Roles of Gravitational Cues and Efference Copy Signals in the Rotational Updating of Memory Saccades

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Klier, Eliana M., Dora E. Angelaki, and Bernhard J. M. Hess. Roles of gravitational cues and efference copy signals in the rotational updating of memory saccades. J Neurophysiol 94: 468–478, 2005. First published February 16, 2005; doi:10.1152/jn.00700.2004. Primates are able to localize a briefly flashed target despite intervening movements of the eyes, head, or body. This ability, often referred to as updating, requires extraretinal signals related to the intervening movement. With active roll rotations of the head from an upright position it has been shown that the updating mechanism is 3-dimensional, robust, and geometrically sophisticated. Here we examine whether such a rotational updating mechanism operates during passive motion both with and without inertial cues about head/body position in space. Subjects were rotated from either an upright or supine position, about a nasal–occipital axis, briefly shown a world-fixed target, rotated back to their original position, and then asked to saccade to the remembered target location. Using this paradigm, we tested subjects’ abilities to update from various tilt angles (0, ±30, ±45, ±90°), to 8 target directions and 2 target eccentricities. In the upright condition, subjects accurately updated the remembered locations from all tilt angles independent of target direction or eccentricity. Slopes of directional errors versus tilt angle ranged from -0.011 to 0.15, and were significantly different from a slope of 1 (no compensation for head-in-space roll) and a slope of 0.9 (no compensation for eye-in-space roll). Because the eyes, head, and body were fixed throughout these passive movements, subjects could not use efference copies or neck proprioceptive cues to assess the amount of tilt, suggesting that vestibular signals and/or body proprioceptive cues suffice for updating. In the supine condition, where gravitational signals could not contribute, slopes ranged from 0.60 to 0.82, indicating poor updating performance. Thus information specifying the body’s orientation relative to gravity is critical for maintaining spatial constancy and for distinguishing body-fixed versus world-fixed reference frames.

INTRODUCTION

As creatures that rely heavily on visual input, we are constantly moving our bodies (i.e., eyes, head, torso, etc.) to scan objects in the environment. The locations of these objects are typically static in space, although the location relative to the observer changes constantly while the observer is moving. It is well known that primates can program accurate motor commands to the locations of targets in space irrespective of intervening movements. Specifically, they can accurately look to the remembered location of a briefly flashed light even if the eyes/head are subsequently moved from their initial location (Baker et al. 2003; Blohm et al. 2003; Blouin et al. 1998; Hallett and Lightstone 1976; Herter and Guitton 1998; Israel and Berthoz 1989; Mays and Sparks 1983; McKenzie and Lisberger 1986; Medendorp et al. 2002; Ohtsuka 1994; Pelisson et al. 1989; Schlag et al. 1990; Zivotofsky et al. 1996). Hallett and Lightstone (1976) were the first to demonstrate this updating ability for horizontal and vertical displacements of the eyes, whereas more recently, Medendorp et al. (2002) extended this view by demonstrating that updating also accounts for head perturbations in the torsional dimension. Note that by using the term updating we do not necessarily imply that the visual targets are stored in any one particular map or coordinate frame (e.g., eye or space). Rather, we mean that new information about the intervening movement is appropriately taken into account to keep track of the body’s orientation in space.

To update accurately, the brain requires either information regarding the amplitude and direction of the intervening movement or some exteroceptive sensory information (e.g., vision, gravity, etc.) to determine body orientation at various points in time (i.e., before and after a movement). In the case of active head movements used by Medendorp et al. (2002), such information can be provided either by motor signals (in the form of efference copies of the outgoing motor command before the movement is executed) or by sensory signals that arise during and after the movement. These sensory signals include proprioceptive means (directly from the joints and muscles) and vestibular signals (from the canals and otolith organs). In addition, both body proprioceptors (Mittelstaedt 1992) and the otolith organs (Fernandez et al. 1972) are stimulated as the body changes its orientation relative to gravity, so gravitational cues may also represent an important cue for updating. Thus as subjects actively moved their heads (relative to their bodies) from one location to the next, signals from all these sources (i.e., efference copies of the motor command that moved the head, proprioceptive signals from the stretched neck muscles, and vestibular signals during the head rotation) could have been responsible for the rotational updating reported by Medendorp et al. (2002).

To determine whether vestibular signals alone can account for updating in 3 dimensions and whether accurate updating still holds during passive as opposed to active head movements, we used a memory-saccade experiment in which efference copy signals were eliminated. We found that subjects could update the remembered locations of space-fixed targets with sensory signals alone, in the absence of efference copy cues. We then conducted the same experiment with subjects...
lying on their backs, but still rotated about a nasooccipital axis. Without changing their body position relative to gravity, their ability to update was greatly diminished. These results have been presented in abstract form (Klier et al. 2004).

**Methods**

**Subjects**

Eight subjects (4 male and 4 female) ranging in age from 27 to 39 yr old were recruited to participate in the experiment. All but one (EK) were completely naïve to the purpose of the experiment and none had any known neuromuscular or neurological damage. All subjects gave informed consent to the experimental protocol that was approved by the Ethics Committee of the Canton of Zurich, Switzerland.

**Measuring 3-dimensional eye position**

Three-dimensional (3D) eye positions were measured using the magnetic search coil technique and 3D Skalar search coils (Skalar Instruments, Delft, The Netherlands). The magnetic field system consisted of 3 mutually orthogonal magnetic fields, generated by a cubic frame with side lengths of 0.5 m, operating at frequencies of 80, 96, and 120 Hz. The 3D eye position was calibrated by using a new algorithm that simultaneously determined the orientation of the coil on the eye and offset voltages based on 9 target fixations in close-to-primary and secondary gaze positions (see Appendix).

**Experimental protocol**

Subjects sat on a chair that was mounted on a 3D turntable (ACUTRONIC Switzerland, CH-8608 Bubikon, Switzerland) capable of rotating the subjects about the roll axis. Their bodies were fixed to the chair by 3 restraining methods. First, aviation safety belts secured the upper and lower torso to the chair. Second, evacuation pillows filled the empty spaces under the arms and around the neck. Finally, a malleable thermoplastic mask was molded to each subject’s face and fasted to the chair behind the subject’s head. This mask kept the subject’s head fixed relative to the rest of the body so that movement of the chair caused the head and body to move as one unit (i.e., the head on the rotation axis). Visual targets were produced by a computer-controlled laser and projected onto a spherical projection screen (ACUTRONIC Switzerland) located 1.45 m in front of the subject (the screen provided a visual angle of 100°).

A timeline of the torsional updating paradigm is illustrated in Fig. 1. In complete darkness, the subjects were rotated in the roll plane (i.e., torsionally) about a space-fixed, nasooccipital axis (i.e., either left ear down or right ear down) to one of 7 possible tilt angles (0, ±30, ±45, ±90°). Positive tilt angles cause the left ear to move down (i.e., counterclockwise tilt), whereas negative tilt angles cause the right ear to move down (i.e., clockwise tilt). In the 0° tilt condition the subject remained upright and thus it served as a control. The chair moved with a constant acceleration/deceleration phase of 180°/s² so that a strong vestibular signal could be provided throughout the movement. In this rotated position, a central target appeared on which the subjects had to fixate. At 2 s after the onset of the central target, a peripheral target briefly flashed for 100 ms. This peripheral target could appear in any one of 8 directions (4 cardinal and 4 oblique), and at any one of 2 target eccentricities (10 and 20°). Subjects had to ignore the flashed target, but remember its location in space. Subjects were then rotated back to an upright position while continuing to fixate the central target. At 1.5 s after the flash, the central target was extinguished, which cued the subjects to make a saccade to the remembered location of the peripheral target. The subjects were instructed to be as accurate as possible and to make only one eye movement to reach the final target (subjects were clearly able to follow these instructions because the number of trials with second saccades accounted for only 7% of all trials). The peripheral target did not reappear and thus subjects had no feedback about their performance and were not trained in the task. Finally, a tone instructed the subjects to end their fixation and relax before the next trial.

A total of 112 combinations were possible (7 tilt angles × 8 target directions × 2 target eccentricities), and each trial was repeated 3 times for a total of 336 runs. Because each run lasted about 7 s, this caused our experiment to run longer than the 30-min maximum duration recommended for eye coil usage. For this reason, we randomly divided the 112 combinations into 2, and ran each subject twice over a period of 2 wk. Within each of the 2 experimental runs, the trials were randomized into 3 parts (with 18, 19, and 19 randomized combinations in each part), and the 3 parts were repeated 3 times in the same order.

Four out of the 8 original subjects were then retested on the same experiment, except now they were rotated in a supine position. Because of acceleration limits in the axis necessary to produce torsional rotations from a supine position, the experiment could be run with only a constant acceleration/deceleration phase of 90°/s². Thus for a fair comparison of the data, 3 out of these 4 subjects were subsequently retested in the upright condition with similar constant acceleration/deceleration phase of 90°/s² (the fourth subject was no longer available).

**Data analysis**

Raw data from each subject’s right eye, sampled at 833 Hz, was first converted into rotation vectors, which indicate the horizontal, vertical, and torsional positions of the eye. These positions were subsequently transformed into eye velocity by taking the derivative of eye position (dE/dt = where E is the 3D eye position). Finally, angular eye velocity (Ω) was computed from the previous 2 values by the equation $\Omega = 2[(dE/dt + E \times dE/dt)/(1 + |E|^2)]$ (where “×” designs the cross-vector product). All saccade trajectories to the...
remembered target locations were automatically selected using the following criteria. The start of a saccade was selected when the square root of the sum of squares of the horizontal, vertical, and torsional angular velocities exceeded 10°/s. The end of a saccade occurred when the same value decreased below 10°/s. These data, along with the actual locations of the targets in space, allowed us to plot saccade trajectories and endpoints, compute polar and Cartesian errors, and conduct statistical analyses (t-test, ANOVAs, and Tukey post hoc analyses) on our data.

Finally, a 3D analysis, measuring how well Listing’s law was obeyed by the memory saccade endpoints, was made by first fitting the memory saccade endpoints with a 3D plane using the equation $E_T = a + b E_V + c E_H$ (where $E_T$, $E_V$, and $E_H$ are the torsional, vertical, and horizontal components of final eye position). The torsional SD ($T_{SD}$) of the plane (i.e., a measure of the plane’s thickness) was then computed by the formula

$$T_{SD} = \sqrt{\sum_{i=1}^{N} (E_T(i) - a - b E_V(i) - c E_H(i))^2} \over N - 3$$

where $N$ is the total number of endpoints. The thicknesses of these memory planes were compared (using paired t-tests) with planes computed from fixation points during the calibration files (two calibration files were collected, one at the start and one at the end of each experiment). In addition, the parameter “a” described each plane’s torsional offset. Pairwise t-tests were then used to compare the offset differences of the calibration plane versus memory plane offsets.

**RESULTS**

**Trajectories and endpoints**

Saccade trajectories for one subject, toward the 20° targets, are shown in Fig. 2. Saccades to horizontal/vertical targets are shown in gray, whereas saccades to oblique targets are shown in black. As previously demonstrated, the former are straighter, whereas the latter are often more curved (King et al. 1986; Smit and Van Gisbergen 1990; Smit et al. 1990). What is important to note, however, is that from all 7 tilt angles, the saccades seem to be directed rather accurately toward their desired goal. If the subjects were not able to compensate for the intervening movement, then one would expect to see a pattern in which the saccade trajectories are biased in a counterclockwise direction for positive tilt angles and in a clockwise direction for negative angles. Specifically, if subjects were completely unable to update target locations, then, for example, a target flashed directly upward (in space) when a subject is tilted 90° clockwise would be 90° counterclockwise relative to the subject at the time of presentation, and would remain 90° counterclockwise even after the subject was rotated back to an upright position. Also, this bias should be more pronounced as the size of the tilt angle increases. As will be presented quantitatively below, this was generally not the case.

We also examined whether the latency of the saccades differed for the different tilt amplitudes. One might expect that larger head/body tilts, which take place over longer periods of time, require more processing and therefore result in a delay of the first torsional offset. Pairwise t-tests were collected, one at the start and one at the end of each saccade to the target. The average saccade latency (±SD) for the 0° tilt angle was 0.30 ± 0.05 s for the 10° targets and 0.30 ± 0.09 s for the 20° targets. These values are in line with the latencies of memory-guided saccades reported in previous studies (Muri et al. 1996; Wipfl et al. 2001). The average latencies (±SD) for saccades made from the 6 nonzero tilt angles were 0.29 ± 0.04 s for the 10° targets and 0.29 ± 0.03 s for the 20° targets. An ANOVA indicates that the latencies from all 8 tilt angles were statistically different from one another [$F(6,97) = 3.508, P = 0.003$], however, a post hoc Tukey test indicates that none of the differences is found between any of the tilt angles (i.e., ±30, ±45, ±90°) and the upright (i.e., 0°) condition (Tukey HSD, $P > 0.5$; the only significant differences found were between the 30 and ±90° tilt angles). A similar ANOVA shows that eccentricity was not a significant factor in the latency of saccades [$F(1,97) = 0.119, P = 0.731$].

Data representing final trajectory endpoints from all 8 subjects are shown in Fig. 3 for the 20° endpoints. Here, the actual target locations are identified by black X’s, the average endpoint for each subject is shown by the gray or black filled circles (gray for horizontal/vertical endpoints and black for oblique endpoints), and the average endpoint across all subjects is shown by the hollow black(gray circles). Again, as with the trajectories in the previous figure, the endpoints to all 8 possible targets remain in distinct clusters and never overlap with neighboring endpoints. For the various tilt angles, the saccade endpoints to the 10° targets (not shown) seemed to be more tightly clustered than those to the 20° targets. Again, this...

**FIG. 2.** Saccade trajectories from one subject. All saccades made to targets at 20° eccentricity are shown for each of the 7 tilt angles (positive tilt angles indicate clockwise rotations and negative tilt angles indicate counterclockwise rotations). Actual locations of the targets are indicated by the black circles (●). Saccade trajectories to cardinal targets in space are shown in gray, whereas those to oblique targets are shown in black. Trajectories are shown in views from behind the subject according to the axes labels in the 0° tilt box.
type of amplitude-dependent precision has been previously shown (Becker 1972). Across both target eccentricities, some subjects appeared to be undershooting, whereas others seemed to be overshooting the targets, although qualitatively there is no overall observable pattern. Across subjects there also does not seem to be an overall trend for positions to be shifted in a positive or negative horizontal direction. Saccade endpoints from the 0° tilt angles appear to be most closely clustered around the real location of the targets in space. This is also generally true for the 30 and 45° tilt angles. The only tilt angles to display an inkling of the pattern of errors expected if updating were less than optimum are the 90° tilt angles. Here, the final endpoints seem to be deviated in a clockwise direction for 90° tilt angles and skewed in a counterclockwise direction of 90° tilt angles (this is true for both 10 and 20° endpoints). To determine the accuracy of updating, we performed the following quantitative analyses.

Polar coordinate errors

We first quantified endpoint errors in polar coordinates (Fig. 4A). The 2 measurements we obtained were amplitude errors ($\Delta a$) and directional errors ($\Delta \rho$). Amplitude errors indicate whether subjects were either undershooting (negative-amplitude errors) or overshooting (positive-amplitude errors) the targets. Directional errors indicate the direction of subjects’ endpoint errors relative to the direction of the actual target in space. Positive directional errors indicate that the subject’s endpoint was displaced counterclockwise of the real target (e.g., directional error = direction of subject’s endpoint − direction of real target location = $55^\circ - 45^\circ = 10^\circ$), whereas negative directional errors indicate a clockwise error (e.g., directional error = direction of subject’s endpoint − direction of real target location = $35^\circ - 45^\circ = -10^\circ$). Thus this measure is the critical test for determining whether updating had occurred.

Figure 4B shows the amplitude errors (and SD bars) for all 8 subjects, from all 8 tilt angles. Errors to the 10° targets are shown in black, whereas errors to the 20° targets are shown in white. Half of the subjects (right column) consistently undershot the targets irrespective of the tilt angle. Two subjects (MW and SM) were extremely accurate for small tilt angles, but undershot the locations of targets when the targets were originally seen from larger tilt angles (only at 90° for MW, and at 45 and 90° for SM). Finally, 2 subjects (AP and EK) consistently overshot. Thus amplitude errors appear to be subject-specific because no clear trends in overshooting/undershooting were observed across subjects. The fact that the majority of subjects undershot the targets is not surprising.

FIG. 3. Saccade endpoints from all subjects. Final average eye positions made to targets at 20° eccentricity are shown for all 8 subjects, from all 7 tilt angles (0, ±30, ±45, ±90°), to all 8 target locations (4 cardinal and 4 oblique). Actual target locations are indicated by the black “x”; each subject’s averaged endpoints are shown by the filled circles (gray for cardinal targets and black for oblique targets), and the endpoint location averaged across all subjects is indicated by the hollow circles.

FIG. 4. Polar coordinate errors—amplitude errors. A: 2 types of polar coordinate errors were computed. Amplitude errors ($\Delta a$) indicate whether the subject’s endpoint overshot (positive “$\Delta a$”) or undershot (negative “$\Delta a$”) the actual target location. Directional errors ($\Delta \rho$) indicate whether the subject’s endpoint was clockwise (positive “$\Delta \rho$”) or counterclockwise (negative “$\Delta \rho$”) of the actual target location. B: amplitude errors. Amplitude errors (averaged across all 8 target directions) and SDs are plotted as a function of tilt angle for each subject. Black bars indicate errors to 10° targets and white bars indicate errors to 20° targets.
because this has previously been identified as a visuomotor strategy to reach eccentric targets with minimal energy expenditure (Howard 1982). In addition, we performed a multifactor ANOVA to determine the effects of target amplitude, target direction, and tilt angle on these amplitude errors. All 3 variables had a significant effect on these errors, most interestingly tilt angle \[ F(6,1504) = 7.5, P = 0.000 \]. A Tukey post hoc analysis revealed that amplitude errors made from 0, ±30, and ±45° tilts were different from amplitude errors made from −45 and ±90° tilts.

Figure 5 plots directional errors as a function of tilt angle for all 8 subjects. Errors to the 10° targets are indicated by the black circles, whereas errors to the 20° targets are shown by the white circles. Best-fit lines to the 10 and 20° data are also shown by the dotted and dashed–dotted lines, respectively. These graphs indicate the extent to which updating occurs by the following rationale: if subjects perfectly updated the locations of the flashed targets, then one would expect no errors from all tilt angles (i.e., a slope of 0). In contrast, if subjects were completely unable to update the target locations, then, for example, a subject tilted 90° clockwise would consistently mislocalize flashed targets in space in a 90° counterclockwise direction (positive directional errors). Thus no updating would predict a slope of 1 (dashed line). Finally, it is known that when a subject’s head-fixed body is rotated in the roll plane, the eyes counterroll in their orbits by approximately 10% of the roll amplitude (Crawford and Vilis 1991; Haslewanter et al. 1992; Klier and Crawford 1998). Thus a slope of 0.9 (solid line) would be expected if the subjects were updating the location of the target relative to the eyes (as opposed to the location of the target relative to the head).

The directional errors for the 10 and 20° amplitudes were similar, as shown by the overlapping error ranges. Variability in directional errors was smallest for the 0° tilt condition and increased slightly, in some subjects, for the 30 and 45° tilt conditions. The 90° tilt condition exhibited the largest variability; however, note that this variability was nearly equally split in the clockwise (positive directional error) and counterclockwise (negative directional error) directions. Results of the linear regressions to the data are shown in the top left-hand corner of each plot and these slope values, along with their corresponding upper and lower 95% interval boundaries, are given in Table 1. The average regression slopes (±SD) across all subjects was 0.08 ± 0.08 for the 10° targets and 0.06 ± 0.05 for the 20° targets. Although a slope of 0 was not always included in the 95% confidence intervals, the slopes were still extremely small and were always different from a slope of 1 and a slope of 0.9. This indicates that subjects were quite successful in updating the locations of visual targets in space from all tilt angles, and that this ability, previously reported for active rotations (Medendorp et al. 2002), also holds for passive movements. Incidentally, note that conducting a statistical analysis similar to the \( t \)-tests conducted by Medendorp et al. (2002) also reveals that our slopes were significantly different from 0 (a repeated-measures \( t \)-test in which a column of computed slopes is compared with a column of zeros, \( P = 0.009 \) for the 20° amplitude targets), whereas the Medendorp (2002) subjects’ slopes were not statistically significantly different from 0. This is also revealed by showing that our subjects’ slopes were statistically significantly higher than the slopes in the Medendorp (2002) study (\( t \)-test on 20° target eccentricities, \( P = 0.01 \)).

A multifactor ANOVA was also performed to determine the effects of target amplitude, target direction, and tilt angle on these directional errors. Again all 3 variables had a significant
The slope values and lower and upper confidence intervals (CI) are given for the regression line fits to the data in Figs. 5 and 6. *indicates that a slope of 0 was within the 95% CIs (note that for the upright data, slopes of 0.9 and 1 were never included in the 95% interval range).

effect on these errors, including tilt angle \( F(6,1504) = 27.5, P = 0.000 \). A Tukey post hoc analysis revealed that directional errors from 0°, ±30°, and ±45° were different from directional errors from ±90°, and that the ±90° errors were different from each other.

Finally, we examined whether the torsional eye position at the time of target presentation was correlated with the observed directional errors. If such a correlation exists, this would imply that a visual mislocalization arising from ocular counterroll was partly the cause of the observed errors. For individual subjects, plots of directional error versus torsional eye position across trials produced slopes that covered a large range from -0.07 to 1.80, and across the population average slopes were -0.67 \( (r^2 = 0.03) \) for 10° targets and -0.55 \( (r^2 = 0.04) \) for 20° targets. These large ranges and extremely low correlations imply that no such relationship existed. However, when we then compared subjects’ individual directional error slopes in Fig. 5 to their average torsional eye position at the time of the flash, a pattern emerged. The larger the ocular torsion was when the target was presented, the larger the directional error slopes were in Fig. 5 [10° targets, slope = -10.93 \( (r^2 = 0.78) \); 20° targets, slope = -6.22 \( (r^2 = 0.42) \)].

**Cartesian coordinate errors**

Final endpoint errors were also analyzed in Cartesian coordinates. This type of analysis complements the previous one by indicating whether subjects consistently missed the targets to the right (positive Δx errors) or left (negative Δx errors) of the targets, or whether they consistently landed above (positive Δy errors) or below (negative Δy errors) the targets. Average Δx Cartesian errors \( (±SD) \), across all 7 tilt angles and 8 target directions, were 0.11 ± 0.20 and -0.42 ± 0.28°, whereas average Δy errors were 0.62 ± 0.17 and 0.59 ± 0.54°, for the 10 and 20° eccentricities, respectively. In contrast to the polar coordinate amplitude errors, these errors were generally smaller and centered around zero.

**Supine directional errors**

If efference copies of the motor command are not required for updating, as the previous analyses indicate, then which of the remaining sensory commands provide the necessary cues? To answer this question we had several of the subjects repeat the passive torsional updating task in a supine position where their bodies no longer rotated relative to gravity. Supine polar coordinate directional errors were computed similarly to the upright errors (directional error = direction of subject’s endpoint – direction of real target location). Plots of directional error as a function of tilt angle are plotted in Fig. 6 for the 4 subjects who were retested, along with best fit slopes for the 10 and 20° amplitudes (red lines) and slopes of 1 and 0.9 (black lines). Note that errors were generally larger in the supine position.
condition, sometimes exceeding 180°. [We do not convert these large angles to their complementary angles (i.e., \(360 - \theta\)) because the sign indicates the direction in which the targets were mislocalized; positive/negative errors indicate counterclockwise/clockwise mislocalizations, respectively.] The average slopes (±SD) were 0.69 ± 0.05 for the 10° amplitudes and 0.71 ± 0.10 for the 20° amplitudes (red lines). As in the upright condition, these slopes were significantly different from slopes of 0, 0.9, and 1, although they were also different from the subjects’ slopes in the upright condition (\(t\)-test, \(P = 0.000\) for both 10 and 20° amplitudes). This indicates that the subjects’ ability to update was significantly reduced. Average saccade latencies in the supine position for all 7 tilt angles were 0.29 ± 0.07 s for the 10° eccentricities and 0.28 ± 0.07 s for the 20° eccentricities. These latencies were not different from those in the upright condition (\(t\)-test, \(P = 0.85\) for 10° amplitudes and \(P = 0.81\) for 20° amplitudes).

Interestingly, although all subjects felt that they had performed accurately in the upright condition, once supine, one subject reported that he felt they had been rotated through a greater angle than he had actually been rotated. Another subject remarked that she had trouble differentiating between the world-fixed and body-fixed locations of the targets and that she had to try much harder to make saccades specifically to world-fixed locations. This is evidenced by the much larger range of directional errors in the supine condition. Especially with the ±90° tilt conditions and in subject CB, it appeared as if the errors were clustering into 2 groups (one group closer to 0 and ideal performance and the second with exaggerated errors). As in the upright condition, we examined whether initial torsional eye position was correlated with these directional errors. Here, there was no such correlation in the absence of gravity.

Finally, because the subjects could be rotated only at a constant acceleration/deceleration phase of 90°/s² in the supine position, we repeated the upright experiment with this new acceleration/deceleration profile. This was conducted on the 3 available subjects and their slopes are also plotted in Fig. 6 (blue lines). As expected, accurate updating was obtained with average slopes (±SD) of 0.08 ± 0.05 for the 10° amplitudes and 0.07 ± 0.08 for the 20° amplitudes. These slopes were not different from the upright slopes at the higher acceleration rate (\(t\)-test, \(P = 0.12\) for the 10° amplitudes and \(P = 0.62\) for the 20° amplitudes). Thus the ability to update correctly was maintained in the upright condition, even with this slower acceleration.

**DISCUSSION**

These experiments illustrate 2 important findings. First, we show that a rotational updating mechanism operates even for passive head and body motion, and thus effference copies of the active movement are not necessary to keep track of the locations of visual targets in space with great accuracy. This updating occurred not only for a number of different tilt angles but also for different target eccentricities, suggesting that both the direction and eccentricity of a target are correctly updated. Second, by repeating the experiment with subjects supine, we find that gravity cues play a critical role in this updating mechanism. These gravity cues are sensed both by the otolith organs (Fernandez et al. 1972) and body proprioceptors (Mittelstaedt 1992; Yates et al. 2000).

The fact that vestibular information can be stored and used by the oculomotor system to reproduce a body displacement with a saccadic eye movement has been suggested by a number of studies. The classical paradigm typically used in these studies has been the “vestibular memory-contingent” saccade task, where subjects match the amplitude of a preceding horizontal or vertical angular head displacement conducted in the dark with voluntary oculary saccades of equal but opposite cumulative angular displacement (Bloomberg et al. 1988,
1991; Israel et al. 1993). The accuracy of these saccades was preserved in patients with lesions of the posterior parietal cortex (PPC) (Berthoz 1997; Israel et al. 1995). In contrast, patients with supplementary eye field (SEF) lesions had no abnormalities of retinotopic saccades, although vestibular memory saccades were affected (Israel et al. 1995; Pierrot-Deseilligny et al. 1991, 1993).

Despite a clear contribution of vestibular signals to memory-contingent saccades, their role in visuospatial updating has been more controversial. The difference between the 2 tasks is that only with visuospatial updating in a memory-saccade paradigm do the vestibular signals interact with the retinotopic goal for a saccade. When subjects have performed such tasks with yaw rotation, Israel et al. (1999) reported improvement in updating accuracy after a few trials of performing the task in the presence of visual feedback. Similarly, in monkeys trained to perform either retinotopic or nonretinotopic saccades after an intervening horizontal rotation of the head and body, Baker et al. (2003) demonstrated clear updating, although with greater variability than double-step or retinotopic memory saccades. However, note that here too the memorized target reappeared at the end of each trial and the animals were highly trained. In contrast, when subjects underwent yaw rotations in the absence of visual feedback, little or no updating was reported (Blouin et al. 1998). In the present torsional updating experiments, we provided no visual feedback while rotating the subjects both from upright and supine positions and found minimal errors in the former condition (i.e., with gravity cues) and larger errors in the latter condition (i.e., without gravity cues). Therefore we suggest that these gravitational signals play a critical role in head-on-body and whole-body updating. In their absence, subjects must either be overtrained or provided with visual feedback to properly localize the remembered targets in a world-fixed reference frame. Because world-fixed targets could be localized in the upright but not supine orientations, we speculate that gravity cues maybe important for defining an allocentric reference frame.

Although our subjects were able to update quite well to 20° eccentric targets while passively rotated to upright positions, they did not perform as well as those in the related Medendorp (2002) study in which subjects actively rotated their heads. The difference can be attributed to several factors including the amplitude of head rotation. In the latter study, subjects never had to take into account head rotations that exceeded 45°, whereas in the present study, the largest errors were seen with the larger body rotations. In addition, directional errors were correlated with initial torsional eye position when the target was flashed and this mislocalization error was greater with the larger torsional eye positions from our larger tilt angles. Also, the additional signals provided by an active paradigm (i.e., efference copies and neck proprioception) may be responsible for the smaller errors observed. So although efference copies are not essential for updating, they may still be used when present.

Three-dimensional aspects of updating

Medendorp et al. (2002) were the first to show that updating occurs in the torsional dimension (in addition to horizontal and vertical dimensions). Our study not only corroborates their finding, but suggests that vestibular/body proprioceptive signals represent a key source of this updating signal. If a 3D, rotational vestibular signal is used for updating, this would imply that the process by which updating occurs cannot geometrically be explained by simple vector subtraction (Duhamel et al. 1992; Goldberg and Bruce 1990; Quaia et al. 1998). For example, with such a model and targets represented in a retinotopic frame, a target initially seen 15° to the right would be remapped to a location 10° right if the eye made a 5° rightward movement (i.e., old target location − eye movement = new target location, or, 15° − 5° = 10°). However, if this arithmetic were to hold true for roll rotations about the torsional axis, then any uniform subtraction of torsion about the line of sight would result in final gaze positions with large systematic horizontal and vertical errors as well as large torsional components (e.g., extend a pointing arm straight out and rotate it about the index finger). Rather, in 3 dimensions, the remembered target location must be rotated about the axis of rotation during the intervening movement, but in the opposite direction.

Alternatively, this 3D mathematical rotation would be unnecessary if the target was not kept in its original retinotopic frame, but rather was placed in some gravity-related spatial frame of reference immediately after viewing. In this situation, the target’s location could be derived after any rotation made relative to gravity as the target’s location is in a space-fixed frame immutable by the subjects’ movements and the gravity vector sensed by the otoliths and other proprioceptors is constantly available. In this case, the computational burden would shift from updating the target’s location in a retinotopic, egocentric frame toward maintaining a space-fixed, allocentric frame based on graviceptive inputs. Our current results cannot support or refute either of these 2 models, but points to experiments exploiting gravitational cues as a possible means of differentiating between these reference frames for updating.

In a recent set of experiments, Sommer and Wurtz (2002, 2004a,b) provided evidence for a neural pathway from the superior colliculus (SC), by mediodorsal thalamus (MD), to the frontal eye fields (FEF). After inactivation of MD, the authors found deficits in a monkey’s ability to perform a double-step saccade task, and thus they speculated that this pathway represents a neural substrate for the updating mechanism that uses corollary discharge signals, stemming from the SC, to update spatial information in the frontal cortex. Although there is no doubt that multiple extraretinal signals and probably multiple pathways implementing updating exist (including different sources for eye and head movements), there is a conceptual problem in embracing the notion that SC signals can represent the major source of appropriate extraretinal information. As has been demonstrated by several studies, the SC represents gaze (i.e., both eye and head)-related information in only 2 dimensions (Klier et al. 2001; Van Opstal et al. 1991). Thus the output of the SC does not provide the correct 3D information required to perform accurate updating for eccentric object locations. Even when considering shifts in gaze arising from saccadic eye movements, one could argue that corollary discharge signals must originate from motor centers downstream from the colliculus, areas where torsional signals are added on to motor commands (Klier et al. 2003). In fact, there is ample evidence that the efference copy signals used for visuospatial updating arise mostly downstream of the SC and upstream from oculor motoneurons (Schiller and Sandell 1983; Sparks and Mays 1983; Sparks et al. 1987; Tanaka 2003).
from electrical stimulation–induced perturbations in eye position before the execution of memory saccades. For example, appropriate visuospatial updating occurs for perturbations in eye position produced by electrical stimulation of most pontine sites that contain medium lead burst neurons (Sparks et al. 1987). In contrast, the saccadic system does not appropriately update for the eye movements elicited by stimulation of either the abducens or trochlear nerve (Schiller and Sandell 1983; Sparks and Mays 1983; Sparks et al. 1987).

Pathways for vestibular signals to sensorimotor cortex

When the concept of updating is generalized to include head and body movements, like those used in the present study, or those previously used by Medendorp et al. (2002), it is immediately obvious that the necessary extraocular signals must originate from motion centers in the brain stem (and/or cerebellum). Under the assumption that spatial updating and the underlying rotational remapping of retinal signals occurs in the visuomotor cortex (Andersen et al. 1997; Duhamel et al. 1992; Goldberg and Bruce 1990), there exist at least 2 possible pathways by which vestibular signals can reach these sensorimotor areas. The first pathway involves vestibular projections through the ventrolateral thalamus to the so-called parieto-insular vestibular cortex (PIVC) (Grusser et al. 1990a,b), an area that is bidirectionally interconnected with the FEF (Guldin et al. 1992; Huerta et al. 1987). Because no interconnection was found between frontal oculomotor areas and any of the other vestibular cortical areas (Guldin et al. 1992), it has been suggested that PIVC provides the necessary vestibular signals for vestibular memory-contingent saccades (Berthoz 1997). However, the FEF–PIVC connection is weak in rhesus monkeys (Huerta et al. 1987). Second, there is no evidence that PIVC is connected to SEF, the cortical area that, based on lesions studies, has been implicated in the control of vestibular memory saccades (Israel et al. 1995; Pierrot-Deseilligny et al. 1991, 1993).

Alternatively, the vestibular signals needed for spatial updating could follow a similar route as other extraretinal signals, i.e., through projections to the paralaminar mediodorsal and intralaminar nuclei of the thalamus (ILN). In support of this notion, labeled terminals have been reported in the ILN after tracer injections into the vestibular nuclei (Asanuma et al. 1983; Kotechabakhdi et al. 1980a,b; Lang et al. 1979; Magnin and Kennedy 1979; Nakano et al. 1985; Warren et al. 2003), and retrograde transport after HRP injections into the ILN have labeled cells in the rostral medial, superior, and lateral vestibular nuclei (McGuinness and Krauthamer 1980; Royce et al. 1991; Russchen et al. 1987). In turn, the ILN has widespread projections to both the frontal and parietal cortices, including FEF (Huerta et al. 1986; Jasper 1949; Kaufman and Rosenquist 1985; Orem and Schlag 1973; Scollo-Lavizzari and Akert 1963; Starzl and Magoun 1951), SEF (Huerta and Kaas 1990; Shook et al. 1990, 1991), and the PPC (Kaufman and Rosenquist 1985). In support of the hypothesis that the vestibular contributions to spatial updating follow a pathway through the ILN, patients with thalamic lesions localized in the internal medullary lamina are unable to perform vestibular memory-contingent saccades (Gaymard et al. 1994). This discussion highlights that both the neural mechanisms for this updating, as well as the origin and course of extraretinal signals to the sensorimotor centers in the cortex, remain unclear. It is important that future studies address both the neuroanatomical and computational aspects of these sensorimotor transformations and provide a functional understanding of ascending sensory and motor signals to the visuomotor cortical centers.

A P P E N D I X

Linear algorithm to separate search coil orientation signals from other DC offset voltages

A common problem in search coil measurements is the difficulty of discriminating the output voltages that arise from the rotation of the search coil in the magnetic field from those DC voltages that are picked up by the leads, plugs, and other parts of the measuring chain (Hess et al. 1992). We developed a simple linear algorithm that separates the coil orientation–dependent output signals from the remaining DC signals, which we call collectively DC offset signals. This approach is an extension of the one described by Hess et al. (1992) and is applicable for 3-field magnetic fields without the need of coil recalibration before implantation.

In the following calculations we consider a dual search coil, consisting of a direction coil (d = [dx, dy, dz]T) and a torsion coil (t = [tx, ty, tz]T) in a certain geometric configuration (ideally but not necessarily orthogonal to each other). In the following we use the subscripts 1 to 3 to denote the 3 different outputs according to the x-, y-, and z-magnetic field. The superscript “T” stands for “transpose,” meaning that a row vector becomes a column vector and vice versa. The output of the dual search coil in each of the 3 directions and torsion coil channels can be summarized as the vector sum of the orientation-dependent signals R̂d and R̂t and unknown DC offset signals ̂x and ̂y

\[
\begin{align*}
\vec{u} &= \vec{R}_d + \vec{x} \\
\vec{v} &= \vec{R}_t + \vec{y}
\end{align*}
\]

Here, R describes the orientation (= rotation) of the direction (d) and the torsion coil (t) in the magnetic field. If the dual search coil is in reference position, R, expressed as a rotation matrix, is the unity matrix, \( R = I \) (diagonal elements = 1, off-diagonal elements = 0). If the orientation R of the dual search coil and the DC offset signals ̂x and ̂y are known, we can compute the sensitivity and the relative orientation of the direction and torsion coil from the 6 output signals ̂u and ̂v as follows (‖ denotes the length of a vector, · denotes scalar product)

\[
\begin{align*}
Pd\vec{P} &= PR^{-1}(\vec{u} - \vec{x})P = P\vec{u} - x\vec{P} = \text{const} \\
Pt\vec{P} &= PR^{-1}(\vec{v} - \vec{y})P = P\vec{v} - y\vec{P} = \text{const}
\end{align*}
\]

\[
\begin{align*}
\vec{d} \cdot \vec{t} &= R^{-1}(\vec{u} - \vec{x}) \cdot R^{-1}(\vec{v} - \vec{y}) = (\vec{u} - \vec{x}) \cdot (\vec{v} - \vec{y}) = \text{const}
\end{align*}
\]

Equations A3–A5 hold true under the assumption that the sensitivities and the mutual orientation of the direction and torsion coil as well as the offset voltages do not depend on the orientation of the dual search coil in the field. Calculating the gradients of Eqs. A3–A5 as a function of a single axis rotation R = R(\( \rho \)) through the angle \( \rho \), we obtain the following system of vector equations

\[
\begin{align*}
(\vec{u} - \vec{x}) \cdot \frac{d\vec{u}}{d\rho} &= 0 \\
(\vec{v} - \vec{y}) \cdot \frac{d\vec{v}}{d\rho} &= 0
\end{align*}
\]

\[
\frac{d}{d\rho} [ (\vec{u} - \vec{x}) \cdot (\vec{v} - \vec{y}) ] = \frac{d\vec{u}}{d\rho} \cdot (\vec{v} - \vec{y}) + (\vec{u} - \vec{x}) \cdot \frac{d\vec{v}}{d\rho} = 0
\]

These equations describe the coil vector output signals ̂u and ̂v implicitly as functions of the unknown DC offset vectors ̂x and ̂y and
the vector gradients $\partial u/\partial p$ and $\partial v/\partial p$, which depend on the DC offset vectors $\hat{x}$ and $\hat{y}$ and the particular rotation $R(p)$ as follows

$$\frac{\partial u}{\partial p} = \frac{d}{dp} \left[ (\hat{x} \cdot \hat{R}) \cdot (\hat{R} \cdot \hat{x}) \right]$$

$$(A9)$$

We used a minimum of 5 symmetrically arranged fixations in horizontal and vertical directions around straight ahead to obtain good numerical estimates of the vector gradients $\partial u/\partial p$ and $\partial v/\partial p$. For horizontal fixations (rotation angle $\hat{\theta}$) we estimated Eqs. A9 and A10 by taking the derivative from the sinusoidal least-squares fits of Eqs. A1 and A2 to the direction and torsion coil output

$$\hat{u}(\hat{\theta}) = \left( \begin{array}{c} d \cos \hat{\theta} - d \sin \hat{\theta} + x_1 \\ d \sin \hat{\theta} + d \cos \hat{\theta} + x_2 \\ x_3 \end{array} \right)$$

$$\hat{v}(\hat{\theta}) = \left( \begin{array}{c} t_1 \cos \hat{\theta} - t_1 \sin \hat{\theta} + y_1 \\ t_2 \sin \hat{\theta} + t_2 \cos \hat{\theta} + y_2 \\ y_3 \end{array} \right)$$

Similarly, for vertical rotations (rotation angle $\phi$) we estimated Eqs. A9–A10 by taking the derivative from the analogous curves fitted to the direction and torsion coil output

$$\hat{u}(\phi) = \left( \begin{array}{c} d \cos \phi \cos \theta - d \sin \phi \sin \theta + x_1 \\ d \sin \phi \cos \theta + d \cos \phi \sin \theta + x_2 \\ x_3 \end{array} \right)$$

$$\hat{v}(\phi) = \left( \begin{array}{c} t_1 \cos \phi + t_1 \sin \theta \sin \phi + y_1 \\ t_2 \sin \phi - t_2 \cos \theta \sin \phi + y_2 \\ y_3 \end{array} \right)$$

With the vector gradients $\partial u/\partial p$ and $\partial v/\partial p$ at hand (obtained by taking the derivative of the fitted curves A11–A14) one can solve the system of linear Eqs. A6–A8 for the 2 DC offset vectors $\hat{x} = [x_1 \ x_2 \ x_3]^T$ and $\hat{y} = [y_1 \ y_2 \ y_3]^T$ using singular value decomposition. This approach, which was used in the present analyses, provides an accurate measurement of horizontal, vertical, and torsional eye positions after correction for offset voltages in a 3-field magnetic system.

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