experiments 1-2; Wang & Spelke, 2000), but several other experiments have not (e.g., Holmes & Sholl, 2005; Mou et al., 2006, Experiments 1-3). When comparing these groups of experiments, no obvious differences are apparent that would explain why the former found an increase in configuration error after disorientation and the latter did not. In Waller and Hodgson's (2006) and Wang and Spelke's (2000) studies, participants pointed with either their fingers or a pointing rod and not with a joystick as in Experiment 1. One could speculate that pointing with a joystick would be less accurate and increases in configuration error would therefore be harder to detect. When comparing the levels of configuration error, however, between Experiment 1 and Hodgson and Waller's (2006) experiments, it turns out that these are comparable. Furthermore, an increase in configuration error was found in Mou et al.'s (2006) Experiment 4 in which participants also responded using a joystick, but not in Holmes and Sholl's (2005) Experiment 6 in which participants pointed with their fingers.

Holmes and Sholl (2005) investigated the hypothesis that an increase in configuration error after disorientation would only occur for novel environments, which supposedly were only represented in the egocentric but not the allocentric system, but not for familiar environments, for which supposedly allocentric representations were available. Their results, however, showed no increase in configuration error for either novel or familiar environments. Holmes and Sholl then conducted a long series of experiments in which they tried to approximate Wang and Spelke's (2000) original methods as closely as possible. Across these experiments, they varied, for instance, the proximity of the surrounding objects to the participants, whether participants were disoriented through active or passive rotations, whether participants wore headphones that masked ambient sounds or not, whether participants were told that they would be disoriented, etc. They were, however, unable to replicate the increase in configuration error under any of those conditions.

As described previously, the results of Mou et al. (2006) suggested that an increase in configuration error after disorientation is only observed if participants study the object layout not from an external vantage point but from the inside of the layout and if the object layout is irregular. Follow-up experiments conducted by Xiao, Mou, and McNamara (2008) identified layout irregularity as the deciding factor for an increase in configuration error and not the participant's initial study position. Further experiments, however, showed that an increase in configuration error after disorientation could even be observed for a regular layout if participants were instructed to focus on self-to-object spatial relations during testing (e.g., "Please keep track of all of the locations of the objects relative to yourself while you are turning to face the ball."). By contrast, instructing participants to focus on object-to-object spatial relations (e.g., "Please keep track of all of the locations of the objects relative to other objects while you are turning to face the ball.") did not prevent an increase in configuration error when participants had studied an irregular layout from the inside.

Participants in Experiment 1, as those in the other experiments described in this paper, studied an irregular layout from a position inside the layout and were instructed to keep track of the object locations with respect to their own bodies. Yet, in contrast to the predictions of Xiao et al.'s (2008) results, no increase in configuration error after disorientation was observed. This discrepancy suggests that the increase in configuration error after disorientation must be modulated by a variable in addition to layout regularity, study position, and instructions.

In summary, no clear picture has yet emerged about the specific conditions under which configuration error increases after disorientation. Whereas some studies have replicated the increase in configuration error multiple times (Waller & Hodgson, 2006; Wang & Spelke, 2000) others have failed to replicate this effect despite numerous variations in the methods (Holmes & Sholl, 2005). Once the conditions that underlie this effect are better understood, it would be valuable to rerun Experiment 1 in such a way that these conditions were satisfied. The results would then allow for a decisive judgment on the question whether an increase in configuration error is indeed caused by participants being no longer able to rely on precise dynamic egocentric representations, as many previous disorientation studies have claimed, or whether that increase is caused by participants relying on allocentric representations that lose fidelity after disorientation.

An innovative alternative to testing for an increase in configuration error after disorientation was recently presented by Sargent, Dopkins, Philbeck, and Modarres (2008). In their experiments, participants learned irregular layouts of four objects and then underwent five successive rotations of either 70° or 200° while blindfolded. After each rotation, participants were asked to point to the objects. The authors were interested in whether the represented object locations would drift away from their physical locations interdependently of one another over the course of the multiple rotations or whether they would drift together as an ensemble.

As in previous studies that have tested for an increase in configuration error after disorientation, the key assumption in Sargent et al.'s (2008) study was that disturbances in the updating process would have different consequences for dynamic egocentric representations and for allocentric representations. More specifically, the assumption was that, in the case of allocentric updating, imprecision in the updating process would only affect participants' knowledge about their heading, but not the quality of their configurational knowledge of the object layout. Therefore, errors in updating would lead to object locations drifting together as an ensemble. In the case of dynamic egocentric representations, the assumption was that imprecision in updating would affect the individual self-to-object relations differently and therefore lead to object locations drifting independently of one another.

Sargent et al. (2008) employed three different analyses to contrast their predictions for allocentric and dynamic egocentric updating. The first analysis was based on correlations of within-object and between-object error scores across rotations; the second analysis compared angular separation errors between objects with the common offset of reported object locations for a given rotation; the third analysis used sign tests of the pointing errors for the individual objects for a given rotation. The results of the first two analyses indicated that object locations primarily drifted as an ensemble and not independently of one another, and thereby supported the hypothesis that participants relied on allocentric representations. The third analysis revealed that the pointing errors for the different objects after a given rotation typically had the same sign, which generally supported the allocentric updating hypothesis, but that the frequency of differences in sign was higher than the allocentric updating hypothesis would have predicted. These results have led Sargent et al. (2008) to suggest that spatial updating is primarily based on allocentric representations, but also augmented through the use of dynamic egocentric representations.

One potential criticism of Sargent et al.'s (2008) analyses is that they can be construed as tests of whether participants erred more in assessing their current heading after a rotation than they erred in reporting the object locations in their proper configuration. Proponents of egocentric updating could therefore argue that the observed drifting of the objects as an ensemble was not a consequence of updating errors, but simply a reflection of participants misjudging the amount they had been rotated. This criticism, however, does not apply to their first analysis, in which heading error was removed from the error scores.

Sargent et al.'s (2008) design and analyses were very innovative but the underlying research logic for contrasting dynamic egocentric and allocentric representations was the same as that in previous studies that tested for increases in configuration error after disorientation. At the core of both types of studies is the assumption that participants' abilities to report object locations accurately with respect to each other can only be affected by retrieval conditions (e.g., whether disoriented or not, the amount of movement that preceded retrieval, etc.) if participants relied on dynamic egocentric representations, but not if they relied on allocentric representations.

This assumption that the fidelity of allocentric representations is unaffected by retrieval conditions seems plausible if allocentric representations are considered static, cognitive-map-like representations, as suggested by Wang and Spelke (2000). An alternative view, however, would be that allocentric representations can store object locations at a higher degree of precision while the person is perceptually engaged with the environment, and that this additional precision is lost once the person is disengaged from the environment. In contrast to the prevalent view that the fidelity of allocentric representations is constant, this alternative view would be compatible with the finding of an increase in configuration error after disorientation.

Two general possibilities are conceivable for how precision could be lost in an allocentric representation once the person is disengaged from the environment. The first option would be a general loss of precision that would result in random distortions in the represented object locations. The second option would be that the represented object layout is regularized (e.g., objects are moved towards canonical directions, etc.). This second option would readily explain why an increase in configuration error has typically only been observed for irregular but not for regular layouts (Mou et al., 2006).

Returning to the experiments described in this paper, the goal of Experiment 2 was to explore the possibility that the earlier experiments did not find evidence in favor of dynamic egocentric representations because the task requirements in those experiments went beyond the limitations of the dynamic egocentric system. Two possible limitations of the system were considered: the number of objects that can be tracked simultaneously and the duration that information can be held in the egocentric system before it decays after the loss of perceptual support. Experiment 2 employed single trial testing to minimize the delay between loss of perceptual support and pointing to an object and varied the number of to-be-tracked objects between one and six to assess potential limitations of the system regarding the number of objects that can be tracked simultaneously.

The results showed that pointing error was completely unaffected by the number of tracked objects and even for one tracked object, pointing error was lower for the 270° heading than for the 135° heading, which indicated that participants relied on allocentric representations even when tracking only a single object over the course of a few seconds. For response time, there was an effect of number of objects, suggesting that participants did follow the instructions to track the announced objects. Furthermore, when participants only had to track a single object, the function for tested heading became completely flat and responses for the 135° heading were as fast as those for the 0° and 270° headings, indicating that the response time cost that had been consistently observed for the 135° heading in the earlier experiments was completely eliminated when participants only had to track a single object.

These results showed that participants were able to track one or two objects efficiently, which enabled them to respond considerably faster overall and without a latency cost for the 135° heading, but the pointing error data showed that tracking was done relative to allocentric representations. Hence, participants were able to point to objects faster from the 135° heading when only tracking a subset of the objects, but they were not able to report object directions more accurately from the 135° heading, because that heading did not correspond to a reference direction in their allocentric representation.

Even when tracking a single object over the course of only a few seconds without perceptual support, participants appeared to have relied on allocentric representations. This finding casts substantial doubt on the notion that dynamic egocentric representations are a crucial component in spatial updating. It is entirely possible, though, that dynamic egocentric representations play a central role in obstacle avoidance and navigation through the immediate environment when vision is available, as some theories have claimed (Mou et al., 2004). The current experiments are not able to speak to this issue.

The goal of Experiment 3 was to address a potential methodological weakness of the previous experiments. The headings used in those experiments were selected so that the usage of dynamic egocentric representations and allocentric representations made opposing predictions for performance on these headings. Better performance on the 135° heading, which was associated with the smaller rotation angle but was misaligned with the walls of the surrounding room, indicated the usage of dynamic egocentric representations. Better performance on the 270° heading, which was associated with the greater rotation angle but was aligned with the walls of the surrounding room, indicated the usage of allocentric representations. What these considerations did not take into account was that those headings also differed with respect to their disparity to the 0° learning orientation. Whereas the disparity between the 135° heading and the 0° learning orientation was 135°, the disparity between the 270° heading and the 0° learning orientation was only 90°. Performance in the earlier experiments could have been better for the 270° heading than for the 135° one, purely because of the disparity of these headings to the learning orientation. Such a result would have been predicted, for example, if participants had not relied on allocentric representations but instead on static snapshot-like egocentric representations of the learning view.

In order to examine this alternate hypothesis, that participants relied on representations of the learning view and not on allocentric representations that were specified with respect to reference directions that corresponded to the walls of the surrounding room, participants in Experiment 3 were tested at the 70° heading and the

270° heading. The results showed that participants performed faster and more accurate at the 270° heading, which had the greater disparity to the learning orientation but was aligned with the walls of the room, than at the 70° heading, which had the smaller disparity to the learning orientation but was misaligned with the walls of the room. These findings ruled out the possibility that the results of the previous experiments could simply be explained by differences in the disparity of the tested headings to the learning orientation and further supported the hypothesis that spatial updating is based on allocentric representations.

In conclusion, the experiments presented in this paper provided compelling evidence for the hypothesis that spatial updating is based on allocentric representations. These findings are in stark contrast to the commonly found claim that dynamic egocentric representations play an important role in spatial updating (Wang & Spelke, 2000). The primary evidence for a reliance on dynamic egocentric representations is the finding by some studies that configuration error increased after disorientation. As explained earlier, this evidence is indirect, because it entirely rests on the assumption that the fidelity of allocentric representations could not be affected by disorientation. In contrast, the tested heading manipulation employed throughout this project produced evidence for the reliance on allocentric representations that was more direct. That performance on a given heading was determined by its alignment with the dominant geometric organization of the environment and not by rotation angle was not merely an assumption, but a direct prediction of the allocentric updating hypothesis. In egocentric representations, object locations are, by definition, specified with respect to one's own body and not with respect to features of the surrounding environment. It is therefore not clear how dynamic egocentric updating models can explain the finding that performance was determined by the relation between a tested heading and the dominant geometrical features of the environment.

Furthermore, once the methodological conditions that lead to an increase in configuration error after disorientation are better understood, a decisive conclusion can be reached regarding the question whether an increase in configuration error is caused by the usage of precise dynamic egocentric representations before but not after disorientation, or whether such an increase can occur when allocentric representations are relied on both before and after disorientation, as the results of the experiments presented in this paper suggest. If it is determined that configuration error can increase after disorientation even if participants rely on allocentric representations, further experiments that investigate the nature of the loss of fidelity of allocentric representations will be needed. Specifically, it would be informative to test if object locations were randomly distorted or if they were systematically distorted, for instance, through a process of regularization of the represented object layout.

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 and Psychophysics*, *59*, 404-418.

Bülthoff, H. H., & Edelman, S. (1992). Psychophysical support for a two-dimensional view interpolation theory of object recognition. *Proceedings of the National Academy of Sciences of the United States of America*, *89*, 60-64.

Burgess, N., Spiers, H. J., & Paleologou, E. (2004). Orientational manoeuvres in the dark: Dissociating allocentric and egocentric influences on spatial memory. *Cognition*, *94*, 149-166.

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.

Galati, G., Lobel, E., Vallar, G., Berthoz, A., Pizzamiglio, L., & Le Bihan, D. (2000). The neural basis of egocentric and allocentric coding of space in humans: a functional magnetic resonance study. *Experimental Brain Research*, *133*, 156-164.

Golledge, R. G. (1999). Human wayfinding and cognitive maps. In R. Golledge (Ed.), *Wayfinding behavior: Cognitive mapping and other spatial processes* (pp. 5-45). Baltimore: Johns Hopkins University Press.

Hodgson, E., & Waller, D. (2006). Lack of set size effects in spatial updating: Evidence for offline updating. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *32*, 854-866.

Holmes, M. C., & Sholl, M. J. (2005). Allocentric coding of object-to-object relations in overlearned and novel environments. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *31*, 1069-1087.

Klatzky, R. L. (1998). Allocentric and egocentric spatial representations: Definitions, distinctions, and interconnections. In C. Freksa, C. Habel, & K. F. Wender (Eds.), *Spatial cognition: An interdisciplinary approach to representing spatial knowledge* (pp. 1-17). Berlin: Springer.

Levinson, S. C. (1996). Frames of reference and Molyneux's question: Crosslinguistic evidence. In P. Bloom, M. A. Peterson, L. Nadel, & M. F. Garret (Eds.), *Language and Space* (pp. 77-1017). Cambridge: MIT.

May, M., & Klatzky, R. L. (2000). Path integration while ignoring irrelevant movement. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *26*, 169-186.

McNamara, T. P. (2003). How are the locations of objects in the environment represented in memory? In C. Freksa, W. Brauer, C. Habel, & K. F. Wender (Eds.), *Spatial cognition III: Routes and navigation, human memory and learning, spatial representation and spatial reasoning, LNAI 2685* (pp. 174-191). Berlin: Springer.

McNamara, T. P., Rump, B., & Werner, S. (2003). Egocentric and geocentric frames of reference in memory of large-scale space. *Psychonomic Bulletin and Review*, *10*, 589-595.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford, England: Oxford University Press.

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*, *32*, 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.

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.

Sargent, J., Dopkins, S., Philbeck, J. W., & Modarres, R. (2008). Spatial memory during progressive disorientation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*, 602-615.

Shelton, A. L., & McNamara, T. P. (2001). Systems of spatial reference in human memory. *Cognitive Psychology*, *43*, 274-310.

Sholl, M. J. (2000). The functional separability of self-reference and object-to-object systems in spatial memory. In S. O. Nuallain (Ed.), *Spatial cognition: Foundations and applications: Selected papers from Mind III, annual conference of the Cognitive Science Society of Ireland, 1998* (pp. 45-67). Amsterdam: John Benjamins.

Sholl, M. J., & Nolin, T. L. (1997). Orientation specificity in representations of place. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *23*, 1494-1507.

Soechting, J. F., & Flanders, M. (1992). Moving in three-dimensional space: Frames of references, vectors, and coordinate systems. *Annual Review of Neuroscience*, *15*, 167-191.

Tarr, M. J. (1995). Rotating objects to recognize them: a case study of the role of viewpoint dependency in the recognition of three-dimensional objects. *Psychonomic Bulletin and Review*, *2*, 55-82.

Tarr, M. J., & Bülthoff, H. H. (1998). Image-based object recognition in man, monkey and machine. *Cognition*, *67*, 1-20.

Valiquette, C. M., McNamara, T. P., & Mullen, V. (in preparation). Egocentric, exocentric, and intrinsic frames of reference in spatial memory. *Unpublished manuscript*.

Valiquette, C. M., McNamara, T. P., & Smith, K. (2003). Locomotion, incidental learning, and the selection of spatial reference systems. *Memory & Cognition*, *31*, 479-489.

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.

Waller, D., Montello, D. R., Richardson, A. E., & Hegarty, M. (2002). Orientation specificity and spatial updating of memories for layouts. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *28*, 1051-1063.

Wang, R. F. (1999). Representing a stable environment by egocentric updating and invariant representations. *Spatial Cognition and Computation*, *1*, 431-445.

Wang, R. F., Crowell, J. A., Simons, D. J., Irwin, D. E., Kramer, A. F., Ambinder, M. S., et al. (2006). Spatial updating relies on an egocentric representation of space: Effects of the number of objects. *Psychonomic Bulletin and Review*, *13*, 281-286.

Wang, R. F., & Spelke, E. S. (2000). Updating egocentric representations in human navigation. *Cognition*, *77*, 215-250.

Wang, R. F., & Spelke, E. S. (2002). Human spatial representation: Insights from animals. *Trends in Cognitive Sciences*, *6*, 376-382.

Woodin, M. E., & Allport, A. (1998). Independent reference frames in human spatial memory: Body-centered and environment-centered coding in near and far space. *Memory & Cognition*, *26*, 1109-1116.

Xiao, C., Mou, W., & McNamara, T. P. (2008). Use of self-to-object and object-to-object spatial relations in locomotion. *Unpublished manuscript.*