Vestibular Contributions to Gaze Stability During Transient Forward and Backward Motion

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Hess, Bernhard J. M. and Dora E. Angelaki. Vestibular contributions to gaze stability during transient forward and backward motion. May 28, 2003. Neurophysiology 90: 1996–2004, 2003. First published May 28, 2003; 10.1152/jn.00302.2003. The accuracy with which the vestibular system anticipates and compensates for the visual consequences of translation during forward and backward movements was investigated with transient motion profiles in rhesus monkeys trained to fixate targets on an isovergence screen. Early during motion when visuomotor reflexes remain relatively ineffective and vestibular-driven mechanisms have an important role for controlling the movement of the eyes, a large asymmetry was observed for forward and backward heading directions. During forward motion, ocular velocity gains increased steeply and reached near unity gains as early as 40–50 ms after motion onset. In addition, instantaneous directional errors also remained <1° for forward headings. In contrast, backward motion was characterized by smaller vestibular gains and larger directional errors during the first 70 ms of the movement. To evaluate the accumulated retinal slip and vergence errors during the early epochs of motion when vestibular-driven mechanisms dominate gaze stability, the movement of a virtual fixation point defined by the intersection of the two gaze lines was quantitatively compared with the respective movement of the extinguished target in head coordinates. Both conjugate retinal slip and vergence errors were <0.2° during the first 70 ms of the movement, with forward motion conjugate errors typically being smaller as compared with backward motion directions. Thus vestibularly driven gaze stabilization mechanisms can effectively minimize conjugate retinal slip errors as well as keep binocular disparity errors low during the open loop interval of head movement.

INTRODUCTION

Translational disturbances of the head and body elicit short-latency vestibuloocular reflexes that help to stabilize gaze in space, known as the translational (or linear) vestibuloocular reflex (TVOR) (Angelaki and McHenry 1999; Busettoni et al. 1994; Gianna et al. 1997; McHenry and Angelaki 2000; Paige and Tomko 1991a,b; Schwarz and Miles 1991; Schwarz et al. 1989; Telford et al. 1997). Because no single eye movement could generally result in stabilization of the whole visual field, the TVOR is organized such that it cares to stabilize images on the fovea (Angelaki and Hess 2001; Angelaki et al. 2003). In addition, motion parallax dictates that the amplitude of the eye movements required to maintain fixation should be inversely proportional to viewing distance during translation. Thus simple geometrical calculations dictate that eye movements during translation should be scaled by a signal related to a neural estimate of the inverse of target distance as well as a signal proportional to a sinusoidal function of monocular eye position. Behavioral studies have indeed shown that vestibularly evoked eye movements are organized to reflect these geometrical requirements, not only during lateral and fore-aft motion (McHenry and Angelaki 2000; Paige and Tomko 1991b; Seidman et al. 1999) but also along in-between heading directions (Angelaki and Hess 2001; Tomko and Paige 1992).

Even though the TVOR has been shown to depend on viewing distance, this scaling is less than optimal (Schwarz and Miles 1991; Schwarz et al. 1989; Telford et al. 1997). As a result, gains are typically lower than unity and eye velocity is undercompensatory during near target viewing (Angelaki et al. 2000; Paige and Tomko 1991a,b; Schwarz and Miles 1991; Schwarz et al. 1989; Telford et al. 1997). These conclusions were typically drawn based on an analysis of velocity gains, that is, through a comparison of the instantaneous velocity of the eye relative to ideal velocity that would keep images stable on the retina. In addition, almost all previous studies have concentrated on small sinusoidal perturbations, requiring small eye movements to keep images stable on the fovea. Using such velocity analysis during high-frequency sinusoidal movements, it was found that although version (i.e., conjugate) velocity gains are strongly undercompensatory, vergence velocity was compensatory with gains near unity (Angelaki and Hess 2001; McHenry and Angelaki 2000). These results were interpreted to suggest that the TVOR’s goal is to minimize binocular disparities and optimize binocular coordination during movements along forward/backward headings. However, how these velocity gains relate to the limits of monocular visual acuity and binocular fusion during natural motions consisting of transient motion profiles and whether these suboptimal TVOR behaviors are still consistent with an efficient and effective visual acuity and stereocuity remain unknown. Finally, the role of the TVOR and the quality of gaze stability during transient forward motions, which are the most commonly experienced head and body movements in everyday life, have remained uncharacterized. It is possible, for example, that, through a selective evolutionary process, the visual consequences of forward movements are better anticipated and com-
compensated for by the TVOR. Because only small amplitude, high-frequency sinusoidal stimuli have been used so far, the role of vestibular signals in gaze stabilization for forward versus backward movements has remained uncharacterized. The present study aimed to investigate the vestibular contribution to binocular gaze stability during forward and backward movements using transient movement profiles. In particular, data analyses focused on the first 100 ms of motion during which translational visuomotor reflexes remain relatively ineffective (Busettini et al. 1996b, 1997; Miles 1993, 1998; Schwarz et al. 1989; Yang et al. 1999). To provide a quantitative assessment for the efficacy of the TVOR to compensate for the visual consequences of translation, we used not only an instantaneous velocity analysis but also a fixation position analysis that would allow us to calculate the accumulated error in retinal slip and disparity during the early epochs of motion when vestibular-driven mechanisms dominate gaze stability.

**METHODS**

**Animal preparation and training**

Three juvenile rhesus monkeys were implanted with a lightweight delrin head ring that was anchored to the skull by stainless steel screws and dual eye coils (Hess 1990) in each eye. Binocular three-dimensional eye movements were recorded inside a fiberglass cubic magnetic field frame of 16-in side length (CNC Engineering). Eye movements were calibrated using both daily fixation routines as well as preimplantation calibration values (Angelaki 1998; Hess et al. 1992). All animals were trained with juice rewards to fixate targets paired with an auditory cue for variable time periods (300–1,000 ms), then to maintain fixation after the target was turned off for as long as the auditory target was present (≥250 ms). Adequate fixation was determined on-line by comparing binocular horizontal and vertical eye positions with ideal target position windows of ±1°–2°. The monkey was assumed to be fixating the target binocularly when the right and left eyes fell within separate behavioral windows whose center was computed based on the geometrical relationship between target distance, interocular distance (2.8–3.2 cm), and target eccentricity (see APPENDIX). Animals were usually trained 5 days/wk with free access to water on the weekend. All animal surgeries and experimental protocols were in accordance to Institutional and National Institutes of Health guidelines.

**Experimental setup and protocols**

During vestibular testing, animals were rigidly secured to the inner axis of a three-dimensional rotator mounted on a linear sled (Acutronics). Animals were secured with lap and shoulder belts to a primate chair with their limbs loosely bound. In all experiments, the head was statically pitched 18° and the room was illuminated (through small red lights) such that the background lights were extinguished immediately before the onset of acceleration and remained off for the entire motion. Within a random time of 2–20 ms after the target was turned off, the stimulus profile commenced. Throughout the first ~250 ms of movement, the auditory tone remained on to provide guidance for the trained animals regarding the duration of the required fixation. Animals received a juice reward after completion of the movement. This reward was contingent on the initial fixation of the target, and no performance requirements were reinforced either during the movement or after the sled came to a stop. Intermingled runs where animals were required to fixate, but no sled movement occurred were also routinely used. In all experimental protocols, the direction of sled motion (positive, negative, and no motion) and the target illuminated were presented in a pseudorandom fashion. Intermingled between days of experimental sessions were additional training sessions that were identical to the pretraining sessions (with animals stationary) such that animals continued to be trained to fixate and maintain fixation under the auditory tone guidance for a minimum of 1 s after the target light was turned off.

Demodulated eye coil signals and the outputs of a three-axis accelerometer (rigidly attached to the fiberglass members to which the magnetic field coil assembly and the animal’s head were firmly attached) were anti-alias filtered (200 Hz, 6-pole low-pass Bessel). The signals were digitized at 833.3 Hz (Cambridge Electronics Design, model 1401 plus, 16-bit resolution) and stored for off-line analysis.

**Data analyses**

Binocular, three-dimensional (3-D) eye position was computed as rotation vectors (Haustein 1989) with straight ahead as the reference position. All three components of the calibrated eye position vectors were smoothed and differentiated with a Savitzky-Golay quadratic polynomial filter (Press et al. 1988; Savitzky and Golay 1964). Angular eye velocity was computed accordingly (Hepp 1990) and expressed as vector components in a head-fixed, right-handed coordinate system, as defined in the 18° nose-down position (typical position of all animals during experiments). Torsional, vertical, and horizontal eye position and velocity were the components of the eye position and eye velocity vectors along the naso-occipital, interaural and vertical head axes, respectively. Positive directions were clockwise (as viewed from the animal, i.e., rotation of the upper pole of the eye toward the right ear), downward, and leftward for the torsional, vertical, and horizontal components, respectively.

An automated analysis routine displayed each experimental run sequentially and allowed the experimenter to select only saccade-free runs to be included for grand averages constructed in each animal for each heading direction and each target on the isovergence screen. Horizontal left and right eye position and velocity at different times after motion onset was then calculated from these grand-averages (5 heading directions, backward/forward motion and 13 different targets positioned at 2.5° intervals along the horizontal isovergence screen) and used for subsequent analyses. In this study, the analyses focused on horizontal eye position (θ_r, θ_l) and velocity (θ_\dot{r}, θ_\dot{l}) because the fixation targets were all in the horizontal plane, i.e., vertical eye...
position during fixation of these targets was close to zero. Head velocity and position was computed by integrating the output of a 3-D linear accelerometer that was mounted close to the animal’s head using the trapezoidal rule. Positive linear acceleration and velocity was defined to be rightward and backward for the y and x components of the linear accelerometer output, respectively.

INSTANTANEOUS EYE VELOCITY ANALYSIS. The instantaneous velocity gain analysis was similar to that previously performed for sinusoidal motion stimuli (Angelaki and Hess 2001). As presented in detail in the APPENDIX, the time-varying horizontal eye velocity of each eye \( \dot{\theta}_e(t) \) can be computed as a function of head velocity, \( \mathbf{v}_h \), the respective eye-to-target distance \( d_{eT}(t) \) (right eye to fixation point distance; \( d_{lT}(t) \) (left eye to fixation point distance) and the sine of the difference between the gaze angle (\( \theta_r \) or \( \theta_l \)) and heading direction (\( \alpha_t \)), as follows (Fig. 1A)

\[
\dot{\theta}_r = \frac{\mathbf{v}_h}{d_{eT}} \sin(\theta - \alpha_t) \quad \text{and} \quad \dot{\theta}_l = \frac{\mathbf{v}_h}{d_{lT}} \sin(\theta - \alpha_t)
\]

Using the nonlinear least-squares algorithm of Levenberg-Marquardt (Mathlab, MathWorks), Eq. 1 was fitted to the right and left eye-velocity data, sampled at different times after motion onset, and plotted as a function of instantaneous eye position (\( \theta_r \) or \( \theta_l \)). Thus parameters \( \mathbf{v}_h \) and \( \alpha_t \) representing the amplitude and heading direction of a virtual fixation point reconstructed from the motions of both eyes, were computed at different times during the motion profile, separately for each heading direction (but simultaneously for all 13 targets). Instantaneous velocity gain was then calculated as the ratio of the computed value of \( \mathbf{v}_h \) over the actual instantaneous velocity of the head. Similarly, the directional error of instantaneous velocity was calculated as the absolute difference between the computed value for \( \alpha_t \) and the actual heading direction.

BINOCULAR EYE-POSITION ANALYSIS. The second set of analyses was based on the actual displacement of the virtual fixation point as a function of time during motion. Thus as explained in detail in the APPENDIX, we computed the time-dependent path of the virtual fixation point \( \mathbf{y}_e(t) = [x_{eT}(t), y_{eT}(t)] \) for each of the 13 fixations and each of the \( 5 \times 2 \) heading directions (= 130 different stimulus configurations). Similar to the eye-velocity analyses, these computations were done on average response profiles that were obtained from five or more single trials in each stimulus configuration. We assumed that at \( t = 0 \), the target and fixation point coincided \( \mathbf{T} = \mathbf{F} \) at \( t = 0 \); Fig. 1B), but that the virtual fixation point defined by the intersection of the two gaze lines traced a path, \( \mathbf{F}(t) \), that in general differed from the relative target motion, \( \mathbf{T}(t) \). We then computed the angular position error of each eye (\( \delta_r; \mathbf{F} \); Fig. 1B) as the difference between actual and ideal eye position. From these values, we also computed the conjugate (version) and disconjugate (vergence) position errors as \( (\delta_r + \delta_l)/2 \) and \( (\delta_r - \delta_l) \), respectively. We also calculated the conjugate and vergence velocity errors by taking the time derivatives using Savitzky-Golay quadratic polynomial filters with a seven-point wide moving smoothing window. The reported conjugate position and velocity errors were calculated as the absolute value of \( (\delta_r + \delta_l)/2 \) and \( (\delta_r - \delta_l)/2 \). Vergence position and velocity errors were positive, if the fixation point, \( \mathbf{F}(t) \), moved closer to the animal than the extinguished target, \( \mathbf{T}(t) \). Accordingly, during forward motion, positive position errors would correspond to larger than expected increases in vergence angle. In contrast, during backward motion, positive position errors corresponded to smaller than expected decreases in vergence angle. These parameters were used as a direct measure of the ability of the vestibular system to anticipate the visual consequences of translation as a function of time throughout the first 100 ms of motion.

All statistical comparisons were based on analyses of variance with repeated measures.

RESULTS

Geometrical dependence of horizontal eye velocity on gaze and heading directions

Stabilization of a target on the fovea during translational disturbances of the head depends on both the direction of linear motion and the relative location of the target. The influence of these two parameters on the TVOR is illustrated in Fig. 2 for three different fixation targets and five different headings of forward translation. To keep the effect of vergence on the VOR constant, all targets were arranged on an isovergence screen such that fixations subtended a constant vergence angle of \( \sim 8^\circ \)–\( 9^\circ \) (see METHODS). When the animal was translated in a direction that was nearly parallel to gaze direction, only a small eye movement needed to be elicited to keep gaze on the previously lit target during motion. For example, during straight-ahead (0°) motion, the smallest eye velocity was observed for the central (green) target. In contrast, during forward motion along a heading 15° to the left of straight-ahead (15°L), the smallest eye velocity was observed for the leftward (red) target. Similarly, during forward motion along a heading 15° to the right of straight-ahead (15°R), the smallest eye velocity was observed for the rightward (blue) target.

The more eccentric the gaze direction was relative to head-
ing direction, the larger was the elicited eye movement. For example, forward motion along the 30° heading elicited a rightward (negative) rotation of both eyes with angular velocities that increased for the rightward-located targets (Fig. 2).

The opposite was true for heading directions to the right of straight ahead, where the largest eye movement was seen for leftward-located targets. To study these dependencies of eye velocity on gaze and heading directions, we "sampled" the instantaneous eye velocity at different times (e.g., 30, 50, and 70 ms shown in Fig. 2) after motion onset. We then computed at those sampled times how well (in terms of both instantaneous velocity and displacement) the movement of a virtual fixation point defined by the intersection of the two gaze lines in the horizontal plane anticipated and followed the relative motion of the extinguished target during translation. In the presentation that follows, we will first present the results based on the instantaneous velocity analysis, followed by those when the actual fixation point trajectories were considered.

Instantaneous velocity gains and directional errors

The dependence of horizontal eye velocity on gaze and heading directions is illustrated in Fig. 3, by plotting eye velocity 50 ms after motion onset for each of the 13 fixation targets as a function of the corresponding eye position for the five different heading directions (30°L, 15°L, 0°, 15°R, 30°R). The graphs show that ocular velocity systematically increased as a function of horizontal eye position for each eye. Furthermore, there was a horizontal equilibrium position for each eye, i.e., a position for which head translation induced no eye movement (i.e., zero velocity). This equilibrium position depended in a systematic way on heading direction. For example, for heading straight ahead the equilibrium position was close to straight-ahead for each eye (Fig. 3, short vertical dotted lines for 0° heading). In contrast, during leftward heading, the equilibrium positions shifted leftward (positive eye position values). Similarly, during heading to the right, the equilibrium positions shifted rightward (negative) eye positions. Such a dependence on heading direction is a direct consequence of Eq. 1.

To quantify the efficacy of the vestibular-driven instantaneous eye velocity in anticipating the visual consequences of relative target motion as a function of time during the imposed transient motion profiles, we computed the velocity amplitude ($v_t$) and direction ($\alpha_t$) of the movement of a virtual fixation point defined by the intersection of the two gaze directions in Fig. 2. Eye- and head-movement profiles during forward motion along 5 different heading directions. Panels from left to right show averages of horizontal eye and head velocity traces during heading 30° to the left (30°L), 15° to the left (15°L), straight ahead (0°), 15° to the right (15°R), and 30° to the right (30°R) while fixating 1 of 3 targets −15° to the left (red traces), straight ahead (green traces), or 15° to the right (blue traces). Center: the 5 different heading directions and the three fixation targets schematically.

Data represent averages over 5 or more trials. Solid/dashed color traces denote right/left horizontal eye velocity, respectively. Black traces illustrate head velocity (vel) and head acceleration (acc). Dashed vertical lines indicate 30, 50, and 70 ms after motion onset.
the horizontal plane (see METHODS and APPENDIX). Accordingly, parameters \( v_F \) and \( \alpha_F \) were calculated by fitting Eq. 1 to the eye-velocity data simultaneously for all 13 fixation points but separately for each of the 5 \( \times \) 2 heading directions. This analysis was performed at different times after motion onset and separately for right and left eye velocity (Fig. 3, gray and black solid lines, respectively). Ideally, if the animal maintained binocular fixation on the extinguished target during motion, parameters \( v_F \) and \( \alpha_F \) would be identical to the velocity and heading direction of the imposed head motion. Thus an instantaneous velocity gain was defined as the ratio of the computed versus actual velocity. Similarly, a velocity directional error was defined as the absolute value of the difference between the computed heading direction of the virtual fixation point and the actual heading direction of the animal. Average (\( \pm \) SD) values of the instantaneous velocity gains and directional errors measured at three different times (30, 50, and 70 ms) after motion onset have been plotted in Fig. 4 (\( \circ \), \( \triangledown \), and \( \Delta \), respectively). As parameters were independent on whether right or left eye-velocity data were used for the computation \( [v_F : F(1,40) = 0.2; \alpha_F : F(1,40) = 3.1, P > 0.05] \), values have been averaged together.

Forward directions of motion were characterized by larger instantaneous velocity gains than backward movements \( [v_F : F(1,50) = 70.8, P < 0.05] \). Backward motions were also typically characterized by larger directional errors than forward motions, particularly so early into the motion and for oblique headings \( [\alpha_F : F(1,50) = 10.8, P < 0.05] \). Only at 70 ms after motion onset were the directional errors for backward motions as small as those during forward movements (\( \sim 5^\circ \)). The time dependence of instantaneous velocity gain and directional errors is better illustrated in Fig. 5, A–C, which plots average gains and directional errors for all heading directions in each animal as a function of time after stimulus onset. A consistent and significant asymmetry in velocity gains during forward and backward motions was observed early into the motion.
Trajectories of fixation point and position error analyses

The instantaneous eye velocity analyses, as typically used in VOR studies, are important to compute the instantaneous performance of the reflex. We were in addition interested in characterizing the position and velocity errors that accumulate as a function of time during motion. Thus for each heading direction and target position, we calculated the trajectory followed by the virtual fixation point (defined by the intersection of the 2 gaze lines) during the first 100 ms of motion. The two-dimensional (2-D) spatial trajectories for all 13 targets (aligned at the beginning of motion and plotted only for the first 70 ms) have been summarized for the five heading directions separately for forward and backward headings in Fig. 6, A and B, respectively. Typically, the fixation point underestimated the equivalent target trajectory as illustrated by comparing the mean fixation point trajectory with that of the target for each heading (Fig. 6, compare thick black with gray lines and circles). As expected from the lower velocity gains reported in the instantaneous velocity analyses, this underestimation was largest for backward movements (Fig. 6B). In addition, early into the motion there was often a small movement of the fixation point in the opposite direction from that of the target. During backward 30°R motion, for example, an initial curvature in the trajectory was observed, as the virtual fixation point first moved in the opposite direction from that expected based on the relative target motion. In two of the three animals, this initial movement in the wrong direction was typically small and was quickly compensated by an eye movement, and thus a fixation point trajectory, in the correct, compensatory direction. The third animal, however, exhibited large initial anticompen- satory movements.

From these trajectories we computed the absolute magnitude of the conjugate retinal slip (version position and velocity error) as well as the corresponding disconjugate (vergence position and velocity) error at different times during the first 100 ms of motion. Average error values have been presented as a function of time in Fig. 7, A and B. The corresponding velocity errors have been illustrated in Fig. 7, C and D. Conjugate position errors 70 ms after motion onset averaged 0.10 ± 0.06 and 0.14 ± 0.08° for forward and backward motion, respectively. Corresponding velocity errors were 3.2 ± 1.9 and 4.3 ± 2.4°/s. Both position and velocity errors were larger during backward than forward motions [\(F(1,4) = 18 \text{ and } 27, P < 0.01\)].

Vergence errors were negative for forward motion and positive for backward motion. Thus during forward motion, vergence angle increased less than that required for binocular gaze stability. During backward motion, vergence angle did not decrease quickly enough for optimal binocular fixation on the target. Vergence position errors 70 ms after motion onset averaged −0.09 ± 0.07 and 0.07 ± 0.04° for forward and backward motions, respectively. Vergence velocity errors 70 ms after motion onset averaged −1.9 ± 1.9 and 2.3 ± 1.6°/s for forward and backward motions, respectively. The magnitude of vergence position and velocity errors were not significantly different for forward and backward directions [\(F(1,4) = 0.4 \text{ and } 0.01, P > 0.05\)].

DISCUSSION

The effectiveness of the VOR system to anticipate and compensate for the visual consequences of translation during forward and backward movements was for the first time investigated here using transient movement profiles in rhesus monkeys trained to fixate near targets. The present analyses, in particular, focused on the first 100 ms of motion during which visuomotor reflexes remain relatively ineffective and vestibular-driven mechanisms have an important role for controlling the movement of the eyes. We used both an instantaneous velocity gain and a fixation trajectory analyses that allow calculation of the accumulated error in retinal slip and disparate. Results can be summarized as follows: first, the retinal slip and vergence position errors that were accumulated during the open-loop portion of the movement were small, in the range of 0.1° (position) and 2°/s (velocity) 70 ms after motion onset. Second, there was an initial gain asymmetry during forward and backward headings. Specifically, instantaneous velocity gains during forward motion increased steeply and reached near unity gain values as early as 40–50 ms after motion onset. Instantaneous directional errors also remained <10° for forward headings. In contrast, vestibular gains during

![Image](http://jn.physiology.org/content/images/090/i05a0211.jpg)

**Fig. 6.** Summary of fixation point spatial trajectories in 1 animal (same data as those of Fig. 1 and 2) during forward motion (A) and backward motion (B). Colored traces illustrate average fixation point trajectories (0–70 ms) for each of the 13 targets and the five heading directions (as indicated by the monkey sketches and arrows). For easier comparison across different targets, all 13 target trajectories were aligned at time = 0 ms for each heading direction. The color scale from blue to red symbolizes targets from right to left. Solid gray lines and circles, the respective trajectories of the target motion relative to the head; black lines and circles, the mean fixation point trajectory for all 13 targets.
stimuli using both sinusoidal and transient movements have studied binocular eye movements during left/right motion stabilization during forward/backward motions, several studies in contrast to the relatively paucity of work addressing ocular cillations, stimuli that typically result in small eye excursions and Tomko 1991b; Seidman et al. 1999). To our knowledge (Angelaki and Hess 2001; McHenry and Angelaki 2000; Paige and Tomko 1991b; Seidman et al. 1999) or depth and binocular disparity cues (Busettini et al. 1994, 1996a,b). However, these visually driven gaze stabilization mechanisms have latencies in the range of 50–80 ms, leaving the vestibular system as the sole sensory information source for gaze stabilization in the first <70 ms of motion.

Relationship to previous studies

Only a few studies have characterized the vestibular contribution to binocular gaze stability during forward and backward translations. Most studies used high-frequency sinusoidal oscillations, stimuli that typically result in small eye excursions (Angelaki and Hess 2001; McHenry and Angelaki 2000; Paige and Tomko 1991b; Seidman et al. 1999). To our knowledge only one study to date utilized more natural, transient forward and backward motion stimuli, although analyses focused mainly on response latencies (Angelaki and McHenry 1999). In contrast to the relatively paucity of work addressing ocular stabilization during forward/backward motions, several studies have studied binocular eye movements during left/right motion stimuli using both sinusoidal and transient profiles. During lateral motion stimuli, numerous investigations have shown that TVOR gains are strongly undercompensatory during near target viewing (Angelaki and McHenry 1999; Angelaki 2002; Busettini et al. 1994; Crane et al. 2003; Gianna et al. 1997; McHenry and Angelaki 2000; Paige and Tomko 1991b; Ramat and Zee 2002; Ramat et al. 2001; Schwarz and Miles 1991; Schwarz et al. 1989; Telford et al. 1997; Zhou et al. 2002). In contrast, high-frequency sinusoidal responses during different heading directions exhibited vergence velocity gains that were typically higher than the corresponding version velocity gains (Angelaki and Hess 2001; McHenry and Angelaki 2000).

Transient VOR analysis presents several advantages over the more commonly used sinusoidal stimuli. For example, transient movement profiles allow the quantification of the adequacy of gaze stabilization during the open-loop interval when visual stabilization mechanisms are ineffective. Specifically during translation, visual stabilization mechanisms arise from relatively low-level preattentive cortical processing that sense the observer’s motion by decoding either the pattern of optic flow (Busettini et al. 1997; Miles 1993, 1998; Miles and Busettini 1992; Miles et al. 1991; Schwarz et al. 1989; Yang et al. 1999) or depth and binocular disparity cues (Busettini et al. 1994, 1996a,b). However, these visually driven gaze stabilization mechanisms have latencies in the range of 50–80 ms, leaving the vestibular system as the sole sensory information source for gaze stabilization in the first <70 ms of motion.

Conjugate and vergence errors during transient forward/backward motions

The main goal of the present study was to measure the accuracy of the vestibularly-driven gaze stability during large transient displacements in an attempt to determine if the less than optimal TVOR gains would introduce errors that would compromise visual acuity and binocular fusion. For this purpose, we quantified responses during the first 100 ms of motion in complete darkness in animals trained to maintain vergence on near isovergence targets. We found that 70 ms into the motion, position errors remain <0.2° and velocity errors <4–5°/s, values that would be close to the range required for maintaining good visual acuity. Specifically, Ludvigh (1949) and Brown (1972) reported that good acuity is maintained with a position error of 2–2.5°, values larger than the maximum conjugate position errors present during the large transient stimuli used here. Other studies have demonstrated that retinal slip velocities lower than ~2–3°/s do not degrade visual acuity (Demer and Amjadi 1993; Demer et al. 1994; Murphy 1978; Steinman et al. 1973, 1982; Westheimer and McKee 1975).

Whereas monocular and conjugate retinal slip would be within the limits of dynamic visual acuity, the vergence errors observed seem to be incompatible with the very low threshold observed in stereoscopic tests. Stereacuity in standard stereoscopic tests is based on judgements of a set of relative distances and have been reported to yield sensitivities typically in the order of 10 s of arc (Ogle 1967; Sarmiento 1975). In our experiments, we measured binocular position errors that would be more analogous to the absolute disparity of a single imaginary target $T$ (if it was visible). Disparity values observed under such conditions cannot be compared with those obtained in usual tests of stereacuity because such tests rely on stimulus configurations that contain relative disparities. Stereacuity thresholds for simultaneously presented line pair stereograms raise by about an order of magnitude if the lines are presented successively at different absolute disparities (Foley 1976; Westheimer 1979). Steinman and Collewijn (1980) have also shown that relative binocular image motion can be on the order of 2°/s and still maintain clear and stable visual perception during natural head movements. Further studies of the effects of instabilities of gaze and vergence have shown that stereofusion and stereacuity is preserved in the presence of fast and large changes in vergence (Patterson and Fox 1984; Steinman et al. 1985; see Collewijn et al. 1991 for a review). Thus the vergence position and velocity errors reported here suggest that vestibular mechanisms are capable to keep absolute disparities to a minimum, thus allowing for the slower visual mechanisms to take over and to fine tune convergence.
Asymmetries between forward and backward motions

The significant difference in instantaneous velocity gains between forward and backward motion might be related to a functional adaptation of the vestibular system to the most commonly experienced forward movements. This asymmetry shows mostly in the monocular and conjugate response gains but not in vergence position or velocity errors. To our knowledge, such a difference in gain during forward and backward headings has never been reported previously. Largely asymmetric responses to different motion directions have been reported in the majority of translation-sensitive vestibular nuclei neurons (Musallam and Tomlinson 2002). How and why these asymmetries are introduced remains unknown. It is clear that forward motion has a quite different biological meaning than backward motion. Under normal visual conditions, during translational motion it is most important to avoid blur of the retinal image to facilitate evaluation of predictive information about the distance to a target or object. During backward motion, this information is less relevant because there is no visible threat to bump into an object. This difference could explain why the initial gain is larger during forward than during backward motion. Despite these asymmetries and a nonideal TVOR gain, the present results demonstrate that both monocular and conjugate vestibular-driven mechanisms exist that help to stabilize the eyes during the open-loop interval of natural head movements and facilitate further stabilization by slower visual mechanisms.

APPENDIX

In this section, we briefly summarize the steps necessary to compute the motion parameters of the virtual fixation point defined by the intersection of the gaze directions of the two eyes as a function of horizontal eye position (θ₁, θ₂), the interocular distance, Δ, as well as the velocity (v = v_{head}) and direction (α) of the animal’s displacement. Equations will be presented in an orthogonal Cartesian coordinate system, with the x axis straight ahead relative to the right eye and the y axis passing through the rotation centers of the right and the left eye (Fig. 1). Computing the fixation point coordinates from binocular eye movements

Let x_{RF} and y_{RF} be the x-y coordinates of the fixation point (F) before motion onset, as the animal fixated a target on a isorevergence screen. The tangent of eye position can thus be expressed as a function of x_{RF} and y_{RF}, as follows (Fig. 1A)

\[
\tan \theta_{RF} = \frac{y_{RF}}{x_{RF}} \quad \text{and} \quad \tan \theta_{RF} = \frac{y_{RF} - \Delta_{RF}}{x_{RF}} \quad (A1)
\]

Using these relations, the coordinates of the fixation point (x_{RF}, y_{RF}) can be expressed as

\[
x_{RF} = \frac{\Delta_{RF}}{\tan \theta_{RF} - \tan \theta_{RF}} \quad \text{and} \quad y_{RF} = \frac{\Delta_{RF} \tan \theta_{RF}}{\tan \theta_{RF} - \tan \theta_{RF}} \quad (A2)
\]

From the coordinates of the fixation point we computed the right- and left-eye-to-target distance (d_{RF}, d_{LF}) as follows

\[
d_{RF} = \sqrt{x_{RF}^2 + y_{RF}^2} \quad \text{and} \quad d_{LF} = \sqrt{x_{RF}^2 + (y_{RF} - \Delta_{RF})^2} \quad (A3)
\]

Equation A3 can be expressed as functions of eye position (θ₁, θ₂) and the interocular distance (Δ) using Eq. A2.

Estimation of heading velocity and direction from fixations

As the subject starts moving with heading velocity (v) and direction (α), the motion of the target in head coordinates can be expressed as

\[
x_{F}(t) = x_{RF} + v \sin(\alpha) \quad \text{and} \quad y_{F}(t) = y_{RF} + v \cos(\alpha) \quad (A4)
\]

At motion onset we have: x_{F}(t = 0) = x_{RF}, y_{F}(t = 0) = y_{RF}, and x_{F}(t = 0) = v \sin(\alpha), y_{F}(t = 0) = v \cos(\alpha). To derive a relationship for the changes in horizontal eye movements that are required to maintain fixation, we calculate first the time derivative of horizontal eye position, d/dt(θ₁) = d/dt[tan⁻¹(y_{F}/x_{F})], as a function of the (premotion) fixation point using the relations (Eqs. A1, A4). Specifically, for the right eye we obtain from the right-eye-to-target distance, d_{RF} (Eq. A3), and the relations sin θ_{RF} = y_{RF}/d_{RF} and cos θ_{RF} = x_{RF}/d_{RF}:

\[
\dot{\theta}_{RF} = \frac{\dot{y}_{RF} x_{RF} + \dot{x}_{RF} y_{RF} - y_{RF} \cos(\theta_{RF}) + x_{RF} \sin(\theta_{RF})}{d_{RF}} \quad (A5)
\]

When the animal tries to keep fixation (i.e., T = F), the instantaneous velocity and direction of the fixation point at motion onset is: v_{RF} = \sqrt{x_{RF}^2 + y_{RF}^2}, and α_{RF} = tan⁻¹(y_{RF}/x_{RF}). Introducing these relations into Eq. A5, we obtain (Θ₁ can be derived analogously to θ₁)

\[
\dot{\theta}_{L} = \frac{\dot{y}_{LF} \sin(\theta_{L} - \alpha_{L}) - \dot{y}_{LF}}{d_{LF}} \quad \text{and} \quad \dot{\theta}_{R} = \frac{\dot{y}_{RF} \sin(\theta_{L} - \alpha_{R})}{d_{RF}} \quad (A6)
\]

Equations A2–A6 describe implicitly the velocity (v_{RF}) and direction (α_{RF}) of the fixation point as a function of right and left eye position (θ₁, θ₂) and either the right or left eye velocity (\dot{θ}_L, \dot{θ}_R) at motion onset. Later into motion, they describe the motion of the virtual fixation point in space and can be used to compute the animal’s estimate of heading velocity and direction under the assumption that the animal tried to maintain fixation during motion.

Error analysis of the virtual fixation point during translation

The spatial deviation of the virtual fixation point from the target was estimated from the fixation-to-target point error vector, F̃, that subtended the angles δ̃_L and δ̃_R, as viewed from the right and left eye (Fig. 1B). Based on this vector F̃, two errors, corresponding to version and vergence, were computed. For this, we define the sign of the angle δ̃_L (δ̃_R) as positive if the cross product of the radius vectors from the center of the right (left) eye to the virtual fixation point (RF̃, LF̃) on the one hand and to the target (RT, LT) on the other hand is positive (Fig. 1B). The version error is defined as δ_{\gamma_{\text{fix}}} = (δ_{\gamma_{\text{f}}} + c)/2 whereas the vergence error was calculated as δ_{\gamma_{\text{ver}}} = c/2 with c = ±1. The sign (c) of this error was chosen to be positive when the plane of the virtual fixation point was closer to the animal than the target plane (Fig. 1B). Thus during both forward and backward motion a positive vergence error corresponded to a relative excess in vergence.

DISCLOSURES

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REFERENCES