

Location memory biases reveal the challenges of coordinating visual and kinesthetic reference frames

Vanessa R. Simmering · Clayton Peterson ·
Warren Darling · John P. Spencer

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Abstract Five experiments explored the influence of visual and kinesthetic/proprioceptive reference frames on location memory. Experiments 1 and 2 compared visual and kinesthetic reference frames in a memory task using visually-specified locations and a visually-guided response. When the environment was visible, results replicated previous findings of biases away from the midline symmetry axis of the task space, with stability for targets aligned with this axis. When the environment was not visible, results showed some evidence of bias away from a kinesthetically-specified midline (trunk anterior–posterior [a–p] axis), but there was little evidence of stability when targets were aligned with body midline. This lack of stability may reflect the challenges of coordinating visual and kinesthetic information in the absence of an environmental reference frame. Thus, Experiments 3–5 examined kinesthetic guidance of hand movement to kinesthetically-defined targets. Performance in these experiments was generally accurate with no evidence of consistent biases away from the trunk a–p axis. We discuss these results in the context of the challenges of coordinating reference frames within versus between multiple sensori-motor systems.

Keywords Vision · Proprioception · Memory · Reference frames · Coordinate transformations

Location memory biases reveal the challenges of coordinating visual and kinesthetic reference frames

Remembering the locations of objects in space is a surprisingly challenging task. Even a simple laboratory task, where a single target location is presented within a local workspace, requires perceiving the location using some sensory system (e.g., visual, kinesthetic/proprioceptive), encoding and maintaining that information over short-term delays, and then reproducing the location by, for instance, generating a pointing movement or visually guiding a cursor to the remembered location. Each of these steps must be grounded in some frame of reference, and typically multiple reference frames must be continuously coordinated. For example, a visually-guided reaching movement in a rich, natural environment (e.g., reaching for a coffee cup on a cluttered desk) typically brings together world-centered reference frames (where the cup is relative to the edge of the desk) and egocentric reference frames (positioning of the arm and torso).

Given the complexity of this problem, the challenges inherent in simple location memory tasks have typically been studied in different ways. For instance, there is a long history within cognitive psychology of studying the use of world-centered reference frames and the processes that underlie the maintenance of spatial information in memory. The spatial cognition literature has established a robust pattern of biases across a variety of situations (see Spencer et al. 2007, for review). These biases are characterized by stable memory for targets aligned with reference frames—like visible edges or symmetry axes—along

V. R. Simmering (✉) · J. P. Spencer
Department of Psychology, University of Iowa,
Iowa City, IA 52242, USA
e-mail: vanessa-simmering@uiowa.edu

C. Peterson · W. Darling
Department of Integrated Physiology,
University of Iowa, Iowa City, IA 52242, USA

J. P. Spencer
Iowa Center for Learning and Developmental Sciences,
University of Iowa, Iowa City, IA 52242, USA

with biases *away from* reference frames for targets to either side (e.g., Nelson and Chaiklin 1980; Tversky and Schiano 1989; Engebretson and Huttenlocher 1996; Spencer et al. 2006). Such biases increase systematically over short delays (e.g., 0–20 s) with an associated delay-dependent increase in response variability (e.g., Spencer and Hund 2002). Theories proposed to explain these biases have focused on interactions between the structure of the task space and information actively maintained in short-term memory (Huttenlocher et al. 1991; Spencer et al. 2007).

Other approaches have emphasized the transformation of reference frames in the context of the motor challenges present in recall and spatial estimation tasks. For instance, researchers have examined the accuracy of kinesthetically-guided reaches to visually-specified targets, both immediately after target presentation (e.g., Soechting and Flanders 1989a, b; Darling and Miller 1993) and with varying delays (e.g., McIntyre et al. 1997, 1998). Such studies have focused on how movements are planned and executed relative to multiple available reference frames (e.g., shoulder-centered or hand-centered frames). Biases over delays in these studies have tended to be idiosyncratic (i.e., different subjects exhibit different patterns of error). There is some suggestion that people use a hand-centered reference frame to guide movements to visual targets (see, e.g., Sainburg et al. 2003). Other studies implicate a role for body midline. For instance, research on unseen hand movements to visual targets in the horizontal plane has shown that subjects underestimate the lateral distance between the hand and body midline axis when planning movements (Ghilardi et al. 1995; van Beers et al. 1998).¹ Thus, kinesthetic perception of hand/fingertip location may be biased toward body midline rather than away from a midline reference frame as reported in the visuospatial cognition literature.

The present work sought to bring these research traditions together by asking whether people show distortion in location memory relative to a bodily frame of reference over delays, comparable to the biases reported with visual reference frames. We investigated this question by varying the availability of a visual reference frame in a location memory task. In Experiments 1 and 2, we asked whether perception of bodily reference frames contribute to repulsion away from a visual midline symmetry axis in a typical spatial recall task (Spencer and Hund 2002). Results from these experiments show robust biases when the midline

axis was specified visually, but less robust reference-related biases when the axis was specified kinesthetically (in this case, in the absence of visual input).² The lack of bias in these kinesthetic conditions may reflect the challenges of coordinating a kinesthetic reference frame with a visuospatial response (moving a mouse cursor). Thus, in three subsequent experiments, we probed whether location memory was biased away from kinesthetic reference frames in a purely kinesthetic task. In contrast to Experiments 1 and 2, results showed no evidence of systematic bias near a kinesthetic reference frame. We conclude by discussing the challenges of coordinating reference frames within versus between sensori and motor systems.

Experiment 1a

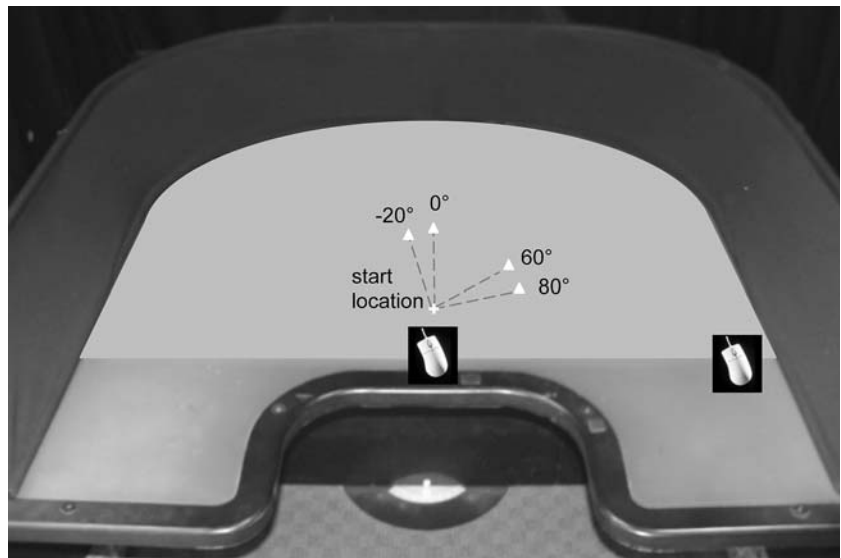
In the first experiment, we used a typical spatial recall task to assess whether body midline contributes to the biases away from midline evident in the spatial cognition literature (e.g., Spencer and Hund 2002). The task we used required subjects to remember a visually-specified target within a visual frame of reference (defined by the edges and midline symmetry axis of a large table; see Fig. 1), and then produce a visually-guided response (move a mouse cursor to the remembered location). Under these circumstances, we have previously observed delay-dependent biases away from the midline symmetry axis of the table, with low mean error and response variability for targets aligned with midline (Spencer and Hund 2002).

To examine whether perception of body midline contributes to this pattern of responding, a second set of subjects completed this task in complete darkness. In this condition, the target was still visually-specified, and the response was still visually-guided; however, in the absence of the visual structure of the table, subjects must rely on a kinesthetically-specified midline (e.g., perception of body midline) to show biases away from this axis. Note that, in this context, we use the term *kinesthesia* to denote the sense of orientation and motion of body segments (including the trunk) in the absence of vision. If we see such biases in this condition, we can conclude that visual perception of the midline symmetry axis is not the only contribution to the biases seen in typical spatial recall tasks.

¹ Note that underestimation reported in some experiments are relative to the body, not to midline; because our interest here is the influence of midline as a frame of reference, we do not address how our experimental manipulations may affect extent errors (i.e., overshooting or under-shooting targets) in this paper.

² Under more typical circumstances, perception of body midline involves multi-modal integration and is not strictly kinesthetically-defined. In these experiments, we specifically limit the availability of other perceptual information such that participants would rely on a kinesthetically specified body midline. The absence of visual input removes vision as a potential source of perceptual information; however, we acknowledge the possibility that participants were also using tactile sensations due to skin–chair contact to specify body midline in this task.

Fig. 1 Experimental apparatus for visual experiments. Targets were presented at two locations per layout (see “Experimental design”). For Experiment 1, the mouse and mouse pad were placed along the right edge of the table; for Experiment 2, they were aligned with the midline symmetry axis of the table



Method

Subjects

Forty-seven subjects (21 males and 26 females, aged 18–44 years) took part in this experiment. All subjects were right-handed and had normal or corrected-to-normal vision. Six additional subjects' data were excluded from analyses (four due to incomplete data, two due to large errors on no-delay trials). Subjects signed informed consent forms approved by the University of Iowa Institutional Review Board prior to participation, and received either research exposure credit or \$7 per hour for participating.

Apparatus

Subjects sat within an arc cut out from the side of a large (0.921×1.194 m) table with a homogeneous dark grey surface. Three edges of the table were covered with a curved border to occlude the corners from view, eliminating the diagonal symmetry axes (Fig. 1). Black curtains covered the walls and ceiling of the experimental room, eliminating distal reference cues. Stimuli were projected onto the surface of the table from below using a Barco 708 Data Projector (Barco, Inc., Belgium). Target stimuli were white isosceles triangle “spaceships” (12 mm base, 15 mm height), presented in a 15 cm square area centered at the midline symmetry axis of the tabletop (aligned with body midline), 30 cm anterior to the subject's chest (see Fig. 1). Targets were presented at radial distances of 15 cm from the “start” location—note that this location was not visibly marked during the session. At response, white crosshairs (15×15 mm) appeared at the start location. Subjects controlled the crosshairs with a wireless mouse located on a

black mouse pad in the bottom right corner of the table, out of their field of view.

Procedure

Subjects sat at the table with a strap secured around the waist to ensure that they would remain stably positioned at the midline of the table. An experimenter explained the task and played a demonstration trial, followed by a 2 min warm-up game to familiarize subjects with the mouse movement. For this game, a grid of white dots appeared on the tabletop. Every 4 s, a tone sounded and a spaceship appeared on a randomly-selected dot. The subject moved the crosshairs with the mouse to follow the spaceship.

Next, the practice trials began. Each trial began when the computer stated, “Beginning search for enemy spaceships.” After a random pre-trial delay, the target appeared for 2 s and then disappeared. To prevent fixation on the location during the delay, subjects were instructed to look up from the table after the spaceship disappeared for a variable delay until they heard “ready, set, go”; during target presentation and response, subjects were allowed to look freely at the display. When subjects heard the “ready, set, go” sequence, they looked down at the table to see the crosshairs at the start location; on “go,” they moved the crosshairs to the remembered spaceship location and clicked the left mouse button.

Each session included 16 practice trials, followed by four blocks of 16 test trials each, for a total of 64 test trials. Breaks were offered between blocks, though few subjects took them. All subjects took a mandatory break half way through the session. Sessions lasted approximately 45 min. Subjects were debriefed at the end of the session.

Experimental design

Subjects were randomly assigned to one of two target layouts (see Fig. 1). In the 0/80 layout, targets were presented at 0° (i.e., along midline) and 80° (i.e., 80° clockwise from midline); this layout allowed us to probe stability for the target aligned with midline by comparing directional errors and variability across targets. In the –20/60 layout, targets were presented –20° and 60° from midline; this layout probed whether targets to either side of midline were biased away from midline over delay. In both target layouts, we used a large separation between targets (i.e., 80°) to avoid interactions between long-term memories for the individual locations (see Spencer and Hund 2002; Schutte and Spencer 2007). Each target was presented eight times at each of four delays—0, 5, 10, and 15 s—for the test trials.

Subjects in each layout were randomly assigned to a reference frame condition. In the Vision with Environment (Vis + Env) condition, subjects responded to the visible targets with the room dimly lit, so that the environment was visible. We expected subjects in this condition to use the midline symmetry axis as a reference frame. In the Vision without Environment (Vis) condition, subjects responded to the same visible targets using the same response type, but the room was dark and subjects wore dark glasses to eliminate vision of the environment. Thus, in the Vis condition, subjects could only see the targets and the mouse cursor (when presented). Because visual information is quite limited in this condition, we expected subjects to use their body midline (trunk anterior–posterior [a–p] axis) as a frame of reference.

Data analysis

For each trial, we recorded the *x*- and *y*-coordinates of the mouse crosshairs when the subject pressed the left mouse button. Then, we computed the angular separation between the vector from the start location to the response and the vector from the start location to the actual target location (in degrees). These directional errors were computed such that positive errors were clockwise (CW) and negative errors were counter-clockwise (CCW). Constant directional errors were computed as the mean of trials to the same target and delay, with variable directional error as the corresponding standard deviation (see, e.g., Spencer and Hund 2002).

We analyzed constant and variable directional error in separate planned comparisons for each layout with a three-way ANOVA with Target (inner [–20°, 0°], outer [60°, 80°]) and Delay (0, 5, 10, 15 s) as within-subjects factors and Condition (Vis + Env, Vis) as a between-subjects factor (with Huynh-Feldt correction for delay effects). All reported effects were significant at $P < 0.05$ unless

otherwise noted. We report only the highest-order interactions in cases where these effects subsume lower-order interactions and main effects. Following significant interactions, we conducted tests of simple effects on the relevant subset of the data (specified for each analysis below). Note that we did not compare across layouts; rather, we chose to focus on within-subjects comparisons to take full advantage of the repeated measures design to test for biases away from midline in both directions (i.e., –20° vs. 60° comparison) and for stability at midline versus lateral targets (i.e., 0° vs. 80° comparison).

Results

Constant directional error

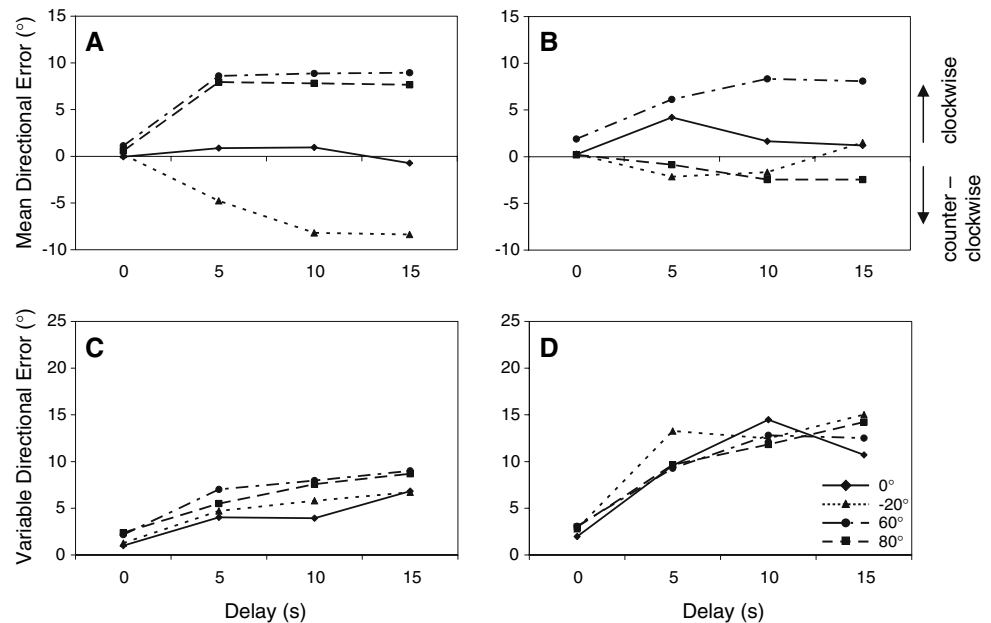
Errors in the Vis + Env condition (Fig. 2a) were low over delays for 0°, with delay-dependent “drift” away from midline/trunk a–p axis for the other targets. In the Vis Condition (Fig. 2b), however, errors were near zero for all but the 60° target, which showed large CW errors.

We first analyzed the 0/80 layout to assess whether subjects’ responses were stable when aligned with the midline symmetry axis (in the Vis + Env condition) or body midline (in the Vis condition). The ANOVA revealed a significant Target \times Delay \times Condition interaction ($F_{3,66} = 4.60$). To explore this interaction further, we conducted tests of simple effects separately for each condition. For the Vis + Env condition, tests of simple effects showed a significant Target \times Delay interaction ($F_{3,33} = 11.05$). Further tests of simple effects revealed a significant Delay main effect for only the outer (80°) target ($F_{3,33} = 13.76$), which was driven by increasing CW errors over delays (see Fig. 2a). Performance to the 0° target, on the other hand, did not change significantly over delay. For the Vis condition, tests of simple effects showed no significant effects; thus, performance for the target aligned with midline (0°) did not differ statistically from performance to the lateral (80°) target in this condition.

Next, we analyzed the –20/60 layout to assess whether subjects’ responses were biased away from the midline symmetry axis (Vis + Env) or body midline (Vis). This ANOVA revealed a significant Target \times Delay interaction ($F_{3,63} = 12.53$). Tests of simple effects showed significant Delay main effects for both the inner (–20°; $F_{3,63} = 5.46$) and outer (60°; $F_{3,63} = 11.92$) targets. These effects were driven by increasing errors away from midline over delay (see Fig. 2a, b).

The ANOVA for the –20/60 layout also revealed a significant Delay \times Condition interaction ($F_{3,63} = 3.61$). Tests of simple effects examining each Condition separately showed a significant Delay main effect for the Vis condition only ($F_{3,30} = 3.50$), which was driven by increasing CW

Fig. 2 Mean constant (a, b) and variable (c, d) directional errors across delays for each target in Vis + Env (a, c) and Vis (b, d) conditions in Experiment 1a. Positive values indicate clockwise directional errors; negative values indicate counter-clockwise directional errors



mean errors over delay. This reflects the asymmetry in bias to these targets in the Vis condition: the 60° target was biased away from midline, but the −20° target was not.

Variable directional error

Variable errors were generally lowest at the 0 s delay, and lower in the Vis + Env Condition than in the Vis Condition (Fig. 2c, d). Additionally, the 0° target had the lowest variability in the Vis + Env condition.

The ANOVA for the 0/80 layout revealed a trend toward a Target \times Delay \times Condition interaction ($F_{3,66} = 2.90$, $P = 0.056$). To explore this interaction further, we conducted tests of simple effects separately for each condition. For the Vis + Env condition, tests of simple effects showed a significant Target main effect ($F_{1,11} = 11.57$), which was driven by lower variability to the 0° target. Tests of simple effects also revealed a significant Delay main effect ($F_{3,33} = 8.19$), driven by a general increase in variability over delay. For the Vis condition, tests of simple effects showed a similar Delay main effect ($F_{3,33} = 5.87$), with increasing variability over delays. Note that targets did not differ in this condition, showing that performance to the 0° target was not stabilized by body midline—if anything, performance to this target was less stable than to the 80° target (see Fig. 2d). In addition, variability to both targets in this layout were higher in the Vis condition than the Vis + Env condition (which contributed to the Condition interaction). These differences across conditions suggest that body midline did not stabilize performance to the 0° target in the Vis condition.

The ANOVA for the −20/60 layout revealed a significant Delay \times Condition interaction ($F_{3,63} = 3.79$). Tests of

simple effects showed significant Delay main effects for both the Vis + Env ($F_{3,33} = 45.63$) and Vis ($F_{3,30} = 19.06$) conditions. Both effects were driven by increasing variability over delays, but variability was much higher in the Vis condition.

The AVOVA for the −20/60 layout data also revealed a significant Target \times Condition interaction ($F_{1,21} = 6.21$). Tests of simple effects for the Vis + Env condition showed a significant Target main effect ($F_{1,11} = 20.43$), which was driven by generally lower variability to the −20° target. Tests of simple effects for the Vis condition showed no such effects.

Discussion

Results from the Vis + Env condition replicated previous findings, with relatively low error and variability to the 0° target and delay-dependent drift away from the midline symmetry axis of the table for the other targets (Spencer and Hund 2002). Results from the Vis condition showed a similar pattern of constant errors, but with several critical differences. Unlike in the Vis + Env condition, performance to the 0° target in the Vis condition showed higher error and variability than in the Vis + Env condition, and did not show lower error and variability compared to 80°. This suggests that body midline did not stabilize memory for 0° target in the Vis condition. In addition, responses to the −20° target were not strongly biased CCW, as seen in the Vis + Env condition. Responses to the 60° target were the most consistent with responses in the Vis + Env condition, showing comparably large CW errors. Thus, the visual structure of the environment clearly contributes to the standard reference effects in this task. The weaker findings from the Vis condition still leave open the question of whether

memory for spatial location is repelled from body midline in a similar fashion.

It is possible that the limited evidence for biases away from body midline reflects a substantive difference in how the sensori–motor system uses visual, world-centered reference frames versus kinesthetically-specified frames. It is also possible, however, that participants *do* show biases away from kinesthetic reference frames in visuo-spatial location memory tasks—just not the one we probed. For instance, several studies have shown that people use shoulder- or hand-centered reference frames in some location estimation tasks (e.g., Lemay and Stelmach 2005). To examine the use of such frames in our spatial recall task, we included a follow-up experiment using conditions identical to Experiment 1a, but with targets presented around a shoulder-centered reference frame.

Experiment 1b

Method

Subjects

The same 47 subjects from Experiment 1a took part in this experiment, in a separate session.

Apparatus, procedure, experimental design, and data analysis

The apparatus, procedure, experimental design, and data analysis were identical to Experiment 1a with one exception. Instead of presenting the targets around midline, they

were presented around a shoulder-centered axis. For each subject, we measured from body midline (sternum) to the right shoulder joint (acromion) to specify the distance (in cm) of the shoulder axis from midline. We then shifted the stimulus presentation area (see Fig. 1) this distance to the right. Directional errors were measured as CW and CCW with respect to this axis.

Results

Constant directional error

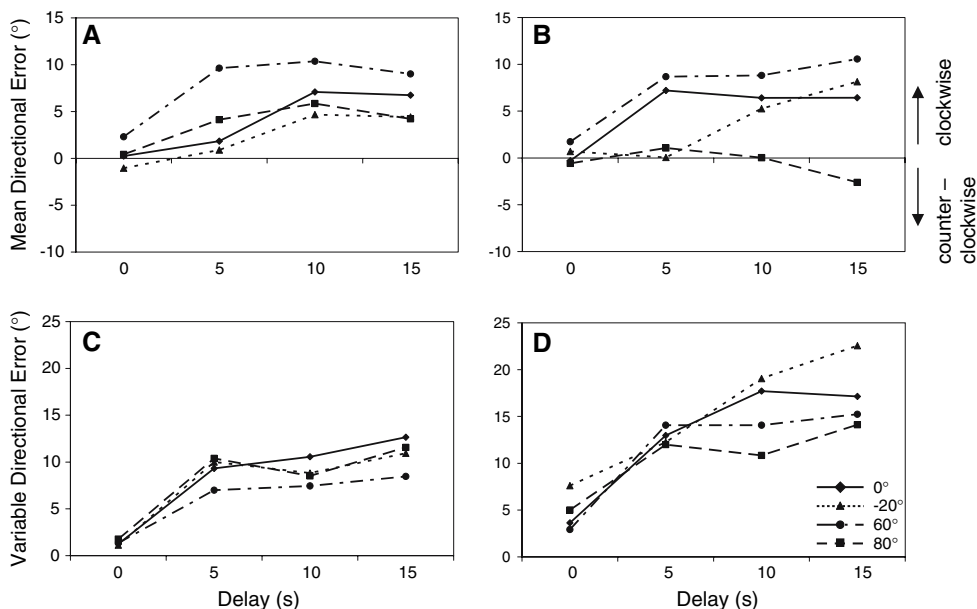
Responses were generally biased CW, with errors increasing over delay (Fig. 3a, b). The only exception to this pattern was errors near zero or slightly CCW for the 80° target in the Vis condition.

The ANOVA for the 0/80 layout revealed only a significant Delay main effect ($F_{3,66} = 5.70$), driven by the overall increase in CW mean errors at longer delays. This suggests that subjects' responses were not stabilized by alignment with a shoulder-centered axis. The ANOVA for the -20/60 layout also revealed only a significant Delay main effect ($F_{3,63} = 13.00$). Again, this effect was driven by CW mean errors at longer delays, suggesting that subjects' responses were not biased away from a shoulder-centered axis, but were instead biased CW. Such biases are consistent with the CW biases observed in Experiment 1a, suggesting that responses here were biased away from a midline reference axis.

Variable directional error

Variability increased over delays (Fig. 3c, d) and was again higher in the Vis condition. In contrast to Experiment 1a,

Fig. 3 Mean constant (a, b) and variable (c, d) directional errors across delays for each target in Vis + Env (a, c) and Vis (b, d) conditions in Experiment 1b. Positive values indicate clockwise directional errors; negative values indicate counter-clockwise directional errors



though, variability to the 0° target was not clearly lower in the Vis + Env condition.

The ANOVA for the 0/80 layout revealed only a significant Delay main effect ($F_{3,66} = 29.71$), driven by increasing variability over delays. The similarity in variability across targets suggests that alignment with a shoulder-centered axis did not stabilize memory for the 0° target. The ANOVA for the $-20/60$ layout also revealed only a significant Delay main effect ($F_{3,63} = 35.11$), again driven by increasing variability of delays. These results confirm that the shoulder-centered axis did not stabilize nearby targets (i.e., 0° and -20°), suggesting that subjects were not using this axis as a frame of reference.

Discussion

Analyses of both constant and variable directional errors suggest that subjects were not using a shoulder-centered frame of reference. Instead, responses in both conditions were mostly biased CW, consistent with the use of the midline symmetry axis in the Vis + Env condition and body midline in the Vis condition. Notably, errors did not differ significantly across condition, in contrast to the findings from Experiment 1a. Together, results from these experiments suggest that subjects may use body midline as a frame of reference in a manner comparable to a visually-specified reference axis; however, the influence of this kinesthetically-specified axis is not as strong as the visually-specified midline of the table.

One reason that body midline may not serve as a strong reference frame in our Vis condition is because it is not as precise or salient as the visible midline in the Vis + Env condition. We tested this possibility by aligning the hand with body midline in Experiment 2. Studies suggest that a hand-centered reference frame is used for programming movements to visual targets in tasks in which a cursor indicating hand position is moved to a visual target (Sainburg et al. 2003; Wang and Sainburg 2005). We therefore hypothesized that bringing these two bodily reference frames into alignment might lead to more robust reference effects in the Vis condition.

Experiment 2

Method

Subjects

Forty-eight subjects (26 males and 22 females, aged 18–46 years) took part in this experiment. All subjects were right-handed and had normal or corrected-to-normal vision. Two additional subjects' data were excluded from analyses

(one due to incomplete data, one due to equipment problems). Subjects signed informed consent forms approved by the University of Iowa Institutional Review Board prior to participation, and received either research exposure credit or \$7 per hour for participating.

Apparatus, procedure, experimental design, and data analysis

The apparatus, procedure, experimental design, and data analysis were identical to Experiment 1a with one exception. Instead of placing the mouse pad along the right side of the table, it was aligned with body midline (see Fig. 1).

Results

Constant directional error

Performance in the Vis + Env Condition (Fig. 4a) showed the same pattern as in Experiment 1a (Fig. 2a), with low error over delays at 0° , and delay-dependent drift away from midline for the other targets. Results in the Vis condition (Fig. 4b) were also similar to Experiment 1a (Fig. 2b), except at the 15 s delay, where errors were generally larger.

The ANOVA for the 0/80 layout revealed a significant Target \times Delay \times Condition interaction ($F_{3,66} = 3.52$). To explore this interaction further, we conducted tests of simple effects separately for each condition. For the Vis + Env condition, tests of simple effects showed a significant Target \times Delay interaction ($F_{3,33} = 17.54$). As in Experiment 1, separate tests of simple effects for each target revealed a significant Delay main effect for only the outer (80°) target ($F_{3,33} = 13.63$), driven by increasing CW errors over delay. For the Vis condition, tests of simple effects showed no significant differences, suggesting that aligning the hand with body midline did not stabilize memory for the 0° target.

The ANOVA for the $-20/60$ layout revealed a significant Target \times Delay interaction ($F_{3,66} = 8.83$). Tests of simple effects showed a significant Delay main effect for the outer (60°) target ($F_{3,66} = 7.66$). As in Experiment 1a, this effect was driven by increasing CW errors over delays. Tests of simple effects also showed a trend toward a Delay main effect for the inner (-20°) target ($F_{3,66} = 2.71$, $P = 0.054$), driven by increasing CCW errors over delays. Note that errors did not differ across condition in this target layout.

Variable directional error

As in Experiment 1a, variable errors were considerably lower in the Vis + Env Condition, with lowest variability to the 0° target in that condition (Fig. 4c, d). By contrast, variable

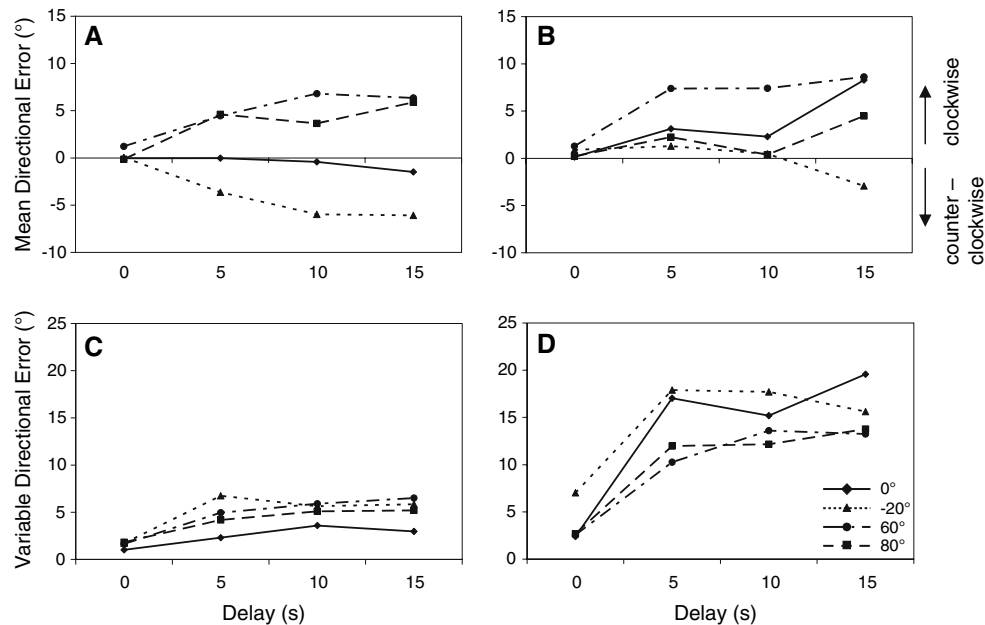


Fig. 4 Mean constant (a, b) and variable (c, d) directional errors across delays for each target in Vis + Env (a, c) and Vis (b, d) conditions in Experiment 2. Positive values indicate clockwise directional errors; negative values indicate counter-clockwise directional errors

errors were slightly lower for the outer targets (i.e., 60° and 80°) in the Vis condition (Fig. 4d).

The ANOVA for the 0/80 layout revealed a significant Delay \times Condition interaction ($F_{3,66} = 8.59$). Tests of simple effects showed significant Delay main effects for both Vis + Env ($F_{3,33} = 18.01$) and Vis ($F_{3,33} = 13.42$) conditions. Both effects were driven by increasing variability over delays, but variability was much higher in the Vis condition. The ANOVA for the $-20/60$ layout also revealed a significant Delay \times Condition interaction ($F_{3,66} = 4.99$). Again, tests of simple effects showed significant Delay main effects for both Vis + Env ($F_{3,33} = 10.35$) and Vis conditions ($F_{3,33} = 19.27$), with increasing variability over delays but higher variability in the Vis condition.

Discussion

Moving the position of the mouse pad and hand into alignment with body midline had little effect on performance. Indeed, constant errors in Experiments 1a and 2 yielded nearly identical results, with one exception: in Experiment 2, there was no Delay \times Condition interaction in the $-20/60$ layout. It is possible that the small CCW errors to the -20° target in the Vis condition reflect a more robust use of body midline in the present experiment, consistent with our goal of making this axis more salient. In the 0/80 layout, however, there was no evidence that placing the hand in front of body midline helped stabilize memory of the 0° target in the Vis condition. This leads us to conclude that, if subjects are using body midline in our task, it does not lead to the

same pattern of biases as the visually-specified midline axis.

Why might the use of body midline differ from the use of the visible midline in our visuo-spatial location memory task? It is possible that subjects had difficulty using body midline in the Vis conditions given the heavy emphasis on visuo-spatial information: the targets were visually specified and responses were visually guided. The absence of accompanying visible, world-centered reference frames places heavy demands on subjects to represent visuo-spatial information egocentrically and to coordinate such information with kinesthetic information on body midline. It is well known that egocentric reference frames are subject to the accumulation of drift and error over time and require re-calibration to anchor points in the world (e.g., Gallistel 1990; Newcombe and Huttenlocher 2000). Perhaps, then, subjects had difficulty keeping visual and kinesthetic information tightly in register. This could explain both the variable performance for targets aligned with body midline in the Vis conditions as well as the inconsistent CCW bias to the -20° target across Experiments 1a and 2. Alternatively, body midline may be specified in a more variable manner than the visually defined midline of the workspace, thereby producing greater inter-subject (and within-subject) variability of errors. If the former view is correct, then we might find more robust evidence for the use of kinesthetic reference frames if we were to keep target presentation and responses within the same sensori-motor system. Moreover, we could also assess whether there was indeed greater variability in kinesthetic location memory. We tested these

possibilities in Experiment 3 by removing vision entirely—subjects were blindfolded, and target encoding and responding were both kinesthetic.

Experiment 3

Method

Subjects

Eighteen subjects (6 males and 12 females, aged 20–46 years) took part in this experiment. All subjects were right-handed and had no history of neuromuscular disorder. Subjects signed informed consent forms approved by the University of Iowa Institutional Review Board prior to participation, and were paid \$8 per hour for participating.

Apparatus

Subjects were blindfolded and seated, back supported, in a dental chair within an arc cut out from a sheet of plywood mounted on a table. Upon the plywood was an array of holes arranged around a 15 cm radius circle centered 30 cm from the subject's chest on midline (see Fig. 5). A peg (0.8 cm diameter, 7.5 cm tall) was placed in the hole corresponding to the target location on a given trial, and the subject's fingertip was placed upon the top of the peg to



Fig. 5 Experimental apparatus for kinesthetic experiments. Targets were presented at two locations per layout (see “Experimental design”)

present the target. Fingertip location was monitored with an electromagnetic system (Ascension Technologies Minibird).

Procedure

Subjects were blindfolded and seated in front of the target array. The experimenter explained the task and then began practice trials. On each trial, the experimenter guided the subject's fingertip passively from the start location (center of the array of holes) to the target. Once the fingertip was in place, the experimenter released the arm, and the subject maintained that posture for 2–3 s. The experimenter then passively guided the subject's fingertip back to the starting location and removed the peg. After a variable delay, an auditory cue (beep) delivered via headphones signaled the subject to move to the remembered location. The subject attempted to place the fingertip at the location of the target, hold the position for several seconds, and then return to the start location. Note that subjects could not grope for the target peg or hole since the target peg had been removed and the subject's finger was approximately 7–8 cm above the plywood array (see Fig. 5). Subjects completed 16 practice trials, followed by 64 test trials. Subjects were told that they could take a break at any time, though no subjects chose to do so. Sessions lasted approximately 45 min.

Experimental design

The experimental design was similar to Experiments 1 and 2, with two exceptions. First, this experiment included only one kinesthetic condition (Kin). Second, exact delays of 0, 5, 10, and 15 s were unattainable due to the time needed to transport the arm from the target to the start location (0.5–1 s). Therefore, the delays in this experiment were approximately 1, 6, 11, and 16 s. In the figures and analyses presented below, we refer to the shortest delay as 1 s to highlight the fact that this design did not include trials with no delay. For convenience, we still refer to the longer delays as 5, 10, and 15 s.

Data analysis

The data analysis was similar to Experiment 1 except response locations were measured by fingertip location rather than the location of the mouse cursor.

Results

Constant directional error

Mean errors were generally low, with little modulation over delay (Fig. 6a). The -20° target showed the highest errors,

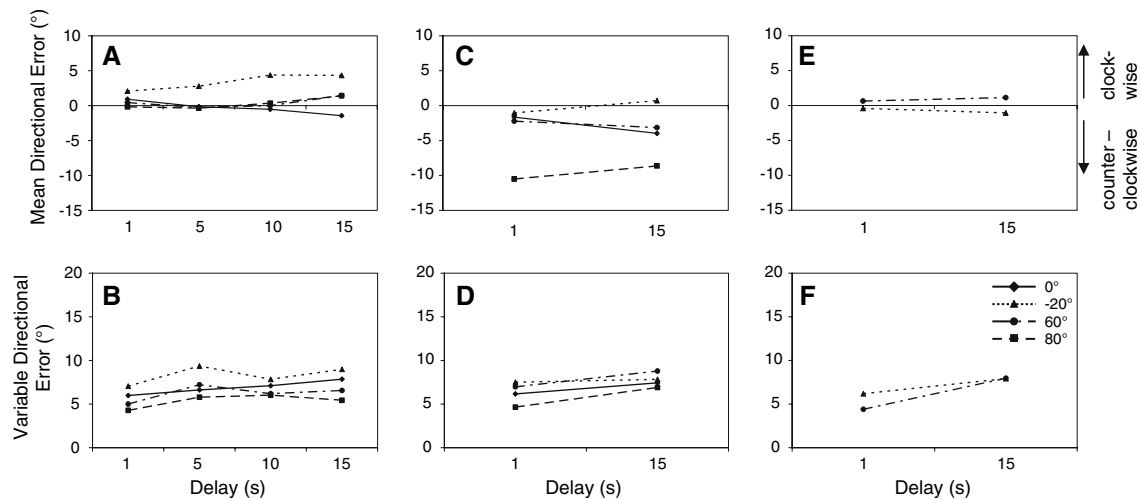


Fig. 6 Mean constant (a, c, e) and variable (b, d, f) directional errors across delays for each target in Experiments 3 (a, b), 4 (c, d) and 5 (e, f). Positive values indicate clockwise directional errors; negative values indicate counter-clockwise directional errors

with biases in the opposite direction of Experiments 1 and 2, i.e., toward body midline.

The ANOVA for the 0/80 layout revealed a significant Delay \times Target interaction ($F_{3,24} = 3.11$). Tests of simple effects showed no significant effects, but a weak trend toward a Delay main effect for the inner (0°) target only ($F_{3,24} = 1.98$, $P = .144$). The shift from small CW errors at the 1 s delay, to small CCW errors at the longer delays suggests that body midline was not producing reference effects comparable to the visible midline.

The ANOVA for the $-20/60$ layout revealed no significant effects ($P > 0.25$). Thus, the CW errors to the -20° target shown in Fig. 6a were not statistically robust due to high inter-subject variability of constant errors. Once again this suggests that body midline did not function as a reference frame in the same manner as the visible midline.

Variable directional error

Variable errors showed little difference across targets or over delays (Fig. 6b), suggesting that subjects had stable kinesthetic perception of location. The ANOVA for the 0/80 layout revealed a trend toward a Target main effect, ($F_{1,8} = 4.60$, $P = 0.064$). As shown in Fig. 6a, variability was generally higher to the 0° target than to the 80° target, similar to the Vis condition, but in contrast to the Vis + Env condition in Experiment 1a.

The ANOVA for the $-20/60$ layout data revealed a significant Delay main effect ($F_{3,24} = 7.54$), driven by small increases in variable errors over delays. There was also a trend toward a Target main effect ($F_{1,8} = 5.10$, $P = 0.054$), driven by higher variability to the -20° target than to the 60° target. Again, this contrasts with the results of the Vis + Env condition in Experiment 1a.

Discussion

Results from this experiment contrasted with those from Experiments 1 and 2. Constant errors showed no significant biases for targets to either side of body midline, and a trend toward a CCW bias for the target aligned with midline. Variable errors were also higher for the inner targets in both layouts. This pattern is opposite what would be expected if body midline served as a reference frame in the same way as the visible midline in the Vis + Env conditions.

One striking aspect of these results, however, is the overall low level of mean errors (although this does not necessarily indicate accurate performance: inter-subject variability of constant errors was rather high, with a mean SD across targets and delays of 7.46°). Indeed, variable errors were comparable to the levels achieved in the Vis + Env condition of the previous experiments, but without the associated systematic constant error distortions. Why were mean errors so low in the purely kinesthetic task? One possibility is that kinesthetic memory for locations is more robust than visuo-spatial memory over 0–15 s delays. Although we know of no studies to date that have directly compared visual and kinesthetic memory over long delays, Chapman and colleagues showed that subjects pointed (without vision) accurately to kinesthetically-specified targets at delays of 10 s, suggesting that this type of memory may be generally resistant to memory decay/drift (Chapman et al. 2001).

It is also possible, however, that errors in this experiment were low compared to Experiments 1 and 2 because subjects used a joint matching strategy, i.e., they remembered the location by memorizing the joint configuration needed to reproduce the target location. We have no a priori reason to expect that memory for joint configura-

tion would be resistant to decay over delays, but we examined this possibility by varying the position of the subject's trunk between encoding and response. This manipulation altered the joint configuration needed to reproduce the target location relative to the configuration used during encoding, thereby making the memorization of joint angles ineffective.

Experiment 4

Method

Subjects

Twelve subjects (six males and six females, aged 18–22 years) took part in this experiment. All subjects were right-handed and had no history of neuromuscular disorder. Subjects signed informed consent forms approved by the University of Iowa Institutional Review Board prior to participation, and received \$8 per hour for participating.

Apparatus, procedure, experimental design and data analysis

The apparatus, procedure, experimental design and data analysis were identical to Experiment 3 with three exceptions. First, the back was no longer supported, allowing subjects to lean forward and backward. Second, the experimenter manipulated the subject's trunk orientation by flexion or extension (total range of trunk motion = 40°) before each target presentation, and then again altered the orientation while transporting the arm back to the starting location. Although the actual movement of the hand required to respond was preserved (i.e., from the fixed start location to the target), this manipulation prevented the subject from employing an upper limb joint matching strategy to place the fingertip at the target location. The trunk orientations were varied pseudo-randomly, and an electromagnetic receiver was placed on the skin over the sternum to measure trunk orientation. Lastly, because Experiment 3 revealed no differences among the 5, 10, and 15 s delays, we used only the 1 and 15 s delays. This reduced the total number of trials (8 practice, 32 test) and the duration of the experiment (~25 min). The reduction from four delays to two also made Huynh-Feldt correction unnecessary.

Results

Constant directional error

As in Experiment 3, responses changed little over delay (Fig. 6c), although responses to the 80° target showed

higher CCW error. Notably, the errors to this target location were in the opposite direction to the CW errors observed in the Vis + Env conditions of Experiments 1 and 2. The ANOVAs for both layouts revealed no significant effects. Thus, the relatively large CCW errors to the 80° target were not statistically robust.

Variable directional error

As in Experiment 3, variable errors show little difference across targets or over delays (Fig. 6d). The ANOVAs for both layouts revealed no significant effects.

Discussion

Results from this experiment were generally consistent with Experiment 3. This suggests that subjects' relatively accurate performance was not solely due to the use of a joint matching strategy. Rather, it appears that memory for location in a purely kinesthetic upper limb task is robust to memory decay/drift and altered trunk orientation between target presentation and reaching to the remembered location. This is perhaps best captured by the low within-subject variable errors evident in Fig. 6d.

Constant errors in the present experiment, however, point toward a different possibility. Although responses to the 80° target did not differ statistically from responses to the other targets, they did differ significantly from zero error at the short delay ($t_5 = -2.91$). This highlights that, although subjects were very good at reproducing the same reaching movements to the same targets across trials, those responses were not always accurate. Indeed, inspection of individual data from Experiments 3 and 4 showed that, in some cases, low mean directional errors resulted from averaging across a mixture of idiosyncratic biases—some subjects showed CW biases while other subjects showed CCW biases. This is reflected by inter-subject variability (SD) across experiments, which averaged 7.71° in experiments 3 and 4 compared to 4.81° for the Vis + Env conditions of Experiments 1 and 2. These data are consistent with previous observations of idiosyncratic differences in perceived orientation of trunk-fixed reference axes (e.g., Darling and Hodzinski 1999; Darling and Bartelt 2005).

Because performance across subjects in the Kin conditions varied considerably more than in the Vis + Env conditions (SD of 7.71° compared to 4.81°), it is possible that inter-subject variation in perception of body midline masked reference-related biases in our kinesthetic task. Thus, in the next experiment, we measured each subject's perception of the trunk a–p axis and aligned the target array to this axis. This allowed us to test whether errors were biased away from this subjective axis.

Experiment 5

Method

Subjects

Six subjects (two males and four females, aged 18–22 years) took part in this experiment. All subjects were right-handed and had no history of neuromuscular disorder. Subjects signed informed consent forms approved by the University of Iowa Institutional Review Board prior to participation, and received research exposure credit as compensation.

Apparatus, procedure, experimental design and data analysis

The apparatus, procedure, experimental design, and data analysis were identical to Experiment 3 with three exceptions. First, we included only the 1 and 15 s delays (as in Experiment 4), resulting in 8 practice and 32 test trials. Second, we included only the –20/60 target layout because Experiments 3 and 4 showed little difference across layouts. We selected the –20/60 layout because results from this layout showed the most consistent use of body midline in the Vis conditions of Experiments 1a and 2. Again, the reduction from four delays to two also made Huynh-Feldt correction unnecessary.

Lastly, we measured each subject's perception of the trunk a–p axis orientation at the beginning of the experiment and aligned the target array to be centered along this axis. To define this axis, the subject (while blindfolded) grasped an electromagnetic receiver between the thumb and forefinger. The experimenter instructed the subject to place the receiver against their chest (sternum), and then positioned it at four locations “about equally spaced” progressing in a straight line along their perceived anterior–posterior axis, with the final position being with a fully-extended elbow. Subjects then relaxed their arm in their lap for several seconds, and were then instructed to repeating the task in reverse by starting from full-extension (along their own perceived midline, i.e., the experimenter did not position the arm), and progressing through four locations to place the receiver against the chest. The points from both tasks were fitted with a straight line, and the deviation of that line from the trunk a–p axis was determined. Subjects repeated this procedure four times; the mean orientation across the four inward and outward movements was used to align the target array such that it was centered along the subject's perceived midline axis. This measure revealed that across subjects, perception of midline varied from about 2° CCW to more than 15° CW ($M = 6.21^\circ$, $SD = 7.33^\circ$). This confirms the high inter-subject variability

suggested by our inspection of individual data in Experiments 3 and 4.

Results

Constant directional error

Mean constant errors were low, even at the long delay (Fig. 6e). The ANOVA for the –20/60 layout revealed no significant differences among targets and delays. Inspection of the data, however, did confirm that inter-subject variability decreased relative to the previous experiments. Specifically, we computed a range of constant errors for each target and delay in the –20/60 Layout, then averaged these across participants. For Experiments 3 and 4, these means were 26.57° ($SD = 8.75^\circ$) and 21.76° ($SD = 6.96^\circ$), respectively; for the current experiment, the mean range was reduced to 13.67° ($SD = 2.52^\circ$). Thus, measuring errors relative to each participant's perceived body midline did reduce the influence of inter-subject variability; however, this had little impact on mean constant errors in the kinesthetic condition.

Variable directional error

Variable errors showed little difference across targets or delays (Fig. 6f). The ANOVA for the –20/60 layout revealed a significant Delay main effect ($F_{1,5} = 6.80$), driven by increasing variability over delay.

Discussion

Subjects' performance in this experiment was measured from their own subjective perception of body midline. This corrected for notable variation in perception of midline across subjects (inter-subject variability of constant errors dropped from 7.71 in Experiments 3 and 4 to 5.42 in Experiment 5); however, constant and variable errors were still quite low and showed no systematic biases in the kinesthetic location memory task. This is consistent with the results from Experiments 3 and 4, and contrasts with results from the visuo-spatial location memory task. Taken together, results from the kinesthetic experiments suggest that, although body midline presumably serves as a reference frame for location memory, under purely kinesthetic conditions the effects of the bodily reference frame are not comparable to the influence of the visible midline in visuo-spatial location memory tasks.

General discussion

These experiments explored the influence of visual and kinesthetic reference frames on location memory. In the

Vis + Env conditions of Experiments 1 and 2, we presented targets visually within a visual reference frame and asked subjects to produce visually-guided responses. Results replicated previous findings of stable memory for locations aligned with the midline symmetry axis of the task space, and biases away from midline for targets to either side (Spencer and Hund 2002). In the Vis conditions of these experiments, we removed the visual reference frame, but maintained visual presentation of targets with visually-guided responses. Results showed some suggestion that subjects were using body midline as a reference frame in a manner similar to the visible reference, although without the stability for targets aligned with body midline. This lack of stability in perception of body midline in dark conditions may be related to contributions from both visual and kinesthetic inputs in the Vis conditions of Experiments 1 and 2 (e.g., Biguer et al. 1988; Karnath et al. 2002). For instance, the locations of visual targets viewed in a dark environment may influence perceived body midline, with potentially enhanced perception of body midline with a broader range of target locations. In Experiments 3–5, we removed vision completely by presenting targets kinesthetically to blindfolded subjects. Results showed generally accurate performance with no systematic reference-related effects, though inter-subject variability was quite high.

One central question raised by these results is why there were strong reference-related biases in the Vis + Env condition, weak biases in the Vis condition, and no reference-related biases in the kinesthetic conditions. At face value, this pattern suggests that reference-related biases arise whenever there is a heavy reliance on the visuo-spatial system. Critically, this was the case regardless of whether the reference-related information was supplied by vision (Vis + Env) or kinesthesia (Vis). Why does the visuo-spatial system use reference frames in a way that produces systematic distortions in memory? We contend that reference-related biases are a behavioral signature of processes that maintain location information while actively coordinating multiple reference frames (see Spencer et al. 2007). In the Vis + Env condition, participants actively maintained a memory of the target location in a world-centered or allocentric reference frame. This required that they continually calibrate/align information perceived in, for instance, retinal or head-centered coordinates with information in an allocentric frame anchored to perception of the midline symmetry axis of the task space (see Spencer et al. 2007, for discussion). When the target was presented at 0°, we observed the benefits of using an allocentric frame—performance was accurate over delays with low response variability. But there were also costs of using an allocentric frame: memory for location drifted away from the reference over delays (for details of a formal model that explains the origin of such effects, see, Spencer et al. 2007).

This view of coordinating multiple reference frames may also explain performance in the Vis conditions. Because the targets and response were visually-specified, subjects still had to maintain location information in the context of head movements, eye movements, and so on; however, in the absence of visual allocentric cues, subjects could not ground visual information in an allocentric frame. Rather, their task was to coordinate two egocentric frames: a retinal or head-centered frame and a body-centered frame. Moreover, when the response cursor appeared at the end of the delay, they had to bring these egocentric frames into register with the visual information in the task space (i.e., perception of location of the mouse cursor), without the benefit of the continuous visual allocentric information available in the Vis + Env condition. Data suggest that subjects were able to use body midline as a reference frame when targets were relatively far (e.g., at 60° or in Experiment 1b), but use of body midline led to less reliable response biases near this reference, as well as high response variability. There are two likely sources of these effects. First, it is likely that body midline is not perceived as precisely as a visual symmetry axis. Indeed, in Experiment 5 when subjects estimated the orientation of their own trunk a–p axis, the range of within subject estimates over four trials averaged 5.6° (SD = 3.0°). In contrast, evidence from perceptual studies suggests that perception of symmetry axes—especially vertical symmetry axes, as the one used in our task—is comparable to perception of weak visible lines (e.g., Palmer and Hemenway 1978; Wenderoth and van der Zwan 1991). A second source of error may have occurred at response generation. It is likely that on some trials, subjects had to re-align their perception of body midline with vision of the response cursor in the task space at the “go” signal. Such updating of reference frames would introduce variance in location memory estimates. It will be important for future studies to clarify the source of differences in performance between the Vis + Env and Vis conditions, perhaps by having people estimate perceived body midline in darkness as we did in Experiment 5.

Finally, in the kinesthetic conditions, participants had to remember locations within a single, egocentric, kinesthetically-defined reference frame. Thus, there was no need to coordinate multiple reference frames. Moreover, because subjects did not have knowledge of results, there was no explicit need to update this egocentric reference frame at the “go” signal to some anchor point in the world. Although this led to very stable performance within subjects across trials, it was also clear that subjects showed idiosyncratic biases in their perception of the trunk a–p axis as well as in how they perceived that this axis was aligned to the task space. We suspect that this was the source of the large inter-subject variability of constant errors.

Our account of the pattern of directional error results also points toward a candidate source of the variability

effects: variability scales with the coordination challenges involved in the task and the precision of the information upon which this coordination is based. In the Vis + Env conditions, subjects had to coordinate egocentric and allocentric information, but that coordination was based on precise, stable, world-centered spatial information. Thus, response variability was quite low, particularly for targets near the reference frame axis (for related effects, see Simmering et al. 2006; Simmering and Spencer 2007). Note that the low variability in the Vis + Env condition is consistent with a Bayesian view of spatial recall biases. For instance, Huttenlocher et al. (1991) have argued that although the use of allocentric spatial information results in systematic memory biases, this reduces the overall amount of response error due to low variance across trials. Subjects also had to coordinate multiple coordinate frames in the Vis conditions, but this coordination was based on less precise egocentric information. Consequently, there was a large increase in response variability. Finally, the kinesthetic conditions presented the simplest coordination challenge since the target and response were kinesthetically specified.

In summary, data from the present study highlight the challenges of putting locations in context, i.e., grounding location memory in multiple frames of reference. We contend that these data also reveal signatures of processes that underlie this coordination, as revealed by systematic biases under some conditions and changes in variability across conditions. More generally, our data highlight important gains that can be made by integrating the multiple perspectives on spatial memory evident in the diverse literatures on this topic.

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