Differences in the Accuracy of Human Visuospatial Memory After Yaw and Roll Rotations

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Klier, Eliana M., Bernhard J. M. Hess, and Dora E. Angelaki. Differences in the accuracy of human visuospatial memory after yaw and roll rotations. J Neurophysiol 95: 2692–2697, 2006. First published December 21, 2005; doi:10.1152/jn.01017.2005. Our ability to keep track of objects in the environment, even as we move, has been attributed to various cues including efference copies, vestibular signals, proprioception, and gravitational cues. However, the presence of some cues, such as gravity, may not be used to the same extent by different axes of motion (e.g., yaw vs. roll). We tested whether changes in gravitational cues can be used to improve visuospatial updating performance for yaw rotations as previously shown for roll. We found differences in updating for yaw and roll rotations in that yaw updating is not only associated with larger systematic errors but is also not facilitated by gravity in the same way as roll updating.

INTRODUCTION

In a previous study (Klier et al. 2005), we showed that gravitational cues play a critical role in visuospatial updating. Specifically, subjects were asked to generate accurate eye movements to the remembered location of a visual target after an intervening whole body roll rotation. They were successful from an upright orientation, when the intervening roll rotation (about a body-fixed naso-occipital axis) changed head and body orientation relative to gravity. In contrast, large errors were seen when the same movements were made in a supine position, a condition that does not reorient the body relative to gravity. The difference between the two conditions lies on the fact that roll rotations in supine orientation only activate semicircular canal afferents in the inner ear. In contrast, because roll displacements from an upright orientation change head and body orientation relative to gravity, they also stimulate both body and head gravitoceptors, the latter found in the vestibular otolith organs. A dependence of the accuracy in visuospatial memory on orientation relative to gravity was also reported by Van Pelt et al. (2005).

Other studies have investigated visuospatial updating performance during yaw rotations from upright orientations (Blouin et al. 1995a,b, 1997, 1998; Israel et al. 1999). Here, naïve subjects were reported to make significant errors when localizing briefly flashed targets after intervening yaw rotations. Note that these updating paradigms are different from those associated with vestibular memory-contingent saccades, in which subjects are rotated in yaw and subsequently asked to report where they perceived their initial starting position to have been (Bloomberg et al. 1988; Israel et al. 1993). In these latter experiments, the vestibularly derived information is only used in its original form, without a need to combine it with other cues (e.g., the memorized location of the visual target).

Because with roll rotations (from upright), the body is reoriented relative to gravity, whereas with yaw rotations (from upright), the body’s position relative to gravity remains fixed, we hypothesized that differences in performance for yaw and roll updating could be caused by gravity. In particular, if gravity is an important factor for maintaining spatial constancy during body rotations about any axis, yaw rotations from supine that change head and body orientation relative to gravity might be more accurate than yaw rotations in upright positions.

Thus to study the effects of gravity during yaw updating, we had subjects memorize a briefly flashed target and subsequently rotated them about a body-fixed yaw axis when their initial body position was either upright, pitch-tilted back by 30°, pitch-tilted back by 60°, or supine. To more systematically compare human ability to update after yaw and roll rotations, in a second experiment, we also directly compared the accuracy of the subjects to update after intervening yaw and roll rotations from upright orientation. We found that subjects only partially updated their saccades to the remembered targets after intervening yaw movements in all orientations, indicating that gravity cues may have differential effects depending on the particular axis of rotation used.

METHODS

Subjects

A total of seven subjects (5 female; 2 male) ranging in age from 27 to 37 yr participated in two experiments that were conducted on different days. Five of the seven subjects participated in both experiments, whereas the remaining two subjects each participated in one experiment, such that data from six subjects were available for each study. All but one of the subjects (EK) were completely naïve to the purpose of the experiment, and none had any known neuromuscular or neurological deficits. Before their participation, they all gave informed consent to the experimental protocols. The study was approved by the Ethics Committee of the Canton of Zurich, Switzerland.

Apparatus

Three-dimensional eye positions were measured using the magnetic search coil technique and three-dimensional Skalar search coils (Skalar Instruments, Delft, The Netherlands). The magnetic field

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Subjects sat on a chair that was mounted on a three-dimensional turntable (Acutronic) capable of rotating the subjects about yaw and roll axes, with their body fixed to the chair by three 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 their body so that movement of the chair caused the head and body to move as a unit. Visual targets were produced by a computer-controlled laser (Acutronic) and projected onto one of three flat projection screens. An upright screen was mounted on the turntable at a distance of 1.47 m from the subject, an oblique screen was used for the 30° and 60° pitch-tilt angles in the yaw updating experiments (it was at a perpendicular distance of 2.16 m for 30° pitch-tilt and 1.98 m for 60° pitch-tilt), and a supine screen was mounted on the ceiling at a distance of 1.54 m from the subject when they were lying on their backs. All tasks were performed in complete darkness.

General visuospatial updating task

Each task began with the subject looking straight ahead at a central fixation target. After 1.5 s, a peripheral target was briefly flashed (100 ms). The subject had to make note of and memorize the location of the flashed target but continue to fixate the central target. After the peripheral target was extinguished, the subject was rotated about either the yaw or roll axis to a new position. The motorized chair moved with a constant acceleration/deceleration phase of 180°/s² so that a strong stimulus to the semicircular canal afferents could be provided. During the rotation, the central, head-fixed target remained illuminated, and the subject continued to fixate it. At the end of the rotation and after a delay interval of 1.5 s, the central target was extinguished, and this cued the subject to make a saccade to the remembered location of the flash (which the subjects were told had remained fixed in space). The subjects were instructed to reach the remembered location as accurately as possible using only one eye movement. Subjects never received visual or verbal feedback about their performance during any of these tasks. Similar instructions in previous studies have shown that subjects can readily do this task (Klier and Crawford 1998; Klier et al. 2005).

Yaw-upright versus yaw-supine

In the first experiment (upright/supine yaw), subjects were passively rotated, 35° in yaw, at four different static head/body orientations: 0° = upright; 30° pitch-tilt nose-up; 60° pitch-tilt nose-up; 90° nose-up = supine. In upright orientation, the head and body were rotated about the yaw axis and did not change orientation relative to gravity. In the tilted orientations, the subjects were rotated about the same body-fixed yaw axis, but this time they were reoriented relative to gravity (in the direction of either right ear down during rightward yaw rotations or left ear down during leftward yaw rotations).

Eight targets were used, four cardinal and four oblique, each at an amplitude of 18° from a central fixation target. Here only eight targets were used because of the time constraints associated with coil usage (maximum 45 min) and the fact that each target was paired with both a rightward and a leftward rotation at each of the four tilt angles (for a total of 8 × 2 × 4 = 64 unique trials). Each trial took ~10 s and was repeated three times for a total experimental duration of 32 min. For each static head/body orientation, trials with different peripheral targets and motion directions were presented in a random fashion. All trials for a given static head/body orientation were presented within the same block, and the blocks were repeated in the order 0, 30, 60, and 90° four times. Although both rotation directions and all eight targets were tested, only those that required a memory-guided eye movement within the normal oculomotor range (i.e., <35°) were used for off-line analyses (5 targets for each motion direction). The targets excluded from analyses were the three right targets during leftward motion and the three left targets during rightward motion (these missing targets would otherwise complete the circles in Fig. 1).

Yaw versus roll

In the second experiment (upright yaw/roll), subjects had to update the spatial location of a memorized target after an intervening movement that was either 35° yaw or 35° roll. A total of 12 possible targets were used that were located at an amplitude of 18° from a central fixation point. The directions of the targets were 30, 45, and 60° in all four quadrants (specifically, the 45° targets were located at 45, 135, 225, and 315° in polar coordinates; the 30° targets were located at 30, 150, 210, and 330°; the 60° targets were located at 60, 120, 240, and 300°). Thus the 30° targets were those closest to the amscissa, whereas the 60° targets were those closest to the ordinate. Each set of yaw and roll rotations was conducted in separate blocks of trials, but each yaw block was followed by a roll block. The pairs of blocks were repeated four or five times in each subject within the same experimental session. Within each block, trials with different peripheral targets and motion direction were presented in a random fashion.

In the yaw trials, rightward whole body rotations were conducted for targets presented in the first and fourth quadrant, whereas leftward whole body rotations were made for targets in the second and third quadrants. In the roll trials, counterclockwise whole body rotations were conducted for targets presented in the upper right and lower left quadrants, whereas clockwise rotations were made for targets in the upper left and lower right quadrants. These combinations were chosen 1) to allow for ample repetitions of memory saccades to each target within the 30–45 min time limit for human eye coil usage, 2) to keep the targets within the oculomotor range of the subject after each rotation, and 3) to match target rotation combinations from a previous experiment (Klier et al. 2005). The total time for this experiment was 20 min [12 targets × 2 rotation directions (yaw and roll) × 5 repetitions × 10 s per repetition]. All rotations began from an upright, forward facing body orientation.

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 3-dimensional eye position). Finally, angular eye velocity (Ω) was computed from the previous two values by the equation Ω = 2 (dE/dt + E × 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 <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 on our data.

Updating ratio quantification

The accuracy of the subjects’ saccades relative to the space-fixed location of the targets was quantified to determine how well subjects
took their intervening body movements into account when making saccades to the remembered location of the flashed target (Fig. 2A).

Three measures were used for this analysis: 1) the space-fixed location of the target (assuming perfect updating for intervening body motion), 2) the head-fixed location of the target (assuming no updating for body motion), and 3) the subject’s final gaze position (i.e., the memory saccade endpoint). For all yaw rotations (upright and supine), the target locations must be updated along the horizontal dimension; thus we examined horizontal updating. First, we computed the horizontal distance between the subject’s endpoint and the head-fixed location of the flash (Xactual). Second, we computed the total distance the subject had rotated by taking the horizontal distance between the space-fixed and head-fixed locations of the target (Xideal). Finally, we divided Xactual/Xideal to obtain an updating ratio representing how much of the rotation the subjects compensated for when executing their saccades. A value of 1 indicates perfect updating for the intervening rotation, whereas a value of 0 indicates no updating (i.e., the subject made a saccade to the head-fixed location of the target).

Values between 0 and 1 indicate partial updating, and values >1 represent saccades that overcompensated for the intervening rotation by missing the actual space-fixed target location in a direction opposite to that of the head-fixed target location. For the roll rotations, the analysis was the same, except that updating in final saccade direction (i.e., angular updating) was examined because the required updating was for a whole-body torsional rotation around the central fixation point (and not a horizontal rotation).

**RESULTS**

We first examined how well subjects performed after upright yaw versus supine yaw rotations. Figure 1 shows each subject’s memory saccades to eight targets after yaw rotations in either upright (left column in each pair) or supine (right column in each pair) conditions. Each space-fixed target location is color matched with its corresponding eye movement trajectory. Movements made after yaw rotations to the right are indicated by solid lines, whereas movements to the left are indicated by dashed lines. The view of the targets and trajectories are plotted relative to the final fixation position at the end of the rotations [0,0]. Thus targets initially flashed to the right of the subject are seen to the left of center after the rightward yaw rotations (semicircle of symbols to the left of [0,0] in each plot), whereas targets initially flashed to the left of the subject are seen to the right of center after the leftward yaw rotations (semicircle of symbols to the right of [0,0] in each plot).

The endpoints of the memory-guided saccades in the upright and supine orientations appeared to be quite similar across each subject (although variability can be seen across subjects). In general, several of the subjects seemed to greatly undershoot the space-fixed locations of the targets in the direction of the targets’ head-fixed locations. These results, quantified using the updating ratio (defined as the distance of the memory saccade endpoint from the head-fixed target location divided by the distance between the head-fixed and space-fixed target locations), are shown in Fig. 2B (see**M**ETHODS and Fig. 2A). A value of 1 indicates perfect updating, whereas a value of 0 indicates no updating (i.e., the subject made a saccade to the head-fixed location of the target). The updating ratios for the upright orientation were significantly correlated with the respective ratios for the supine orientation, with a regression slope that was not different from unity (slope = 0.96, R² = 0.71, 95% CIs = 0.79, 1.07). Across all six subjects, updating ratios averaged 0.65 ± 0.23 (SD) for the upright orientation (where rotation did not change the body’s orientation relative to gravity) and 0.65 ± 0.22 for the supine orientation. The intermediate tilt angles of 30 and 60° had average updating ratios of 0.66 ± 0.21 and 0.64 ± 0.25, respectively. Collectively, across all subjects (6) and all targets (10), there was no significant difference between updating performance at any of the four different tilt angles relative to gravity [1-way, repeated-measures ANOVA, F(3,174) = 0.374, P >= 0.05].
Updating Ratio = \( \frac{X_{\text{actual}}}{X_{\text{ideal}}} \)

**FIG. 2.** Quantification of upright vs. supine yaw updating performance. A: computation of the updating ratio. HF, head-fixed target location; SF, space-fixed target location; SE, subject’s endpoint; X\(_{\text{ideal}}\), space-fixed target – head-fixed target; X\(_{\text{actual}}\), head-fixed target – subject endpoint. Updating ratio = X\(_{\text{actual}}\)/X\(_{\text{ideal}}\). B: average error ratios are plotted for each of 10 different target/direction pairs (5 target locations; 2 rotation directions) in each subject (●, AG; ▲, CB; △, EK; ●, MS; ●, TS; □, TT) for the supine (abscissa) and upright (ordinate) yaw conditions. A regression line through all the data are also shown.

Because of the observed large systematic memory saccades errors (unlike the relatively small systematic errors for roll rotation updating; Klier et al. 2005), we also directly compared how well individual subjects updated for yaw compared with roll rotations. Figure 3 shows trajectories of the memory saccades elicited by the six subjects. The colored circles indicate the final space-fixed locations of the 60° targets (in each of the 4 quadrants) relative to the subject’s final fixation point at the end of the rotation [0,0]. For example, the red circles indicate targets initially flashed at 60° in the upper right quadrant (0°–90° in polar coordinates). For yaw rotations (1st and 3rd columns), the target is now to the left (top left quadrant = 90°–180° in polar coordinates) as the subject was rotated 35° to the right. For roll rotations (2nd and 4th columns), the target’s final position is shown at 25° in polar coordinates (after a torsional clockwise rotation of 35° from 60°). The blue circle represents the 60° target initially flashed in the upper right quadrant (90°–180° in polar coordinates), the magenta circle represents the 60° target initially flashed in the bottom left quadrant (180°–270° in polar coordinates), and the cyan circle represents the 60° target initially flashed in the bottom right quadrant (270°–360° in polar coordinates).

Several subjects tended to perform better in the roll condition than in the yaw condition. For the former, the subjects’ trajectories appear to land on or around the space-fixed locations of the targets (circles), despite variability within and across subjects. For the latter, memory saccades typically undershot the space-fixed location of the target, with the effect being more obvious in some subjects than others (e.g., compare CB with TT). The average updating ratios, for each subject, are depicted in Fig. 4. Two of the subjects (MS and TT) had nearly perfect updating ratios for both the yaw and roll conditions. For the remaining subjects, the updating ratios for yaw rotations (black bars) were always positive and <1, indicating that the saccades always landed in between the space-fixed and head-fixed target locations. The roll ratios (white bars) could be either >1 or <1 (indicating that saccade endpoints landed on either side of the space-fixed target locations), resulting in larger variable errors but smaller systematic errors than in the yaw conditions (large variable errors for roll updating have previously been reported by Klier et al. 2005).

Across all subjects, targets (30, 45, and 60°), and quadrants, memory saccades after yaw rotations had an average updating ratio of 0.71 ± 0.26 compared with memory saccades after roll rotations, which had an average error ratio of 0.92 ± 0.37. A one-way, repeated-measures ANOVA between yaw and roll trials, across all subjects (6) and all targets (3 × 4 = 12), found that the error ratios in the two conditions were significantly different from one another \( [F(1,7) = 20.85, P \ll 0.001] \). The study of Klier et al. (2005) also reported that subjects could account for 90% of the induced upright roll rotation. This study found similar results for roll updating (a \( t \)-test between the roll ratios and a ratio of 0.9; \( P > 0.05 \)), but not for yaw updating (\( P < 0.05 \)). Finally, the study of Klier et al. (2005) examined updating during supine roll rotations (similar to upright yaw rotations in that the body does not change its position relative to gravity and thus the otoliths do not modulate their activity during these rotations). The average updating ratio for supine roll was calculated to be 0.05 ± 0.48 (this value was computed using data from 4 subjects who also participated in the current experiment, a target amplitude of 20°, target directions of 45, 135, 225, and 315°, and roll rotations of ±30°—parameters closest to those found in the current experiment). Thus humans seem to have a graded ability to update for intervening body movements; upright roll performance is best, yaw at any orientation is intermediate, and supine roll is worst.

**DISCUSSION**

The results indicate that visuospatial updating uses gravity cues differentially depending on the specific axis of the intervening movement. Roll rotations seem to use gravitational cues effectively whenever they are present, resulting in relatively accurate memory saccades (current paper; Klier et al. 2005; van Pelt et al. 2005), albeit with large variable errors. In contrast, subjects, on average, can only partially update the remembered locations of visual targets after yaw rotations—irrespective of whether the yaw rotation changes the body’s orientation relative to gravity (supine yaw) or not (upright yaw).

These results, showing that memory saccades after yaw rotations undershoot the world-fixed locations of the targets (also see Blouin et al. 1995a,b, 1997), coupled with previous findings that the ability to appropriately update after roll rotation breaks down in supine orientation (Klier et al. 2005), raise questions as to how well passive rotational signals from
the semicircular canals are used for visuospatial updating by naïve human subjects without extensive training (as occurs in monkeys: Baker et al. 2003; Li et al. 2005). The relative contribution of the otolith organs/body graviceptors is also unclear because yaw updating performance does not improve when the subject is supine and moved relative to gravity (this study), but roll updating does improve when the subject is upright as opposed to supine (Klier et al. 2005). However, vestibular signals (i.e., canals and otoliths) have been shown to be critical in updating for intervening rotational and translational movements (Li and Angelaki 2005; Li et al. 2005). When the vestibular labyrinths are surgically ablated, the ability of trained rhesus monkeys to perform accurate updating during intervening yaw rotations and translations is severely compromised. However, whereas yaw updating deficits recover over time, updating capacity during forward and backward motion remains compromised (Wei et al. 2005).

The larger systematic errors observed for yaw updating are puzzling in the this and previous human experiments, especially given the results from studies using vestibular memory-contingent saccades (Bloomberg et al. 1988; Israel et al. 1993). Here, subjects are first shown a target and are then rotated about an upright or supine yaw axis. Their task is to make an eye movement back to the original location of the flashed target, thereby indicating their perceived rotation. The above studies find that normal subjects can do this task quite accurately. However, the updating paradigm takes this vestibular-to-saccade mapping one step further by requiring the subjects to use this apparently accurate information to update the location of a space-fixed target. Previous experiments examining yaw updating from upright orientations have also found large final eye position errors (Blouin et al. 1995a, b, 1997; Israel et al. 1999) that were only corrected after learning through visual feedback of the target location (Israel et al. 1999). Similar errors were also found when updating visual space after whole body yaw rotations was studied using pointing movements (Blouin et al. 1998). Therefore, while the initial vestibular signals describing the rotation seem to be precise, the updating computations that follow may lead to cumulative errors.

While gravity may not facilitate yaw updating performance in humans, other factors have been shown to be helpful. These include efference copies from self-generated yaw rotations, because subject seem to perform as well in these conditions as when they point to remembered visual targets while stationary (Blouin et al. 1995c, 1998). In addition, neck proprioception from passive head-on-body rotations has been shown to improve updating accuracy (Mergner et al. 1988). Finally, as mentioned above, learning and practice have also been shown to facilitate yaw-only updating in both humans (Israel et al. 1999) and monkeys (Baker et al. 2003; Li et al. 2005). Thus yaw rotations, which in everyday life are actively generated and largely leave the body fixed relative to gravity (e.g.,
turning around when someone calls your name), may rely more on signals associated with self-generated commands and monitoring signals. In their absence, performance is compromised.

In contrast, roll rotations are not generated nearly as often, but when they do occur, they dramatically change the body’s position relative to gravity. Thus it is not surprising that gravity plays a much larger role in updating accuracy for roll movements. Previous studies have shown that roll updating relative to gravity is quite accurate for both self-generated (Medendorp et al. 2002) as well as passive (Klier et al. 2005) whole body rotations. However, when subjects were rotated about a naso-occipital roll axis while supine (and thus not rotated relative to gravity), their performance drastically declined (Klier et al. 2005). It is yet to be determined if, in such gravity-static situations, roll updating can be improved through learning or self-generated movements that allow for additional efference copy and proprioceptive cues.

The differences between updating accuracy after yaw and roll rotations may also be caused by different frames of reference used by the different axes. Several studies have used updating errors to infer the underlying reference frame used for computing and generating saccades to remembered targets. For example, Baker et al. (2003) found that, after upright yaw rotations, saccade endpoints were less variable when targets were memorized in a body-fixed frame as opposed to a space-fixed frame. In contrast, Van Pelt et al. (2005) found evidence for allocentric encoding of targets in space after roll rotations relative to gravity. This difference in ego- versus allocentric coding across axes is initially difficult to reconcile. However, as has been argued previously (reviewed in: Andersen et al. 1997; Battaglia-Mayer et al. 2003; Boussaoud and Bremmer 1999), it is likely that the brain stores spatial memories in various reference frames, depending on the task at hand and the availability of different sensory cues (e.g., the presence or absence of gravity). Thus roll updating in an allocentric frame may rely heavily on gravitational signals, whereas yaw updating in egocentric frames does not. In fact, the brain may choose to represent spatial information simultaneously in various reference frames (Bridgeman et al. 1997; Carrozzo et al. 2002; Snyder et al. 1998) and choose which representation is best suited to the current behavioral task (Crawford et al. 2004). Ultimately, however, all these spatial representations must be converted into appropriate three-dimensional motor commands in the appropriate body-centered reference frames for action (Crawford et al. 2004; Klier and Crawford 1998).

In summary, gravitational cues seem to only be used to facilitate spatial updating after roll, but not yaw, rotations. Updating performance after intervening whole body yaw movements is significantly poorer, irrespective of whether the yaw rotations occur relative to gravity or not. These unexpected results point to different spatial processing mechanisms that are dependent on the axis of rotation and may implicate the use of task-specific reference frames.

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