Accuracy of Saccades to Remembered Targets as a Function of Body Orientation in Space

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Vogelstein, Joshua T., Lawrence H. Snyder, and Dora E. Angelaki. Accuracy of saccades to remembered targets as a function of body orientation in space. *J Neurophysiol* 90: 521–524, 2003; 10.1152/jn.00141.2003. A vertical asymmetry in memory-guided saccadic eye movements has been previously demonstrated in humans and in rhesus monkeys. In the upright orientation, saccades generally land several degrees above the target. The origin of this asymmetry has remained unknown. In this study, we investigated whether the asymmetry in memory saccades is dependent on body orientation in space. Thus animals performed memory saccades in four different body orientations: upright, left-side-down (LSD), right-side-down (RSD), and supine. Data in all three rhesus monkeys confirm previous observations regarding a significant upward vertical asymmetry. Saccade errors made from LSD and RSD postures were partitioned into components made along the axis of gravity and along the vertical body axis. Up/down asymmetry persisted only in body coordinates but not in gravity coordinates. However, this asymmetry was generally reduced in tilted positions. Therefore the upward bias seen in memory saccades is egocentric although orientation in space might play a modulatory role.

INTRODUCTION

Memory saccades show an upward asymmetry whose origin has remained uncharacterized. Other patterns of eye movements that occur over an extended period of time, like memory saccades, have also shown vertical asymmetries. In particular, the vestibuloocular (VOR) and optokinetic (OKN) reflexes show longer time constants and higher gains for upward compared with downward eye movements (Chaudhuri 1991; Clement et al. 1986; Himi et al. 1990; Matsuo and Cohen 1984; Snyder and King 1988). If these asymmetries all derive from the same source, then they should be dependent on the same variables. The low-frequency (long duration) components of the VOR and OKN show asymmetries that cease or change direction when the subjects are reoriented with respect to gravity or when the gravitational field is altered (Angelaki and Hess 1994; Clarke et al. 2000; Clement et al. 1986, 1993; Mittelstaedt and Mittelstaedt 1996; Raphan and Sturm 1991). By convention, we call these gravity-dependent asymmetries allocentric. In contrast, we call any asymmetry that is independent of gravity and maintains a constant relationship with the body an egocentric asymmetry.

The aim of this investigation was to test whether the vertical asymmetry in memory saccades is egocentric or allocentric.

Because all previous studies of memory saccades were performed with subjects oriented upright, this upward asymmetry could be either egocentric or allocentric, or reflect an interaction between the two. Knowing the reference frame of the vertical memory saccade asymmetry will provide clues to its origin. If it is allocentric, then it is more likely to arise from a vestibular-related source; if it is egocentric, then a vestibular origin can be ruled out. We recorded memory saccades while animals were in one of four different orientations in space: upright, left-side-down (LSD), right-side-down (RSD), and supine. Evaluation of the magnitude and direction of the errors in these orientations demonstrated that the up/down asymmetry is egocentric, but the magnitude of the error does decrease in tilted orientations.

METHODS

Three Rhesus monkeys were chronically prepared with skull bolts to restrain body motion during experimental trials. A scleral eye coil was surgically implanted under the conjunctiva while animals were under general anesthesia. Each animal was trained to first perform visually guided saccades and subsequently memory-guided saccades for ≥3 mo prior to data collection. All surgical procedures, animal handling and training were in accordance with institutional and National Institutes of Health guidelines.

During experiments, animals were seated in a head-fixed primate chair inside a three-dimensional turntable (Acutronics) equipped with a three-field magnetic system (CNC Engineering). The animals' bodies were secured with shoulder and lap belts, whereas the extremities were loosely fixed to the chair. The chair and magnetic coils could be tilted in a variety of orientations relative to gravity. Saccades were made from four distinct orientations: upright, LSD, RSD, and supine. This configuration allowed dissociation between gravity and head coordinates, although prohibited dissociation between a head- and a body-centered frame of reference. Because the magnetic coils moved with the animal, the recorded eye movements were measured relative to the animals' head and body axes.

The memory saccade task is outlined in Fig. 1*A*. A laser projected a target on a screen 22 cm from the monkey at the center of his visual field in a completely dark room. After the monkey fixated on the central light for ≥1 s, a peripheral target light flashed for 200 ms. The flash appeared randomly at 1 of 16 possible locations (45° increments around a full circle with 15 or 20° eccentricity). The animal was required to maintain fixation on the central target and ignore the peripheral flash. The central target was turned off between 1.75 and 2.25 s after the peripheral flash, signaling the animal to make a
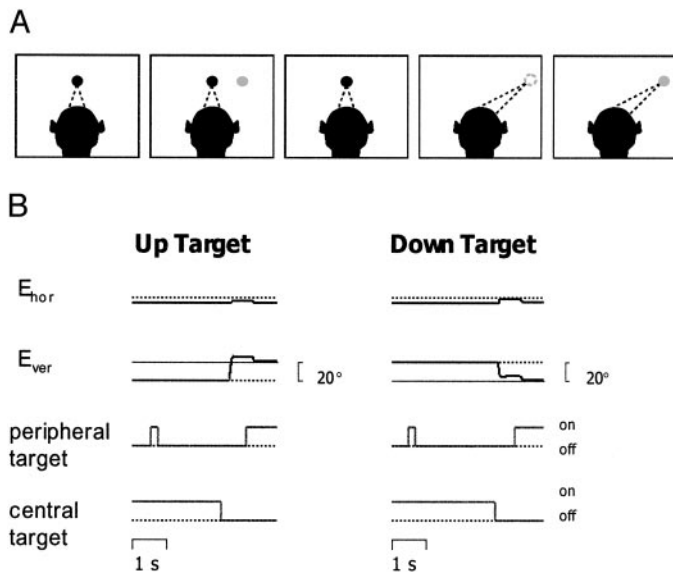
FIG. 1.   The task and 2 example trials. *A*: schematic of the task. Black circle, central target; gray circle, peripheral target; solid circle, visual target; outline circle, remembered target; dotted lines, gaze direction. *B*: horizontal (E_{hor}) and vertical (E_{ver}) eye positions are plotted vs. time. The times of the central and peripheral target onset and offset are illustrated (*bottom*). *Left*: a trial in which the peripheral target flashed directly above the central target. *Right*: a trial in which the peripheral target flashed directly below the central target. Both required a vertical (upward or downward) eye movement of 20°. Data from *animal A*.

saccade to the remembered location of the flash. The animal was required to hold fixation at the extinguished peripheral target location for 400 ms before the peripheral target was turned back on. The animal received a juice reward only after he satisfactorily fixated on the re-illuminated target for 400 ms. Behavioral windows were small for visual fixation (typically ±2°) but large (typically ±10°) for the memory fixation.

Only successful trials (i.e., trials in which a reward was delivered) were saved for off-line analyses. A Cambridge Electronics peripheral interface device (CED Power 1401) using Spike2 software-controlled stimulus presentation, behavioral control, and data acquisition (833.33 Hz, 16-bit resolution). Eye-position signals were anti-alias filtered (200 Hz, 6-pole Butterworth) and calibrated based on a daily horizontal/vertical fixation task. Eye velocity was calculated as the time derivative of eye position.

Saccade onset and offset were defined as the time when the magnitude of eye velocity first exceeded and fell below 25°/s, respectively. Horizontal and vertical pre- and postsaccadic positions were calculated by averaging eye position over a 20-ms period beginning 50 ms before and after saccade onset and offset, respectively. Horizontal and vertical saccade amplitudes were then calculated as the difference between pre- and postsaccadic eye positions.

Systematic error was defined on a trial-by-trial basis as the vector difference between the target location and the eye position immediately after the saccade. Variable error was computed as in White et al. (1994) to indicate variability within each group, where groups are defined as trials that share orientation, direction, target eccentricity, and animal. Positive numbers were defined as upward and rightward errors (relative to the animal) for the vertical and horizontal components, respectively. Systematic errors were analyzed by assuming that the asymmetry was either ego- or allocentric. We therefore defined two distinct coordinate reference frames: allocentric with its ordinate perpendicular to the ground, and egocentric with its ordinate perpendicular to the horizontal (or transverse) body plane. Because these two coordinate systems are identical with the animal upright, non-upright orientations were used to dissociate the two. Specifically, for each

side-down orientation, the egocentric reference frame was rotated by 90° with respect to the allocentric frame. We calculated the mean saccadic errors for each animal in every orientation by averaging the appropriate systematic errors. We then expressed the vertical component of the error in side-down trials as a fraction of the vertical error in upright trials. As a final step, we averaged these ratios across the three animals. Statistical comparisons used ANOVA to ascertain that the upshift was influenced by position, and Student's *t*-test to test the significance of individual comparisons.

RESULTS

Examples of two memory saccades from an upright position to an upward and to a downward target are illustrated in Fig. 1*B* (*left* and *right,* respectively). As previously reported (Gnadt et al. 1991; White et al. 1994), the upward memory-guided saccade overshot its target while the downward saccade undershot its target. When the peripheral target was turned on later in each trial, downward corrective visually guided saccades brought the eyes closer to the target (Fig. 1*B*). To determine whether this up/down asymmetry is egocentric (related to body or head position) or allocentric (related to the direction of gravity), the errors were evaluated in three different body orientations—LSD, RSD, and supine—as well as upright. The systematic (lines) and variable (circles) errors for two monkeys in the eight different 20° target location eccentricities are plotted in Fig. 2, separately for each orientation. For both monkeys and at every orientation, nearly every saccade landed a few degrees above the target. The data are consistent for 15° targets as well, which are not shown for simplicity. Because eye position is expressed relative to the head and body, that is, in egocentric coordinates, it appears that the asymmetry is egocentric. Had it been allocentric, the LSD lines would point to the right, the RSD lines would point to the left, and supine lines would average to no asymmetry at all.

The results for all three animals are summarized in Fig. 3. The up/down asymmetry persisted and remained positive (upward) in all four orientations. However, the upward systematic error decreased in tilted orientations in all three animals (although the difference was statistically significant only for *animal A,* Fig. 3*A, top;* white fills). In contrast to the vertical error, which was always upward, the horizontal error was small and idiosyncratic: to the left for *animal A,* to the right for *animal B,* and variable for *animal C* (Fig. 3*A, bottom*).

A quantitative summary is provided in Table 1 and Fig. 3*B*. The mean up/down asymmetry calculated in an egocentric frame of reference is two-thirds as large as the asymmetry in the upright position (egocentric ratio = 0.68). In contrast, the mean asymmetry calculated in the allocentric frame of reference is close to zero (allocentric ratio = 0.05). Figure 3*B* plots the mean systematic errors separately for each animal and orientation in both ego- and allocentric coordinates. The figure illustrates that the errors in side-down orientation were nearly identical to the errors for the upright orientation, when plotted using egocentric coordinates. However, when the same data are plotted using allocentric coordinates, the error in each side-down orientation clearly diverges from the error in the upright orientation.

DISCUSSION

Up/down asymmetries in memory-guided saccades may arise in either an allocentric or an egocentric frame of refer-
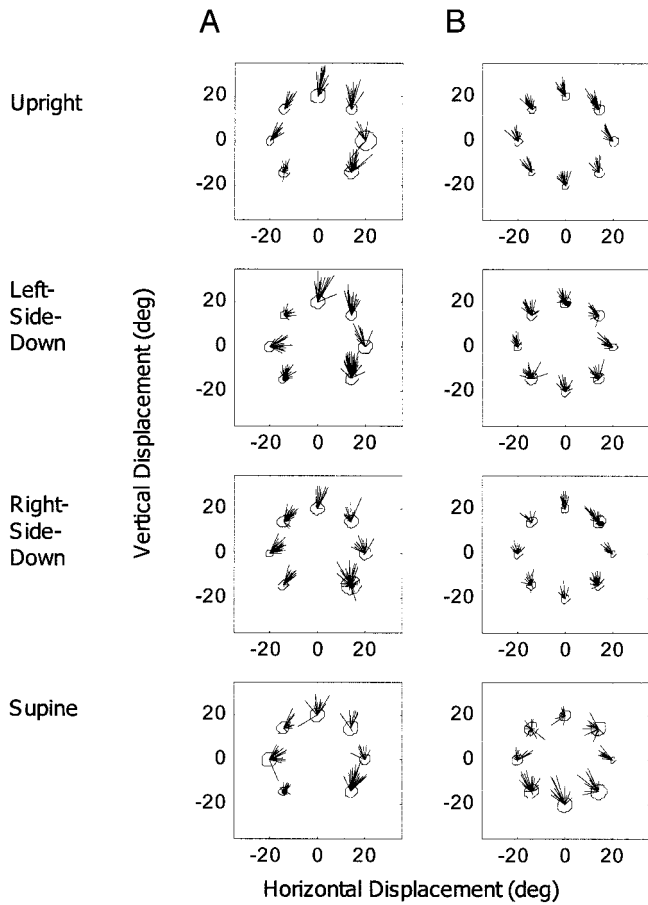
FIG. 2. Systematic and variable errors for 2 animals (*A*) and (*B*) for 20° saccades in the 4 different body orientations: upright, left-side-down (LSD), right-side-down (RSD), and supine. Lines: systematic error drawn from the target position to the actual fixation position after the memory saccade. Circles illustrate variable error (computed as in White et al. 1994). Note: downward saccades were not recorded for *monkey A*.

FIG. 3. (*A*) Average (±1 SD) systematic vertical and horizontal errors (in degrees) for 20° saccades. Positive numbers represent upward and rightward errors for the vertical and horizontal components, respectively. *Animal C* lacks RSD data. Upr, upright; Sup, supine. Data from *animals A–C* (white, gray and black fills, respectively). Asterisks denote LSD, RSD, and supine orientation averages that were significantly different (*P* < 0.05) from the respective average in upright orientation. *B*: errors plotted in either an egocentric (*top*) or allocentric (*bottom*) frame of reference from *animals A–C* (1st–3rd columns, respectively). Black: upright; green LSD; red: RSD.

ence. When upright, these two frames of reference are indistinguishable. However, they can be separated by changing the subject's orientation with respect to gravity. By analyzing the asymmetry in the non-upright (tilted) orientations, we could determine if the effect is ego- or allocentric. If the asymmetry is allocentric, then the allocentric ratio should be unity and the egocentric ratio should be zero. If the asymmetry is egocentric, then the egocentric ratio should be unity and the allocentric ratio should be zero.

Our results from the side-down orientations are consistent with the asymmetry being egocentric (Fig. 3 and Table 1). In addition, the asymmetry persisted for animals in the supine position, which is also consistent with an egocentric frame of reference. However, the egocentric ratio was reduced to approximately two-thirds in the side-down positions, consistent with a second-order modulatory effect of position with respect to gravity on the up/down asymmetry.

Our results indicate that the vestibular system is minimally involved in the vertical asymmetries seen in memory-guided saccades. Asymmetries that are closely linked to the vestibular system, such as those seen in the VOR and OKN, differ from the memory-guided saccade asymmetry in two important respects. First, the low-frequency VOR and OKN effects are allocentric (Angelaki and Hess 1994; Clement et al. 1986;
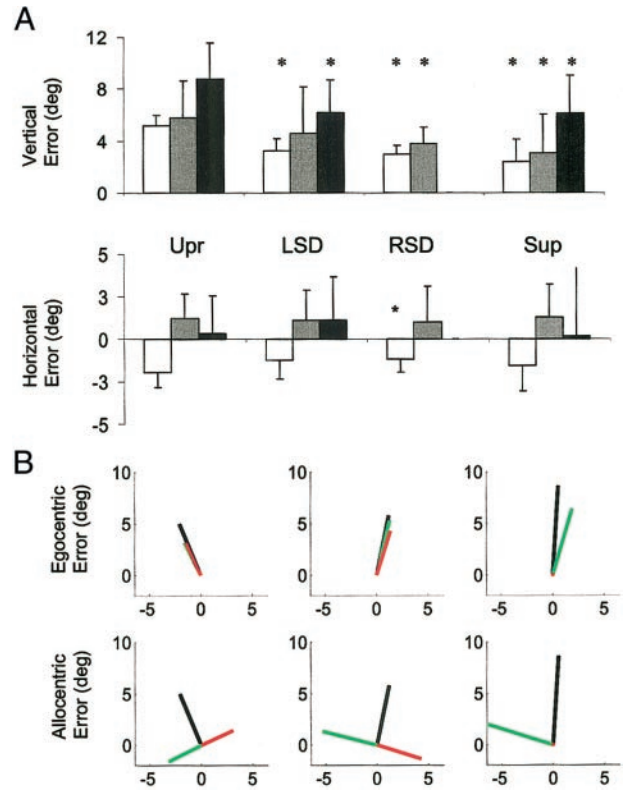
Mittelstaedt and Mittelstaedt 1996; Raphan and Sturm 1991), whereas the memory saccadic effect is egocentric. Second, the up/down asymmetry in the time constant and gain of the VOR and OKN, although present in upright orientations, increases in tilted body positions (Angelaki and Hess 1994; Clarke et al. 2000; Clement and Lathan 1991; Matsuo and Cohen 1984; Pettorossi et al. 1993; van den Berg and Collewijn 1988), whereas the saccadic asymmetry decreases in tilted body positions.

Findings from White et al. (1994) indicate that the up/down

TABLE 1. *Comparison of body- and gravity-coordinate vertical error means to upright*

Orientation Monkeys	Upright	Body Coordinates	Gravity Coordinates
A	5.19 ± 0.76	3.10 ± 0.81* (0.60)	0.00 ± 1.54* (0.00)
B	5.75 ± 2.85	4.19 ± 2.65 (0.73)	0.06 ± 2.18* (0.01)
C	8.73 ± 2.80	6.19 ± 2.50* (0.71)	1.12 ± 2.54* (0.13)
All	—	— (0.68)	— (0.05)

Comparison of asymmetry in egocentric and allocentric coordinates. *, means that were significantly (*P* < 0.05) different from the respective mean values in upright orientation. Ratio, (enclosed in parentheses) was computed as the mean error in ego- or allocentric coordinates divided by the respective mean in upright orientation (see METHODS). Positive values correspond to up and right.

asymmetry in memory-guided saccades does not derive from the memory system itself. In one of their tasks, monkeys initiated saccades as soon as the target light appeared, but the target was extinguished 200 ms later. As a result, the target was absent at the time that the saccade ended. The up/down asymmetry in the saccade persisted despite the fact that the memory period was extremely brief, leading these authors to suggest that memory per se was not responsible for the asymmetry.

If asymmetries in memory saccades derive neither from the vestibular nor the memory system, what is the cause of these errors? One possibility is that the asymmetry reflects a strategic bias rather than an error. Consider three other up/down asymmetries in the visual system. First, the highest density of rods in the retina is found around the superior vertical meridian (corresponding to lower visual field) (Curcio and Allen 1990; Packer et al. 1989; Wikler and Rakic 1990; Wikler et al. 1990). Second, because rods are optimized for scotopic vision, dim targets viewed against a dark background are appropriately placed in the lower visual field (Barash et al. 1998). Third, He, Cavanagh, and Intriligator (1996) have shown that attentional resolution is greater in the lower than the upper visual field.

All three of these asymmetries—higher rod density in the superior retina, a tendency to place dim targets in the lower visual field and better attentional resolution in the lower visual field—suggest that a target that has disappeared from sight against a dim or dark background would be more easily found if it lay below rather than above the current fixation point. This might explain why saccades to a target that has disappeared from view would land above the best estimate of that target's location. Because the eyes generally rotate with the head (ocular counter-roll is minimal at steady state) (Haslwanter et al. 1992), these asymmetries are head-fixed, that is, egocentric. Therefore the finding that the upward asymmetry for memory-guided saccades is egocentric rather than allocentric is consistent with our hypothesis of a strategic bias. When a target has disappeared from view, placing the fovea slightly above the best estimate of its location may optimize the speed with which the target can be reacquired.

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