Visuospatial Memory Computations During Whole-Body Rotations in Roll

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Van Pelt, S., J.A.M. Van Gisbergen, and W. P. Medendorp. Visuospatial memory computations during whole-body rotations in roll. *J Neurophysiol* 94: 1432–1442, 2005; doi:10.1152/jn.00018.2005. We used a memory-saccade task to test whether the location of a target, briefly presented before a whole-body rotation in roll, is stored in egocentric or in allocentric coordinates. To make this distinction, we exploited the fact that subjects, when tilted sideways in darkness, make systematic errors when indicating the direction of gravity (an allocentric task) even though they have a veridical percept of their self-orientation in space. We hypothesized that if spatial memory is coded allocentrically, these distortions affect the coding of remembered targets and their readout after a body rotation. Alternatively, if coding is egocentric, updating for body rotation becomes essential and errors in performance should be related to the amount of intervening rotation. Subjects ($n = 6$) were tested making saccades to remembered world-fixed targets after passive body tilts. Initial and final tilt angle ranged between $-120°$ CCW and 120° CW. The results showed that subjects made large systematic directional errors in their saccades (up to 90°). These errors did not occur in the absence of intervening body rotation, ruling out a memory degradation effect. Regression analysis showed that the errors were closely related to the amount of subjective allocentric distortion at both the initial and final tilt angle, rather than to the amount of intervening rotation. We conclude that the brain uses an allocentric reference frame, possibly gravity-based, to code visuospatial memories during whole-body tilts. This supports the notion that the brain can define information in multiple frames of reference, depending on sensory inputs and task demands.

INTRODUCTION

How the brain represents space and how this information is used to generate goal-directed behavior has been subject of longstanding debate (Andersen et al. 1985; Duhamel et al. 1992; Howard 1982; Von Helmholtz 1867). Whereas currently viewed targets impinge on the retina and are always available, locations of previously viewed targets must be stored in memory if needed for actions at later time. It is known that these memories remain quite accurate over long times, even after we have moved around (see e.g., Baker et al. 2003; Hallett and Lightstone 1976; Israel and Berthoz 1989; Medendorp et al. 2002, 2003b; Mergner et al. 2001; Sparks and Mays 1983).

What are the computational strategies that underlie this behavior? The brain could store spatial memories in egocentric as well as allocentric coordinates (see Battaglia-Mayer et al. 2003 for review). Target representations computed and stored in an allocentric frame of reference (or Earth or inertial frame) are most stable because they remain correct for any type of intervening self-motion. In turn, for motor planning, they must be converted backwards to eye-, head-, or limb-related coor-

dinates, depending on the motor system that is being employed. In contrast, target locations stored within an egocentric framework must be continuously recomputed, or updated, whenever the axes of the specific ego-frame (e.g., limb, eye, head, or torso) move, if they are to remain useful for guiding motor action.

There is neurophysiological evidence for either view. For example, hippocampal place cells code self-position in allocentric coordinates (see Best et al. 2001; Burgess et al. 2002 for reviews). Snyder et al. (1998) reported evidence for separate allocentric and egocentric representations within the posterior parietal cortex. In addition, many areas in parietal and other cortical and subcortical brain regions have been shown to update their egocentric information when the egocentric reference frame moves, using extraretinal information about self-motion (Duhamel et al. 1992; Gnadt and Andersen 1988; Goldberg and Bruce 1990; Medendorp et al. 2003a; Nakamura and Colby 2002; Sommer and Wurtz 2002; Walker et al. 1995).

In which reference frame are locations of targets for saccades maintained? Because neurophysiological data suggest that several coding schemes co-exist, they cannot distinguish which of these prevails in guiding behavior. However, behavioral performance can provide important insights. By assessing the operational errors in the system during various task conditions, one may be able to make inferences about the nature of the computations.

Several studies have used this strategy by investigating the variability in the endpoints of saccades to memorized targets, after intervening eye, head, and body movements. On this basis, Baker et al. (2003) found evidence for eye-centered target representations, while Skavenski and Steinman (1970) and Karn et al. (1997) suggested the use of an extraretinal, possibly space-centered frame of reference. These different suggestions may simply imply that no single frame of reference is being employed in these various conditions or that the reference frame question cannot be addressed by looking at the variable errors alone.

In the present paper, we have investigated the internal mechanisms underlying spatial memory by exploiting a robust systematic error that occurs in human external space perception. More specifically, we have designed a paradigm to assess whether human subjects store target locations for saccades, presented prior to a whole-body rotation, in egocentric or allocentric coordinates. Our test is based on the observation that subjects, when tilted sideways in darkness, make systematic errors when indicating the direction of gravity, an allocentric variable. For tilts $>60°$, these errors are in the same
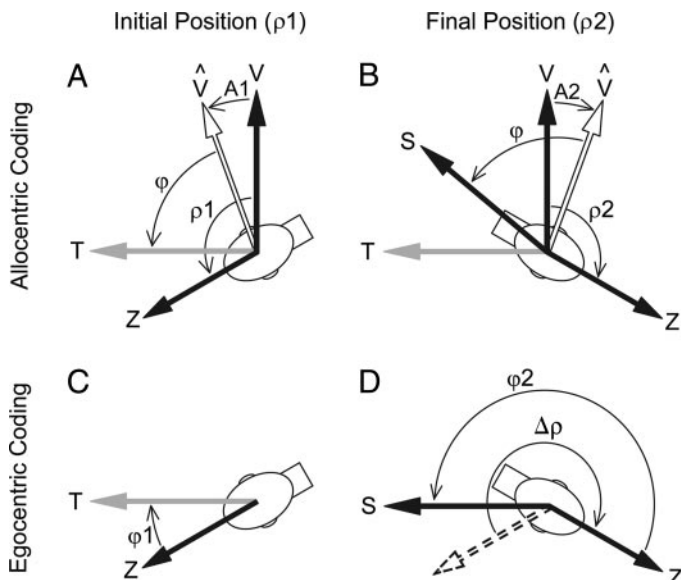

FIG. 1. Allocentric vs. egocentric spatial memory computations during whole-body rotations in roll. In our tests, a subject stores a world-fixed target to memory at initial tilt position ($\rho1$). After being rotated to a new final position ($\rho2$), the subject directs a saccade to the memorized location of the target. *A* and *B*: allocentric coding. *A*: if the direction of a target T is stored in an allocentric, world-centered frame of reference, its memory representation (φ) will be affected by the perceived distortion of this frame (A-error, A1) and thus be encoded relative to the internal representation of the physical world-frame $\hat{V}$. *B*: a similar error (A2) will be incorporated in the read-out (*S*) of this allocentric memory, depending on subject's representation of the world-centered axes at the new position ($\hat{V}$). *C* and *D*: egocentric coding. *C*: the memory ($\varphi1$) is encoded relative to the axes of an egocentric frame of reference (head/body/eyes). *D*: this representation must be updated during the intervening rotation ($\Delta\rho = \rho2 - \rho1$) in order correctly represent the direction of a space-fixed target location at the new body position ($\rho2$), resulting in an updated memory ($\varphi2$), that is ideally equal to $\varphi1 - \Delta\rho$. Note, it suffices here to refer to this operation by a subtraction, but strictly speaking, rotations do not commute and therefore must be described by multiplicative operations. The dashed arrow represents the previous body-tilt position in the world ($\rho1$). The static tilt position of the head (ρ) is defined as the angle between the direction of the physical vertical (*V*) and the subject's positive long-body axis (*Z*), as seen from behind the subject (positive: rightward tilt; negative: leftward tilt).

direction of the body tilt, mounting up to 50° when the body is tilted at about 130° (Kaptein and Van Gisbergen 2004). This type of error is known as the Aubert effect, or A-effect (Aubert 1861) and has been observed in various test paradigms, such as classical visual-line tests and oculomotor paradigms relying on saccadic pointing (Mast and Jarchow 1996; Van Beuzekom and Van Gisbergen 2000). It is noteworthy that, for small tilt angles ($<30°$), errors in the subjective direction of gravity are much smaller and commonly observed in a direction opposite to the body tilt. Such errors are known as the E-effect (Howard 1982). In the present study, for clarity, both the A- and E-effects will be collapsed and referred to as A-errors unless indicated otherwise. It is important to note that errors are virtually absent when subjects are asked to estimate their body tilt in space (Kaptein and Van Gisbergen 2004). This indicates that the A-error is not merely caused by inaccuracies in the underlying head orientation in space signal but rather reflects a property of the central computation involved in external, world-centered space perception (Eggert 1998; Kaptein and Van Gisbergen 2004; Mittelstaedt 1983).

Figure 1 illustrates how the robust relationship between the A-error and body tilt can be exploited to design a test to

distinguish between ego- and allocentric coding of spatial memory. As Fig. 1*A* shows, if a subject, tilted sideways at a given angle ($\rho1$), stores the direction of a target *T* in an allocentric, world-centered frame of reference, the corresponding memory (φ) will be affected by the perceived distortion of this frame at this tilt angle, (A-error, A1). In other words, the direction of the target will be stored in a distorted world frame, i.e., relative to $\hat{V}$ rather than to the actual world-centered coordinates (*V*). If then this subject is rotated to a final position ($\rho2$) and a read-out of this allocentric memory representation is obtained, the response will also incorporate the error (A2) in the subject's representation of the world-centered axes at the new position (see Fig. 1*B*). Thus the allocentric, world-centered model makes a very precise prediction: the directional error of a saccade *S* toward a target, briefly presented before a whole-body rotation, should be equal to the difference in subjective distortion of the earth-frame when probing the memory and when storing the memory (A2-A1). Accordingly, this model predicts zero response errors in absence of an intervening body rotation ($\rho2 = \rho1$), because A2 will then be equal to A1. This also means that any response error found in this condition would merely imply the involvement of other independent processes, affecting memory preservation.

However, if a spatial memory is stored in egocentric coordinates (Fig. 1*C*), such allocentric distortions, as expressed by the A-error, are supposed to play no role. In that case, the memory ($\varphi1$) is stored relative to the axes of a given egocentric frame of reference, e.g., relative to the subject's positive *z* axis, *Z*. While this reference frame can be the eyes, head, or body, these can be treated equivalently in the present study, ignoring the small effects of eye countertorsion (but see following text). Within an egocentric framework, however, a spatial memory about a target location must be updated when the body rotates to a new position to keep correct registry with its true spatial location, represented by $\varphi2$ (Fig. 1*D*). Therefore if the egocentric model is correct, we would expect the readout of this memory after the body rotation only to be affected by errors, if any, related to the amount of intervening rotation $\Delta\rho$ ($=\rho2 - \rho1$). Note that for the sake of argument, we have assumed here that the brain can calculate the change in angle perfectly, irrespective of initial and final tilt position. We will take up this issue in more detail in RESULTS to test whether this assumption is correct. As with allocentric coding, the egocentric scheme would predict zero updating error in static conditions when intervening motion is absent (excluding the errors caused by deterioration processes of memory).

In the present study, we asked human subjects to make eye saccades to remembered targets after whole-body rotations in roll. We show that the saccadic response is systematically affected by the distorted percept of the external world. We will interpret these results in terms of their computational and physiological significance for the brain.

METHODS

Subjects

Six subjects (1 female, 5 male), aged between 24 and 60 yr, gave their informed consent to participate in the experiment. All subjects were without any known visual, vestibular, or other neurological disorders. Three of them were naïve with respect to the purpose of the

experiments. No systematic differences in performance were found between naïve and nonnaïve subjects.

Setup

The subjects were seated in a computer-controlled vestibular chair. They were secured tightly into the chair using seat belts, trunk and hip supports, a foot rest, and straps around the feet and legs. A padded adjustable helmet firmly stabilized the head in the normal upright position. For each subject, seat adjustments were made so that the eye of which the orientation was measured coincided with the roll axis. During the experiment, subjects were rotated around the roll (naso-occipital) axis in complete darkness. The chair rotated with a constant velocity of 45°/s, with equal values of acceleration and deceleration of 30°/s². Chair orientation was measured using a digital position encoder with a resolution of 0.04° and recorded on disk.

Two-dimensional eye orientation of either the left or the right eye was measured with the scleral search coil technique, using oscillating magnetic fields generated by two sets of orthogonal coils inside the chair (0.77 × 0.77 m). The signals were amplified, low-pass filtered at 200 Hz, and recorded at 500 Hz per channel.

Targets (red light-emitting diodes, LEDs, luminance: 8 mcd) were presented on a chair-fixed screen at a distance of 115 cm in front of the subject's measured eye; the central LED on the screen coincided with the axis of rotation. Peripheral LEDs ($n = 36$) were positioned in an array on this screen, at the intersections of three circles at 11, 22, and 31° of visual angle and 12 equally spaced meridians. Prior to the experiment, the subject fixated each of the LEDs in random order, in complete darkness, to calibrate the search coil.

Experimental paradigm

We used a memory-guided saccade task to test a subject's ability to memorize locations of targets, briefly presented before he or she underwent a whole-body rotation.

ROTATION PARADIGM. This experimental paradigm is illustrated in detail in Fig. 2. Roll angle (ρ) is defined as the angle of the longitudinal body axis with the earth vertical, taken positive for right-ear-down rotations. Each trial began by turning off all lights after which the subject was rotated to an initial body tilt position $\rho 1$ ($t = 0-4$ s). Next, a central fixation LED was presented (at $t = 4$ s) that cued the subject to make self-paced saccades into the four Earth-centric cardinal directions to indicate the perceived world horizontal and vertical directions (Van Beuzekom and Van Gisbergen 2000). These responses, to be completed within 6 s, were used to determine the subject's A-error at this position. Next, the central LED had to be fixated again and a peripheral target was flashed for 1,000 ms, at a retinal eccentricity of 22°. The subject was explicitly instructed to memorize the location of this target as if it were world-fixed, for as long as the central fixation LED was on (9 s). During this period, he or she was rotated to a new orientation $\rho 2$. When the central LED disappeared, this signaled the subject to make an eye movement to the memorized target location and fixate there for a short moment. Two seconds later, with the subject still at the new orientation, the central fixation LED was turned on again and another set of A-error measures was obtained. Finally, the subject was rotated back to the upright position and the room lights were switched on. Each trial lasted 33 s; between trials there was 27 s of rest.

STATIC PARADIGM. This paradigm was identical to the rotation paradigm, except that the subject was kept at the same orientation ($\rho 2 = \rho 1$) after target presentation. These trials served as memory controls, to test the subject's performance in the absence of an intervening rotation.

In both paradigms, initial and final orientations were chosen from the interval of -120 to $+120°$ with steps of 30° (9 possible tilt
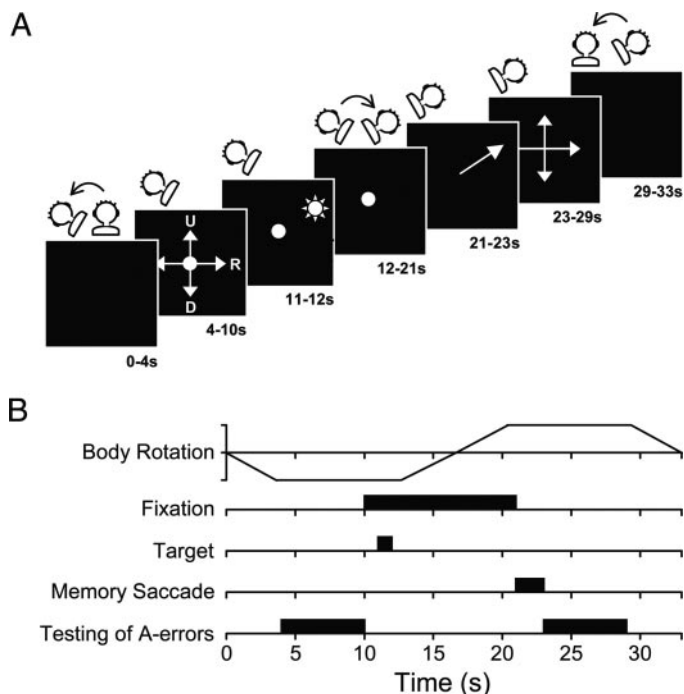

FIG. 2. Experimental paradigm. *A*: sequence of stimuli and subject instructions. After being tilted to an initial position ($\rho 1$), the subject (seen from behind) made saccades to indicate the world cardinal directions (measurement of A-errors). Next, a world-fixed target was flashed for 1 s onto the retinal periphery after which the subject was rotated to a new position ($\rho 2$). Then the fixation point disappeared, cueing the subject to make a saccade toward the remembered target location. Finally, the A-errors were measured at the new position after which the subject was rotated back to the upright position. *B*: temporal order of events for body rotation, stimuli, and saccadic responses during a trial.

positions). This resulted in a total number of 81 possible combinations of which 75 were tested (68 rotation trials, 7 static trials). In the static paradigm, the two orientations, $-30°$ and $+30°$, were not tested. In the dynamic paradigm, rotations from 120 to $-30°$, -120 to 30°, and vice versa were excluded. We never used tilt angles beyond 120° to avoid the complex behavior of the A-effect at very large tilt angles (beyond 135°) (see Kaptein and Van Gisbergen 2004), For each trial, target location was chosen pseudorandomly from 12 possible locations so that all possible target positions were used at least six times. Trials with initial left-ear down and right-ear down rotations were interleaved. For illustration purposes (Figs. 4, 6, and 8), we collected, in addition, some repeated measurements in one subject, using a specific selection of the stimulus set. All subjects were given a few practice runs to get used to the vestibular stimulation and the paradigm. The experiment was divided into three sessions of 25 trials, tested on different days. Each session lasted for ~40 min, including calibration and practice. Typically 2 of the 75 trials per subject had to be excluded from analysis because the subject failed to maintain fixation or make saccades at the requested times.

After completion of all experimental sessions, five of six subjects were tested on their rotation perception in a slightly modified version of the rotation paradigm. Subjects performed 50 trials with pseudorandom initial and final body orientations, chosen from the 240 possible integer values in the interval of -120 to 120°, without assessing the A-errors or spatial memory performance. Instead, when the fixation light went off, subjects had to report verbally the amount of perceived intervening rotation, as minutes on a clock face ($+15$ min $= +90°$).

Analysis

Data analyses were performed off-line using Matlab software (the MathWorks). Using the fixation data of the calibration run, horizontal

and vertical eye-coil signals were calibrated with two neural networks, one for each position component. Each network consisted of two input units (representing the raw horizontal and vertical signal), three hidden units, and one output unit (representing the desired calibrated horizontal or vertical position signal). Raw eye-coil signals were calibrated by applying the resulting feedforward networks. Average calibration errors were typically <0.5°. Off-line saccade detection was performed manually by the experimenter on the basis of the calibrated eye position signals.

In each trial, subjects made saccadic eye movements at both initial and final tilt position to indicate their perceived Earth-centric cardinal directions. The average directional error of these oculomotor responses from the true Earth-centered directions was computed following the method used by Van Beuzekom and Van Gisbergen (2000). In short, the direction of the saccadic endpoints of each arm of the resulting cross-like figure of saccades was determined. The difference of the mean of these directional settings from zero represents a distortion in the subjective earth-referenced frame, known as the A-effect when in the same direction as the body tilt and acknowledged as an E-effect when in a direction opposite to the body rotation. Because the A-effect is most systematic and substantial, as mentioned in the INTRODUCTION, we will refer to both distortions as A-errors.

Subject performance in memorizing a target location, and retaining that location while being rotated during the memory period, was determined by the accuracy of the saccade made to that location at the end of the memory period. As such eye responses often contained several corrective saccades (Medendorp et al. 2002), we measured the directional error of the endpoint of the most eccentric saccade toward the remembered target. Clockwise errors were taken positive. We explored the relationship between the saccadic targeting response, the size of the A-error, and amount of intervening rotation across all trials to test which of the spatial memory models—illustrated in Fig. 1—would best fit our data.

RESULTS

Subjective Earth-centric frame

Our experiments were designed to test whether the location of a target, briefly presented before an intervening whole-body rotation, is stored in egocentric or allocentric coordinates. To make this distinction, we exploited the fact that subjects, when tilted sideways in darkness, make systematic errors when asked to indicate the direction of the gravity vector and the orthogonal horizon (see e.g., Mittelstaedt 1983; Van Beuzekom and Van Gisbergen 2000).

Figure 3 quantifies this measure (the A-errors) for all our subjects. In every trial, at each tested tilt position, subjects made four self-paced saccades to indicate the Earth-centric cardinal directions. The misalignment of these Earth-referenced saccades with the true Earth-centric directions specifies the subjective Earth-reference frame. Figure 3A shows the gaze trajectories of these saccades for one subject for all tilt angles separately. For (absolute) tilt angles ≤60°, the subjective frame corresponds closely to the true Earth-frame, with distortion errors (A-errors) <5°. However, for tilt angles >60°, settings were far from flawless, with distortions of up to 50° in this subject. Statistical analysis revealed that these settings were independent of the preceding amount of rotation ($P <$ 0.01, t-test), i.e., they were only related to the static body tilt position at which the measurements were taken. Figure 3B quantifies these data further by showing the mean A-error (± 1 SD) as function of tilt angle. Similar spatial distortion profiles were observed in all our subjects (Fig. 3C), in correspondence
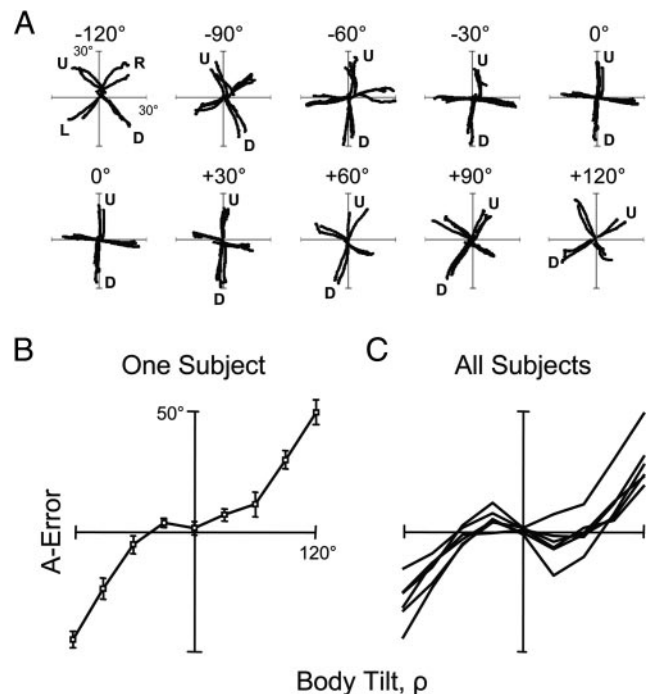

FIG. 3. Quantification of the A-errors. *A*: trajectories of saccades from 1 subject (*JG*) directed along the subject's percept of the Earth's cardinal axes, for the 9 different tilt positions tested. For illustration purposes, data from 2–3 trials per rotation angle (of 8 or 9 measured) are presented. U, D, L, and R indicate the subjective upward, downward, leftward and rightward directions in space, respectively. Substantial A-errors were present for the larger tilt angles ($|\rho| > 60°$). *B*: average A-error ($\pm$SD) as a function of body tilt angle, for the same subject. *C*: A-error for all 6 subjects. For small tilt angles, some subjects showed an E-effect, i.e., errors in a direction opposite to the body tilt.

with previous studies (Kaptein and Van Gisbergen 2004; Van Beuzekom and Van Gisbergen 2000). As we will show in the next sections, these data can be used to test the reference frame underlying spatial memory computations.

Static paradigm

How well can stationary but tilted subjects memorize locations of world-fixed targets? Using the static control condition, we quantified the subjects' performance in making saccades to target locations, remembered for 9 s, without being moved during the memory delay period. Figure 4A shows the results for one subject, tilted at 120°, performing 12 different spatial memory trials, by superimposing the saccade trajectories of all trials toward the four remembered targets located on the cardinal axes in world-space. The responses were fairly accurate even though the subject had memorized the target for 9 s.

Figure 4, *B* and *C*, depict the subject's percept of the Earth-reference frame (A-errors) in the same trials, as indicated by saccades, respectively before and after the spatial memory task was performed. These measures showed a high degree of reproducibility: the saccadic cross-like trajectories, made in separate trials, but at the same tilt angle, are all closely aligned. Thus the A-error remains constant within and across trials in correspondence with Fig. 3. It is noteworthy that the severe distortion in the subject's perception of external, world-centered space (shown in Fig. 4, *B* and *C*) bears no resemblance in the saccade directions to remembered visual targets presented in external space (Fig. 4A).
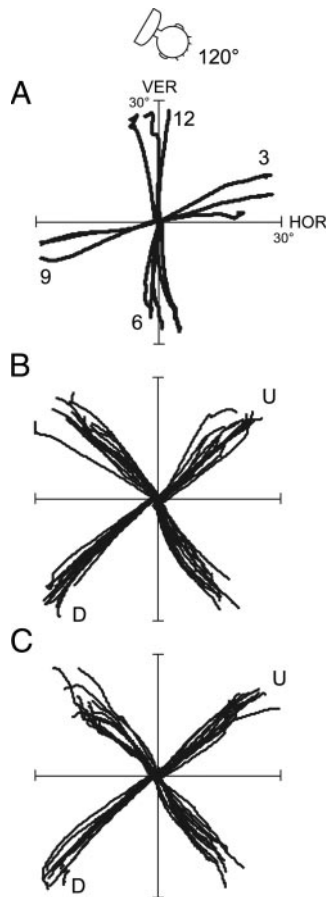
FIG. 4. Saccade trajectories of 1 subject (*JG*), tilted at 120° in the static paradigm. Results of 12 different trials. *A*: spatial memory readout: saccades directed at memorized targets, presented on any of the 4 world-fixed cardinal axes (indicated as hours on a clock scale; e.g., 12 is an upward target location in space). Saccade directions are fairly accurate. *B*: A-errors before target presentation. U and D as in Fig. 3. *C*: A-errors after spatial memory readout was collected.

Figure 5 shows the saccade accuracy averaged across subjects for each tilt angle tested in the static control condition. Saccades directed from tilted body position showed higher variability than saccades made from an upward, natural body position. Across all tilt angles the mean error ranged from −4.8 to +6.6° and was only significantly different from 0 when the subjects were at +120° (*P* = 0.0068, *t*-test). For the purpose of the present study, we take from this that spatial memory is not systematically degraded by our 9 s memory delay.

Rotation paradigm

To what extent are subjects able to look at remembered locations of world-fixed targets, briefly presented before an intervening whole-body rotation? Figure 6*A* shows the performance of a subject in 12 trials in the intervening rotation condition. Here, the subject viewed the flashed targets at a 120° leftward tilted body position before he was rotated to a final body position of 120° rightward and subsequently performed the saccades. As Fig. 6*A* shows, the saccades to the remembered targets show dramatic directional errors. For example, a target initially presented upward in Earth space (the 12 o'clock

direction), is localized, after the body rotation, by a saccade directed rightward in space. In other words, unlike the static condition (compare Fig. 4*A*), a clear deterioration of performance occurs when remembered target locations must be indicated after an intervening body rotation.

For completeness, Fig. 6*B* illustrates the subject's perception of the Earth-centric directions at the initial body orientation (−120°) for the same trials, whereas Fig. 6*C* demonstrates the A-error saccades at the final body orientation (120°). As expected, the A-errors are quite different for these tilt angles, which conforms to the patterns observed in Figs. 3 and 4.

Why do subjects make such severe errors in looking at world-fixed targets after an intervening body rotation? As outlined in the INTRODUCTION, if spatial memory in this task is coded in an allocentric, world-centered frame of reference, it will be affected by the perceived distortion of this frame when storing target location (Fig. 1*A*). In that case, this will also shape the readout of this memory trace, coded in this frame, after the body rotation, based on the perceived distortion of the frame at the new body position (see Fig. 1*B*). As such, we would expect the directional errors in the memory saccade in a given trial be related to the amount of subjective distortion in the perceived Earth frame (A-error) at both the initial and final tilt angle in that trial. In other words, an allocentric coding scheme would predict a saccadic response error corresponding to the difference in A-error at the final and initial tilt angle (A_{net} = A2 − A1) as determined by the saccadic indications of the world's cardinal axes made at final and initial tilt angle, respectively. Figure 7*A* shows the data from one subject by plotting the directional error of the saccade versus the net A-settings for all trials tested (A_{net}). Using linear regression, we quantified the relationship between the saccadic errors and the amount of subjective allocentric distortion (—). This analysis revealed a high correlation ($r = 0.96$). As to the slope of the fitted line, the allocentric coding scheme (Fig. 1*A*) would predict a value of 1 (- - -). For this subject, the slope had a value of 1.15 ± 0.04 (mean ± SD), which clearly seems to favor this model. Figure 7*C* shows the linear regression results from all subjects. In all subjects, we found high correlations ($0.73 < r < 0.96$). Across subjects, the slopes ranged between 0.81 and 1.15. On average, the slope was not significantly different from 1 ($P = 0.74$, *t*-test), indicating almost perfect adherence to the allocentric model.

Could an egocentric model also explain these data? Recall our assumption that an egocentric model would predict the
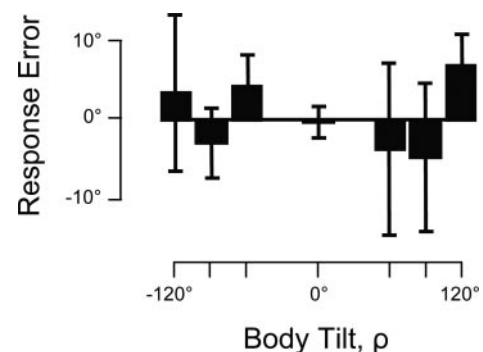

FIG. 5. Response error, averaged across subjects, as a function of tilt angle in the static paradigm. Positive errors denote errors made in the same direction as body orientation. Error bars denote SD.

present results. How then can we distinguish between the putative models underlying the spatial memory computations in the present experiment?

Distinguishing between allo- and egocentric coding

Based on our analyses so far, the directional error in the response saccades to the remembered target locations could be equally well predicted by a distorted allocentric coding mechanism as well as by an imperfect updater in an egocentric model. Why would both models perform about equally well? A confounding effect is that the amount of spatial distortion (A-errors) and tilt angle are so tightly related (see Fig. 3). Therefore a clear dissociation between our models is probably masked by the strong interaction between these two factors.

Can we remove these confounding effects and perform a more sensitive analysis to discriminate between the two models? In the following, we will take advantage of the nonlinearity in the relationship between A-effect and body tilt angle (see Fig. 3) to determine which model is best. In the analysis, we assume that an egocentric model would predict similar errors in the memory-saccades for two trials with the same amount of intervening body rotation, irrespective of initial tilt position ($\rho1$) and final tilt position ($\rho2$). In contrast, the allocentric, world-centered coding scheme allows that the saccadic errors in trials with the same amount of intervening rotation may be different, depending on the A-error at initial and final tilt angle.
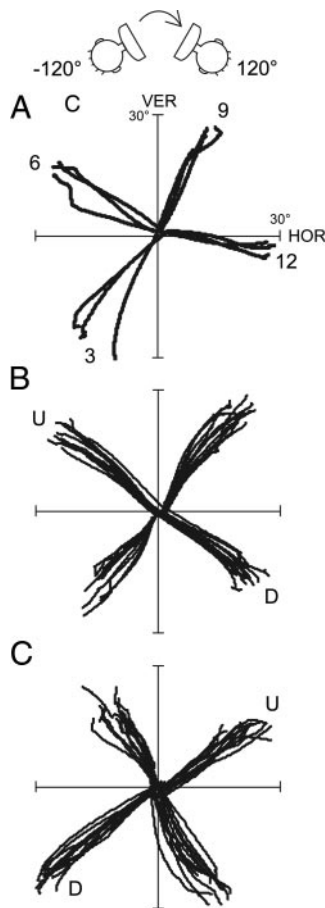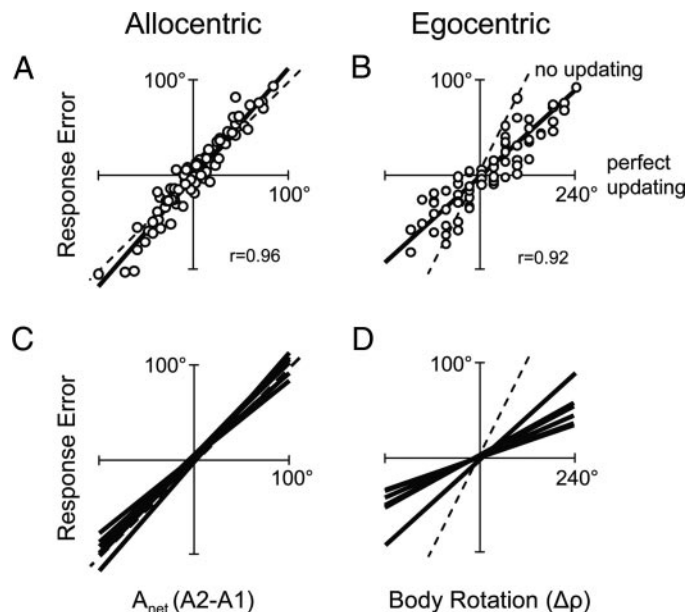

FIG. 6. Response saccades from 1 subject (*JG*) tested in the rotation paradigm. Performance in 12 trials in each of which the subject perceived the target at a 120° leftward tilt, then was rotated to a 120° rightward tilt, and subsequently made a saccade to the memorized target. *A*: spatial memory readouts: saccades directed at memorized targets, presented on any of the 4 world-fixed cardinal axes (indicated as hours on a clock scale), after the intervening body rotation. Note the large directional errors (compare Fig. 4*A*). *B*: A-errors at 120° leftward tilt ($\rho1$) before target presentation. U and D, as in Fig. 3. *C*: A-errors at 120° rightward tilt ($\rho2$) obtained after the spatial memory readout was collected.

saccadic errors to be related to the amount of intervening body rotation (see Fig. 1, *C* and *D*). In Fig. 7*B*, we have plotted this relationship for the same data as presented in Fig. 7*A*. A linear regression, which quantified this relationship, showed a high correlation ($r = 0.92$). If there had been no updating, the slope of the fitted line would have been 1 (- - -). Perfect updating would yield a slope of 0. For this subject, we found a slope of 0.38 ± 0.02, which was significantly different both from 0 (*t*-test, $P < 0.001$) and from 1 (*t*-test, $P < 0.001$). Thus according to this analysis, updating was not perfect—the change in body position seems underestimated in this subject. Similar results were found in all subjects (Fig. 7*D*), with slopes, ranging from 0.14 to 0.38, that were significantly different from both 0 ($P < 0.01$, *t*-test) and 1 ($P < 0.001$, *t*-test). Furthermore, statistical analysis revealed that the observed correlations in these egocentric fits ($0.71 < r < 0.92$) were not significantly different from those observed for the allocentric model ($P = 0.32$, *t*-test). In fact, this means that our analysis so far does not rule out the alternative coding scheme, i.e., an egocentric model. That is, one could still argue that an egocentric model with imperfect updating could describe the

FIG. 7. Directional errors of saccades plotted against the size of the net A-error (A2 − A1) or the amount of the intervening body rotation ($\rho2 - \rho1$) in de dynamic paradigm. *A*: response error plotted as a function of A_{net} (A2 − A1) for 1 subject. The best-fit line had a high correlation ($r = 0.96$) and a slope near 1, consistent with the allocentric model. *B*: response error plotted as a function of intervening body rotation ($\Delta\rho = \rho2 - \rho1$) for the same subject. Regression line had a significant correlation ($r = 0.92$) but a slope >0, consistent with under-compensation for body rotation in an egocentric model. *C*: regression lines of all subjects in an allocentric explanation scheme. All slopes are near 1. *D*: regression lines of all subjects in an egocentric explanation scheme. Slopes vary between 0.14 and 0.38, corresponding to an under-estimation of $\Delta\rho$. Analyses on basis of both schemes reveal significant correlations, suggesting that readout errors of spatial memory can be explained by either of them.
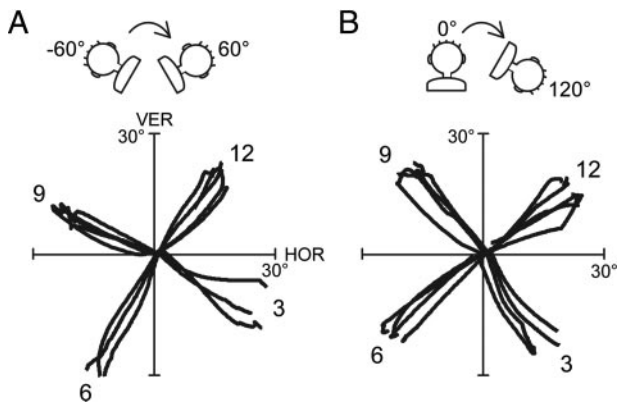
FIG. 8. Spatial memory readouts for 2 testing conditions that had identical intervening body rotation (+120°), but different combinations of initial and final body positions, for 1 subject (*JG*). Traces show the saccade trajectories (12 trials) toward memorized targets that were presented, prior to rotation, on 1 of the 4 world-fixed cardinal axes. *A*: $\rho1 = -60°$; $\rho2 = +60°$. *B*: $\rho1 = 0°$; $\rho2 = +120°$. Saccades in *A* and *B* show considerable but different directional errors despite the equal amount of intervening rotation.

This idea is illustrated in Fig. 8, in one subject, for two different testing conditions that have the same amount of intervening rotation ($\Delta\rho = 120°$) but different combinations of initial and final tilt position, i.e., -60 and $60°$ in the first condition and $0°$ and $120°$ in the second condition. The figure displays the subject's saccade trajectories toward targets flashed at the Earth-centric cardinal directions (indicated by numbers as hours on a clock face). As can be seen, the two conditions lead to different response saccades, with more pronounced errors in the latter condition (Fig. 8*B*). Because the amount of intervening rotation ($\Delta\rho$) was the same in both cases, this result seems to argue against egocentric coding with updating of target location.

To further quantify this for all trials, we computed the difference in the saccadic response direction (ΔResponse Error) for all possible pairs of trials that had identical amounts of intervening body rotation, but different combinations of initial and final body tilt angle. Egocentric updating would predict this difference be 0 (ΔResponse Error = 0), whereas allocentric, world-centered coding would predict this difference be equal to the difference in the net A-settings for the two trials [ΔResponse Error = ΔA_{net}, with $\Delta A_{net} = (A2 - A1)_{trial2} - (A2 - A1)_{trial1}$].

Using this pair-wise comparison, we analyzed all possible combinations of trials contained in our dataset. Figure 9 presents the results of this analysis for each subject. Each data point depicts the difference in saccadic error as function of the difference in net A-setting between two trials with identical amount of body rotation. In case of egocentric coding, the data should scatter around a line with slope 0 ($y = 0$), whereas the data should fall along the diagonal ($y = x$) in case of allocentric coding (- - -). For all subjects, we found significant correlations, $0.36 < r < 0.77$ (ANOVA, $P < 0.001$). Averaged across subjects, the slope was significantly different from zero (*t*-test, $P < 0.001$) but not significantly different from 1 (*t*-test, $P = 0.15$). Thus this analysis shows that our data are most consistent with an allocentric coding of visuospatial memory even though it does not entirely rule out an egocentric contribution.

Finally, one could argue that the conclusion of the latter analysis would be invalid if the amount of perceived interven-

ing body rotation depends on the initial tilt position ($\rho1$) and final tilt position ($\rho2$). Even in an egocentric model, this would allow for various amounts of updating in situations in which there is equal amount of rotation ($\Delta\rho$) but different initial and final body orientations. Therefore, we performed a final experiment to control for this contingency (see METHODS). Five subjects were tested again, similarly as in the rotation paradigm, and verbal reports about the amount of their perceived rotation were obtained. Figure 10*A* shows these estimates of $\Delta\rho$ as function of actual $\Delta\rho$, for one subject. A linear fit with a slope of 0.89, shown by —, captures this pattern very well ($r = 0.99$). In all subjects tested, we found high correlations ($r > 0.98$), and slopes in the range of 0.89 to 1.07, as demonstrated by Fig. 10*B*. This means that whatever the computations or signals involved, our subjects can estimate the amount of intervening rotation in roll quite accurately, much better than could be expected on the performance in the spatial memory task (see Fig. 7). To investigate whether the amount of estimated rotation had any systematic relationship with starting orientation, we fitted the following relationship to the data: estimated $\Delta\rho = a*\Delta\rho + b*\rho1 + c*(\rho1)^2$. Coefficient a specifies the linear dependence of the perceived $\Delta\rho$ on the actual amount of rotation, while parameters b and c represent any first- or second-order effect of $\rho1$ on the estimation of $\Delta\rho$. The values of each of these coefficients are presented in Fig.
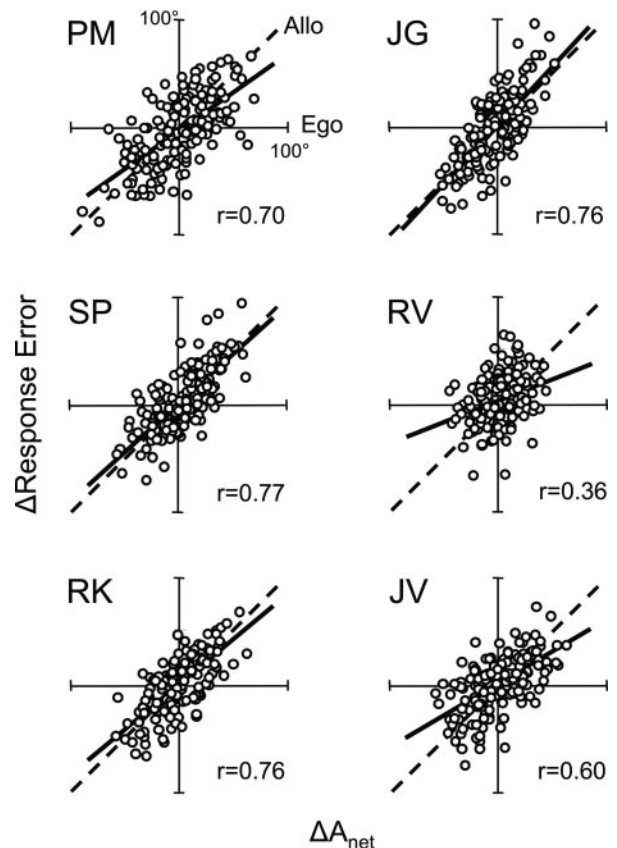
FIG. 9. Difference in response errors (ΔResponse Error) for pairs of trials that had identical egocentric but different allocentric predictions. Scatterplots for all 6 subjects display data of all possible comparisons. Plots show the difference in response error as a function of the difference in the net A-error [$\Delta A_{net} = (A2 - A1)_{trial1} - (A2 - A1)_{trial2}$]. Egocentric scheme predicts a slope of 0; allocentric coding predicts a slope of 1. Linear regressions (—) favor the allocentric predictions.

FIG. 10. Verbal reports on the perceived amount of rotation in the rotation paradigm. *A*: results as function of actual $\Delta\rho$ for 1 subject. A linear fit line had slope 0.89 and correlation $r = 0.99$. *B*: best-fit lines for all subjects tested. *C*: coefficient values of the fit that relates the perceiv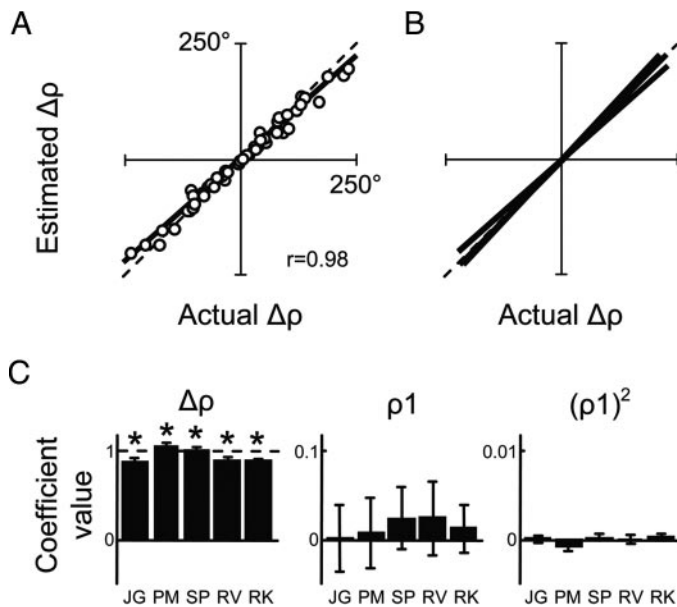ed amount of rotation to the actual amount of intervening rotation $\Delta\rho$ and the initial body position ($\rho 1$), following $\Delta\rho = a*\Delta\rho + b*\rho 1 + c*(\rho 1)^2$. Asterisks in C denote coefficients significantly different from 0 ($P < 0.05$). Error bars denote SD.

10*C* for all subjects separately. As can be seen, the estimated $\Delta\rho$ depends solely on the actual $\Delta\rho$, by values for *a* that were significantly different from 0 (*t*-test, $P < 0.001$). This was not the case for the *b* and *c* coefficients (*t*-test, $P > 0.05$), indicating that the estimates of $\Delta\rho$ did not depend on the starting orientation. Thus our control experiment shows that the perception of the amount of rotation is linearly related to the actual amount of rotation and not dependent on the starting and finishing orientations of the body relative to gravity. This confirms the assumption of the egocentric model and hence the conclusions drawn in the preceding text.

DISCUSSION

We have designed a novel paradigm to test whether human subjects code spatial memories of space-fixed targets during whole-body rotations in an ego- or allocentric frame of reference. Our test exploited the well-documented fact that subjects, when tilted sideways in the dark, make systematic errors in indicating the world-centered cardinal directions (Kaptein and Van Gisbergen 2004; Mittelstaedt 1983). We observed and quantified this distortion of the world-fixed reference frame in all our subjects as illustrated by Fig. 3. We then investigated whether this distortion would be incorporated in the accuracy of saccades directed at memorized locations of visual targets briefly presented prior to a whole-body rotation in roll. Our results show clear evidence for this (Fig. 7). The memory-guided saccades showed an error pattern that was qualitatively and quantitatively predicted by the combination of subjective distortion of the Earth-frame when storing the memory (at initial tilt angle) and probing the memory (at final tilt angle). These data are suggestive for the use of an allocentric frame of reference to represent the location of the target in the present experiments, as we will further argue in the following text.

In contrast with the observed systematic errors in spatial localization in our experiments, previous studies have shown that spatial memory copes well with horizontal and vertical body rotation (Baker et al. 2003; Blouin et al. 1998; Israel et al. 1999; Mergner et al. 2001), provided that the vestibular afferents veridically reflect head rotation (Blouin et al. 1998; Mergner et al. 2001). Is there a discrepancy between these results and our current findings? Perhaps, but it should be emphasized that the present study tested for large body rotations in roll in which the body changes orientation relative to gravity, which may complicate sensorimotor processing. So far, few studies have tested object localization in space during torsional body movements. In fact, our previous study was the first in this domain (Medendorp et al. 2002), in which we found that subjects made almost no systematic errors when compensating for active head torsions within their anatomical limitations (-45–$45°$). One could explain this difference by the availability of additional signals, such as neck efference copies or neck proprioception, that would allow subjects to improve their performance. However, the fact that the current report demonstrates marked response errors in a similar paradigm is more likely due to testing within a wider motion range (-120–$120°$). More specifically, when we analyzed performance in the limited amount of trials comparable to those of Medendorp et al. (2002) (here, trials with rotations from ±60 and $\pm30°$ to the upright position), we virtually found no errors either. Moreover, it is known that A-errors also occur when subjects actively tilt their bodies such that the head adopts orientations beyond 90° (Van Beuzekom et al. 2001). It is known from previous studies, and confirmed here (Fig. 3), that the distortion of the subjective Earth-frame is small for head tilts <60° (Mittelstaedt 1983; Van Beuzekom and Van Gisbergen 2000). Because performance is accurate for these head tilts, studies that examine spatial memory accuracy in this tilt range cannot readily distinguish between the underlying frames of reference.

Our evidence that in the present task conditions, it is indeed an allocentric frame of reference in which a target location for a saccade is encoded is as follows.

First, saccadic response errors cannot be attributed to a memory degradation effect because they did not occur in the absence of intervening body rotation (Fig. 4). The errors that occurred were virtually negligible and did not show any systematic relationship with tilt angle (Fig. 5). From these stationary tilt results, it is interesting to note that saccadic performance is rather accurate, while yet the subjects' perception of external space is so severely distorted. Should these observations be seen as a one more demonstration that visual perception and action are dissociated and employ different frames of reference (Goodale and Milner 1992)? Not necessarily. It could also mean that the processing errors that occur to establish a world-centered memory representation of the visual stimulus are cancelled by the errors involved in transforming this allocentric representation into an eye-centered saccadic command at later time. At least, as we will further argue, during torsional whole-body rotations, the brain seems to store world-fixed object locations in a (perhaps perceptual) allocentric reference frame (Wexler 2003) rather than in an action-oriented egocentric frame of reference.

Second, the size of the errors in the direction of the saccades in the rotation paradigm is in good correspondence with the

predictions of the allocentric coding scheme (Fig. 7, *A* and *C*). In contrast, the egocentric model would predict much smaller errors, taking the rather accurate rotation percepts in the control experiment in Fig. 10 as measure for the quality for the rotation signal. It is interesting to note that in this control test, subjects perceived the amount of rotation so well, despite the constant velocity stimulation, which is a less effective stimulus for the semicircular canals.

Third, we observed clear differences in the saccadic responses for two trials requiring equal amounts of egocentric updating (see Figs. 8 and 9), which makes it problematic to accept this coding scheme as interpretation of our results. In two such trials, the semicircular canals receive identical stimulation, whereas the otoliths are stimulated differently. Therefore, saccade performance in our task seems more related to a spatial reference frame, established by the otoliths, than to one constructed using the canal signals. One could still argue in favor of egocentric updating assuming the rotational updating signal is detected by the otoliths in a tilt-dependent fashion. Following this interpretation, the otolith signals are gain-modulated with a factor smaller than one for tilt-positions further away from upright. This would allow for various amounts of updating in situations in which there is equal amount of rotation ($\Delta\rho$) but different initial and final body orientations. However, it has been shown that subjects can estimate their body orientation in space rather well, at each tilt angle (Kaptein and Van Gisbergen 2004). Moreover, as our control, rotation estimation experiment showed (see Fig. 10, *B* and *C*), there was no significant effect of initial tilt position on perceived $\Delta\rho$, making the idea of a variable tilt-dependent gain factor rather unlikely.

Fourth, we can rule out a possible under-compensation for ocular-counter roll (OCR) as an explanation for our results. Previous studies have reported that the eyes counter-rotate by $<10°$ within their orbits when the head rotates (Bockisch and Haslwanter 2001; Klier and Crawford 1998). This value is virtually negligible in relation to the size of errors that we have observed here. Moreover, the fact that we observed no or only small response errors in the static condition, where subjects were tilted but underwent no intervening body motion (Fig. 5) argues against the OCR as an important factor in the explanation of our results.

Taken together, our results are most consistent with an allocentric, world-centered coding of a spatial memory during whole-body rotations in roll. Previous work has strongly suggested that the brain is capable of constructing an inertial, world-centered representation of head velocity and position during tilt rotations (Angelaki and Hess 1994; Hess and Angelaki 1997; Merfeld et al. 1993a,b, 1999; Pettorossi et al. 1998). Indeed, earlier reports have shown that subjects have a nearly veridical percept of their self-orientation in space (Kaptein and Van Gisbergen 2004; Mast and Jarchow 1996; Mittelstaedt 1983). Because vestibular afferent signals are coded in head-centered coordinates, these signals must be centrally transformed relative to an inertial, gravitocentric reference frame (Hess and Angelaki 1999). This also means that the distorted Earth reference frame reflects a property of a central computation for a gravitocentric, inertial representation rather than an inaccuracy in the underlying source signals (Eggert 1998; Van Beuzekom and Van Gisbergen 2000). The striking relationship between the saccadic targeting responses

and the A-errors, even in individual trials, suggests that the same internal representation, perhaps anchored to the direction of gravity, may underlie these observations (Fig. 7). Again, we reiterate that the response measures here were saccades. It would be useful to perform experiments that exploit this paradigm in other motor systems (e.g., pointing).

Our conclusions agree with results from other behavioral studies claiming that the brain incorporates allocentric information when directing saccades to visual stimuli (Dassonville et al. 1995; Honda 1999). Using pointing, Carrozzo et al. (2002) have shown that when allocentric cues are given about the relation of targets, these cues are used to code target location. In this study, subjects who were instructed that all possible targets would fall along an (imaginary) line showed errors in the endpoints of pointing movements to these remembered locations that were aligned with this line. Similarly, when a visual target is presented within the context of a large frame the center of which is located left or right of the observer's midline, the perceived location of the target is biased toward the opposite direction, an allocentric phenomenon called the induced Roelofs effect (Bridgeman et al. 1997; Dassonville et al. 2004).

However, our findings seem at odds with previous psychophysical studies suggesting egocentric, often eye-centered, updating in other task conditions, including saccadic targeting and pointing (e.g., Baker et al. 2003; Henriques et al. 1998; Medendorp and Crawford 2002). Baker et al. (2003) directly compared saccadic precision after horizontal whole-body rotations, smooth-pursuit eye movements, and saccadic eye movements to memorized targets that remained either fixed in the world or fixed to gaze. Based on the assumption of noise propagation at various processing stages in the brain, they rejected explicit world- or head-centered representations as an explanation of their results. An important difference between our study and the one by Baker et al. (2003) is the change of the body relative to gravity. It is conceivable that the brain relies on this allocentric cue, if readily available, and employs the invariant direction of gravity as a reference for storing target locations during torsional body motion. This would also be compatible with the recent results of Klier et al. (2005), who found reduced performance in a spatial updating task that lacks useful gravitational cues. In this respect, more work is needed to elucidate how the present results on allocentric, world-centered coding generalize to other movement situations. It could be argued that in conditions lacking such allocentric cues, e.g., during horizontal body rotations, the brain resides to sole egocentric coding (and updating) of remembered target locations (Baker et al. 2003; Medendorp et al. 2003b).

To reconcile these various findings, the suggestion can be made that the reference frame used to encode a spatial memory is not fixed but may depend on the sensory context and the task at hand (Battaglia-Mayer et al. 2003; Hayhoe et al. 2003). Alternatively, these findings could imply that the brain can concurrently define information in multiple frames of reference, co-existing at the same time (Bridgeman et al. 1997; Carrozzo et al. 2002; Snyder et al. 1998). Egocentric representations by themselves may not always represent the most efficient means to code information. In most favorable circumstances, the brain may interchange information between allocentric maps and egocentric representations to optimize motor behavior (Crawford et al. 2004). In this respect, one should

note that an allocentric representation alone cannot drive the motor response. Ultimately, allocentric information must be transformed backward into an egocentric representation, to limb-, eye-, or head-related coordinates, for motor planning, requiring nonlinear operations to deal with properties of three-dimensional rotations (Crawford et al. 2004; Klier and Crawford 1998; Medendorp et al. 2002).

Finally, it remains a matter of speculation how and where the allocentric representation that we have probed here, using saccadic eye movements, is encoded in the brain. Hippocampal regions are known to construct allocentric memory representations. However, they are only implicated in the active control of long-term spatial memory, for delays >20 s, whereas the present study probed a short-term memory representation (Pierrot-Deseilligny et al. 2002). Moreover, it is not very likely that hippocampal regions are involved in the memory of single target locations for saccades (Muri et al. 1994). A more likely place to look for is an area where information about body position in space is integrated with information coded in the coordinates of the retinal frame. A major multisensory center for this integration seems to be the parietal cortex. There is currently evidence for separate body and world-referenced coding of stimulus locations in parietal cortex based on implicit representations constructed by gain-modulation of visual signals (Snyder et al. 1998). A possible role could also be attributed to the parieto-insular vestibular cortex (PIVC), which has been implicated in the perception of verticality and self-motion (Brandt and Dieterich 1999). Neurons in the PIVC receive inputs from both the semicircular canals and the otoliths, as well as visual and neck proprioceptive inputs (Brandt and Dieterich 1999; Grusser et al. 1990). In addition, patients with lesions in the PIVC have been shown a distorted perception of verticality (Brandt et al. 1994; Yelnik et al. 2002). Thus the PIVC may have the signals necessary to implement the spatial memory representation that we have revealed.

To conclude, the present study clearly showed that humans make errors in directing saccades to remembered target locations presented prior to a whole-body rotation in roll. The errors could be linked to an internal mechanism that keeps target locations in an allocentric reference frame rather than an action-oriented egocentric frame of reference. It remains a challenge to understand how and where the central computations underlying this finding are implemented by the brain.

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