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Human Gaze Stabilization During Natural Activities: Translation, Rotation, Magnification, and Target Distance Effects

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Crane, Benjamin T. and Joseph L. Demer. Human gaze stabilization during natural activities: translation, rotation, magnification, and target distance effects. *J. Neurophysiol.* 78: 2129–2144, 1997. Stability of images on the retina was determined in 14 normal humans in response to rotational and translational perturbations during self-generated pitch and yaw, standing, walking, and running on a treadmill. The effects on image stability of target distance, vision, and spectacle magnification were examined. During locomotion the horizontal and vertical velocity of images on the retina was $<4^\circ/\text{s}$ for a visible target located beyond 4 m. Image velocity significantly increased to $>4^\circ/\text{s}$ during self-generated motion. For all conditions of standing and locomotion, angular vestibulo-ocular reflex (AVOR) gain was less than unity and varied significantly by activity, by target distance, and among subjects. There was no significant correlation ($P > 0.05$) between AVOR gain and image stability during standing and walking despite significant variation among subjects. This lack of correlation is likely due to translation of the orbit. The degree of orbital translation and rotation varied significantly with activity and viewing condition in a manner suggesting an active role in gaze stabilization. Orbital translation was consistently antiphase with rotation at predominant frequencies <4 Hz. When orbital translation was neglected in computing gaze, computed image velocities increased. The compensatory effect of orbital translation allows gaze stabilization despite subunity AVOR gain during natural activities. Orbital translation decreased during close target viewing, whereas orbital rotation decreased while wearing telescopic spectacles. As the earth fixed target was moved closer, image velocity on the retina significantly increased ($P < 0.05$) for all activities except standing. Latency of the AVOR increased slightly with decreasing target distance but remained <10 ms for even the closest target. This latency was similar in darkness or light, indicating that the visual pursuit tracking is probably not important in gaze stabilization. Trials with a distant target were repeated while subjects wore telescopic spectacles that magnified vision by 1.9 or 4 times. Gain of the AVOR was enhanced by magnified vision during all activities, but always to a value less than spectacle magnification. Gain enhancement was greatest during self-generated sinusoidal motion at 0.8 Hz and was less during standing, walking, and running. Image slip velocity on the retina increased with increasing magnification. During natural activities, slip velocity with telescopes increased most during running and least during standing. Latency of the visually enhanced AVOR significantly increased with magnification ($P < 0.05$), probably reflecting a contribution of the visual pursuit system. The oculomotor estimate of target distance was inferred by measuring binocular convergence, as well as from monocular parallax during head translation. In darkness, target distance estimates obtained by both techniques were less accurate than in light, consistently overestimating for near and underestimating for far targets.

INTRODUCTION

The ability of the vestibulo-ocular reflex (VOR) to stabilize images frequently has been tested by having subjects

either voluntarily move their heads in a steady state sinusoidal pattern or by passively rotating the subjects in such a pattern. Significant retinal image motion occurs in humans during self-generated head movement (Steinman and Collewyn 1980). Evidence suggests that human visual acuity is tolerant of retinal image motion of $\leq 2\text{--}4^\circ/\text{s}$ (Barnes and Smith 1981; Demer et al. 1994) although during vigorous voluntary head rotations, image slip can be as much as $70^\circ/\text{s}$ (Grossman et al. 1989). Retinal slip computed from angular measurements during unconstrained, natural movements was found by Grossman et al. (1989) to be $<4^\circ/\text{s}$ during standing and walking and $\sim 9^\circ/\text{s}$ during running. However, Grossman et al. did not consider eye translation because the target was at optical infinity.

The traditional measure of VOR function has been gain, typically defined as the angular velocity of the eye relative to that of the head. However, in many experimental paradigms as well as during natural movements, ocular translation occurs simultaneously with head rotation. This causes ideal VOR gain to vary with the axis of rotation and viewing distance (Crane et al. 1997; Snyder and King 1992; Takeda et al. 1991; Viirre et al. 1986). Because significant ocular translation occurs during locomotion (Bloomberg et al. 1992; Demer and Viirre 1996; Pozzo et al. 1990), the VOR probably must correct for both translational and rotational movement.

Target distance has been shown to significantly influence the VOR. This has been demonstrated with a purely linear stimulus in both animals (Paige and Tomko 1991; Schwarz et al. 1989) and humans (Bronstein and Gresty 1988; Paige 1991), as well as for combined linear and angular stimulation during rotation about an eccentric axis (Crane et al. 1997; Snyder and King 1992; Viirre et al. 1986). Target distance is thought to influence the linear (otolithic) component of the VOR, such that the response is approximately inversely proportional to target distance (Crane et al. 1997; Paige 1989; Viirre et al. 1986). However, some evidence suggests that, additionally, the angular (semicircular canal) component of the VOR (AVOR) may depend on target distance (Snyder and King 1992). The enhancement of AVOR gain seen with near targets does not depend directly on visual tracking (Crane et al. 1997; McCrea et al. 1996; Viirre and Demer 1996). The binocular vergence angle has been shown to be correlated strongly with the linear VOR response under some conditions (Paige 1991), but not in all subjects (Schwarz and Miles 1991) and not during voluntary convergence (Shirado et al. 1997). In addition to vergence, other cues such as accommodation and the size and context of a visual target, have been suggested as influential on the linear

VOR (Busettini et al. 1994). The factors that determine the oculomotor response to target distance are controversial.

The behavior of the VOR depends also on the mode in which head movement was generated. Single-unit recordings in monkeys have shown that the firing rate of second-order vestibular neurons is dependent on the behavioral context in which head movements are made (Boyle et al. 1996). Boyle et al. found that externally applied head or whole-body perturbations were encoded by these neurons but self-generated movements were not. During rotation of the body beneath the fixed head, no significant vestibular response was observed, indicating a lack of contribution from neck proprioception. Motor efference copy and other factors depending on volitional state have a large role in the second-order vestibular unit response during self-generated head movement (McCrea et al. 1996). This physiology is supported by neuroanatomic studies showing that second-order vestibular neurons receive inputs from the vestibulocerebellum, fastigial nucleus, reticular formation, and cervical spinal cord (Büttner-Ennever 1992) in addition to input from the vestibular nerve. Head movements occurring during standing, walking, and running do not squarely fall into either the realm of self-generated movements or passive movements. It is therefore difficult to draw conclusions about VOR function during locomotion based on studies made of the VOR during purely active or passive head movements.

How retinal image stability is maintained during demanding conditions such as running is not well established. Demer and Viirre (1996) found that during locomotion, the human head translates up as it rotates down and vice versa. They found a similar relationship in the horizontal plane. It also has been observed that the ratio of head translation to rotation decreases when visual targets are moved closer and that vertical reversing prisms change this ratio (Bloomberg et al. 1992). These findings suggest that head translation may play an active role in gaze stabilization rather than being a simple mechanical effect of the linkage between the head and the body. Although this pattern of head motion would seem to stabilize gaze, image motion on the retina has yet to be quantitatively examined. Only after translation is taken into account can it be known how adequately images are stabilized during locomotion.

The effect of visual magnification by telescopic spectacles on the visually enhanced AVOR (VVOR) has been characterized previously during locomotion (Demer and Viirre 1996) and during sinusoidal head motion (Demer et al. 1990). Although VVOR gain increased with magnification under these conditions, the degree of gain enhancement was inadequate to stabilize images on the retina. The effect of translation on retinal image stability with spectacle magnifiers has not previously been studied.

METHODS

Subjects

Fourteen normal paid volunteers gave written consent to participate in this study according to a protocol approved by the Human Subject Protection Committee in conformity with the tenets of the Declaration of Helsinki. There were five women and nine men of average age 27 ± 7 yr (mean $\pm$ SD, range 19–44). Subjects underwent ophthalmologic examination to verify that they were

free of disease and would be able to converge and focus the targets clearly. Each subject stood on a motorized treadmill (1.1 kW) throughout the experiment, although the tread was moving only during selected trials. Subjects were monitored via closed-circuit television and intercom.

Apparatus

Angular eye and head positions were measured with magnetic search coils as employed by other investigators (Grossman and Leigh 1990; Grossman et al. 1989). Reference magnetic fields were generated by three pairs of solenoid coils, each 2 m in diameter, and arranged to form the sides of a cube (C-N-C Engineering, Seattle, WA). This configuration placed the center of the cube near eye level for subjects standing in the center. The two vertically oriented coil pairs were driven by 120 kHz sinusoidal currents in phase quadrature (Collewijn et al. 1975). The horizontally oriented coil pair was driven by a 60 kHz sinusoidal current (Robinson 1963). Dual-winding scleral magnetic search coil annuli were placed on each eye in six subjects, and on one eye only in eight subjects, to measure three-dimensional angular position of the eyes in space. Three-dimensional angular head position was measured with a pair of orthogonal search coils mounted on a head band. The ocular coils were embedded in an annular suction contact lens (Skalar Medical, Delft, The Netherlands) that adhered to the eye under topical anesthesia with proparacaine 0.5% (Collewijn et al. 1975). Search coils were connected to external detectors (C-N-C Engineering). Horizontal positions were demodulated by a phase angle method that is linear over a range of $\pm 100^\circ$.

The search coil arrangement employed here has been reported to have a translational artifact of $<0.03^\circ/\text{cm}$ within a 30-cm central cube (Grossman and Leigh 1990) within which the subject's head was located throughout the experiment. The homogeneity of the reference magnetic field was verified directly. Gain calibration curves were constant to $\pm 5\%$ within a central cube 58 cm on each side and $\pm 1.6\%$ within a central cube measuring 11 cm on each side. During experiments, subjects' heads always remained within the larger region. The measured peak-to-peak position noise level of the search coil system at a bandwidth of 0–100 Hz was 2 min arc. The root-mean-square (RMS) horizontal velocity noise of the system over a bandwidth of 0–43 Hz was 30 min-arc/s. The presence of the treadmill did not have a detectable effect on search coil measurements.

Three-dimensional linear head position and a redundant measure of angular position were obtained with a flux gate magnetometer sensor (FGM; Flock of Birds, Ascension Technology, Burlington, VT). The transmitter for the FGM was mounted rigidly 55 cm behind the center of the cube. The receiver was mounted on top of the subject's head via a head band worn by the subject. Measurements of the position of the receiver relative to the eye were taken before and after the experiment to ensure the receiver did not slip. The FGM had a maximum range of ~ 90 cm that was never exceeded. The position resolution of the FGM was 0.2 mm with an accuracy of 2.5 mm. Accuracy was verified by placing the FGM receiver at points on a measured grid located near the center of the cube and extending 20 cm in each direction. With the FGM sensor in a fixed location and without activation of the search coil field, the reported location had an absolute error of ~ 0.5 mm, with 10% of measurements being 0.2 mm (1 digital bit on the FGM) higher or lower than the mean for each location. When the search coil field was energized, the mean measurement and variation in an indicated location remained the same, except 50% of measurements were 0.2 mm higher or lower. The search coil system thus introduced noise into the FGM measurements near the level of resolution of the system. Angular FGM measurements had a resolution of 0.1° and an accuracy of 0.5° . Because FGM was less accurate

in determining angular head position than the search coil system, the angular search coil data were used for analysis.

Data were acquired by a Macintosh Quadra 950 computer running the MacEyeball software package (Regents of the University of California). Search coil measurements (horizontal and vertical gaze and head positions) were displayed on a digital polygraph and low-pass filtered over a bandwidth (4-pole Butterworth) of 100 Hz before simultaneous digital sampling with 16 bit precision at 400 Hz. The FGM was controlled by a dedicated microprocessor (Ascension Technology). Data from the FGM was collected at 100 Hz and synchronized with search coil sampling via a synchronization pulse from the Macintosh. Synchronization was verified by attaching a search coil and the FGM receiver to a rigid body, which was oscillated at ~ 5 Hz. The data from the FGM was stored in a buffer (GPIB-232CV-A, National Instruments, Austin, TX) until the end of each trial when it was read by MacEyeball. The FGM data were interpolated linearly to match the 400-Hz sampling rate of the search coil system.

Measurement conditions

The activities tested consisted of quiet standing, walking, running, and self-generated angular head movements, each in epochs of 10 s. Each trial in which there was no magnification of vision was performed in the light and repeated immediately afterward in darkness with the subject asked to remember the earth-fixed target in the location where it had been previously visible. When vision was magnified with telescopic spectacles, trials were done only in the light because previous studies have shown that telescopes have no effect in darkness (Crane et al. 1996). Standing trials were done with a subject's feet together without external support. Walking trials were done on the treadmill at 0.9 m/s; running trials were done at 1.4 m/s with the subject employing a jogging gait. Although the treadmill provided the feel of running and walking, no attempt was made to simulate optic flow. For safety reasons, locomotion in darkness was done with subjects grasping a hand rail. A safety interlock stopped the treadmill if the subject did not maintain the pace. Trials conducted in the light were done both with and without the subject grasping the rail to determine any effects of touching a stationary object during locomotion. Subjects were trained to make self-generated head movements in pitch or yaw at an amplitude of $5\text{--}15^\circ$ in synchrony with a sinusoidal tone modulated at 0.8 Hz. Mean rotation frequency achieved was 0.797 ± 0.005 Hz (mean $\pm$ SE) with a range from 0.66 to 0.88 Hz.

In addition to unaided vision, two sets of telescopic spectacles were used. Each was adjusted so that a distant (5 m) target was in focus for the subject. The $\times 1.9$ spectacles had a field diameter of $\sim 16.8^\circ$. The $\times 4$ spectacles had a field diameter of $\sim 10.3^\circ$. Both sets of spectacles were mounted in custom-made adjustable frames with rubber hoods to occlude peripheral vision. Frames were stabilized to the head with straps. The telescopic spectacles were not observed to move relative to the head even during vigorous high-frequency movement (Demer 1992).

Before each trial, the coordinates of the center of the eye relative to the FGM receiver were determined with a metric scale. For binocular experiments, the interpupillary distance also was determined so the position of both eyes relative to the FGM receiver was known. Because the subject was free to move over a small area, target distances were measured relative to the FGM transmitter. The target used at 100 and 150 cm consisted of a 4-cm black cross surrounded by radiating lines at the center of a white background 50×43 cm. The target located at 500 cm was a 14-cm cross on a 102×81 cm background. Before each experiment began, all targets were centered to match the height of the subject's right eye. With unaided vision, all three target distances were tested. With $\times 1.9$ magnified vision, only the 150 cm and 500 cm

distances were tested, and with $\times 4$ magnification, only the 500 cm distance was used due to difficulties converging on close targets with magnified vision.

During each experiment, subjects were tested during standing and self-generated rotation with 500, 150, and 100 cm distant targets in that order. Next running and walking trials were performed starting with the target at 100, 150, and 500 cm. This order was used to minimize possible fatigue effects from running and walking on standing stability. This sequence then was repeated for each of the two types of telescopic spectacles. Each time conditions were altered, a 2-s, three-dimensional position calibration recording was made with the subject standing as still as possible while grasping a fixed rail while aligning the eyes and head directly to the target. The calibration trial allowed for geometric correction of any head band or eye coil slippage that may have occurred during previous trials.

Data analysis

Data were analyzed automatically using custom software written using the LabView package (National Instruments) running on a Power Macintosh compatible computer. Data collected during calibration trials were averaged and used to define a rotation matrix giving the central (0) position for gaze and angular head position (see APPENDIX). The data in test trials were rotated by these calibration matrices so as to place search coil and FGM data in a common coordinate system (see APPENDIX). For binocular recording, a separate rotation matrix was calculated for the left eye assuming that the vertical component of the eye position was 0° and the horizontal component was the inverse tangent of the interpupillary distance divided by the distance to the target. This assumes the subject was foveating the target during the calibration trial, a capability verified by clinical examination of each subject. The purpose of this calibration was to eliminate errors introduced by possible misalignment or slippage of the search coil on the eye or the head band on the head.

Although care was taken to ensure that FGM data and search coil data were sampled synchronously, the starting point of the FGM data collection varied during a range of ~ 100 ms due to variable delays in the FGM microprocessor. We corrected for this offset by cross-correlation analysis between corresponding pairs of head pitch, yaw, and roll values collected redundantly from the coil system and the FGM, respectively. The peak cross-correlation time was taken to be the synchronization offset for that trial. If any of the three peak cross-correlation values was $< 1 \text{ deg}^2$, the time offset was discarded as unreliable. A weighted average was computed on the remaining cross-correlation offsets (which were nearly always within 4 ms of each other) to determine the final offset. This method proved reliable even for trials with a relatively low signal-to-noise ratio such as during standing. In a few trials, however, no cross-correlation values were found greater than the threshold value of 1 deg^2 . In these cases, the analysis was insensitive to the exact offset value and the average offset value was used.

Before further analysis, the data were low-pass filtered (6 pole Bessel, 0–42 Hz). Saccades and other quick phases were infrequent in this protocol, their effects were removed only for computation of AVOR gain.

The intersection of gaze with the target plane was calculated by projecting the line of sight from the translational center of the eye (see APPENDIX for details). Average gaze position in this plane was taken to be the actual target position. Gaze position in the target plane was converted into angular position on the retina by taking the inverse tangent of gaze displacement from the target divided by the distance from the eye to the target. This angular measure was used because it can be compared across a variety of target distances. Both the horizontal and vertical gaze positions in the target plane were differentiated, low-pass filtered (0–8 Hz)

and used to calculate RMS velocity of image slip. Trials where subjects did not comply with instructions to fixate the target (usually voluntary pitch or yaw movements) were discarded.

During experiments when telescopic spectacles were worn, telescope magnification was considered. The gaze angle was reduced by the reciprocal of spectacle magnifying power. The reduced gaze line was intersected with the target plane. Gaze error then was multiplied by spectacle magnification factor. Using this technique, we were able to determine retinal error with telescopic spectacles. Gaze position in the dark was determined in the same manner as during unaided vision.

A measure of the oculomotor system's estimate of target distance can be calculated by considering two eye positions and their corresponding lines of sight. Because these lines do not usually intersect, the point where these lines most closely approach each other was taken to be the internal estimate of target position (see APPENDIX). This technique was applied to binocular trials using the angular and translational positions of both eyes in space to calculate the two lines of gaze (convergence method). The technique also was applied using the position of a single eye translating at two different times to calculate the two lines of gaze (parallax method). To minimize noise with the parallax method, the technique was only applied to eye positions that differed by ≥ 1.0 cm. Values of target distance were constrained to positions in front of the eyes and closer than 10 m. The final trace of target distance estimates was low-pass filtered (0–2 Hz).

For each trial, gain and the time delay between eye and head movement were calculated for pitch and yaw. Angular head and eye position traces were differentiated and plotted against one another for corresponding directions. Linear regression was performed iteratively for corresponding eye and head velocity pairs and over a range of time offsets between 50 ms (eye lead) and –175 ms (eye lag). For each of these fits, the mean standard error was calculated. The time offset minimizing mean standard error was taken as AVOR latency. Eye and head velocities then were low-pass filtered (0–20 Hz). After latency correction, another linear regression of eye velocity against head velocity was obtained, and data points found to lie >2 SD from this fit were excluded as quick phases or noise (Demer 1992). The regression and exclusion of outlying points was iterated three additional times after which the slope was taken to be AVOR gain. Coefficients of determination (R^2) were calculated for the regressions in each axis after statistical outliers were removed. When the R^2 value was ≥ 0.7 , the corresponding gain was considered reliable.

Fourier analysis of head and gaze positions was performed using a rectangular window. The peak frequency component was taken as the maximum Fourier component >0.1 Hz. Statistical analysis was performed using super analysis of variance (SuperANOVA) (Gagnon et al. 1991). Results were considered to be significant for $P < 0.05$.

RESULTS

Using three-dimensional translational and rotational measurements, it was possible to determine the position of the target image on the retina during unrestrained head movements (Fig. 1, *top*). Image position always underwent small perturbations associated with head and eye motions in all 6 df. For example, with a distant target viewed with unmagnified vision, retinal position error as measured by standard deviation was $\leq 0.5^\circ$ and RMS retinal velocity error was $<4^\circ/\text{s}$ for running, walking, and standing (Fig. 2). By both measures, gaze instability was greater under conditions of active head movements, closer targets, magnified vision, and darkness. Effects of these factors are considered in detail below. We repeated our analysis ignoring the eye torsion

data and found no significant differences in any of the values. This indicates that two-dimensional eye position measurements would have sufficed.

Head translation and rotation

All subjects exhibited a phase-locked relationship between orbit translation and head rotation at the peak frequency of head motion during standing, walking, and running in both the horizontal and vertical directions (Fig. 1, *bottom*). As the orbit translated upward, it rotated downward and vice versa. Likewise, as the orbit translated laterally, it rotated medially. This relationship between orbital translation and rotation had a stabilizing effect on retinal images. We investigated a possible frequency dependence of this antiphase behavior using Fourier cross spectral analysis. In spectral analyses over the range 0–20 Hz for each trial, we determined those frequencies where orbit translation and head rotation were antiphase ($180 \pm 45^\circ$). The

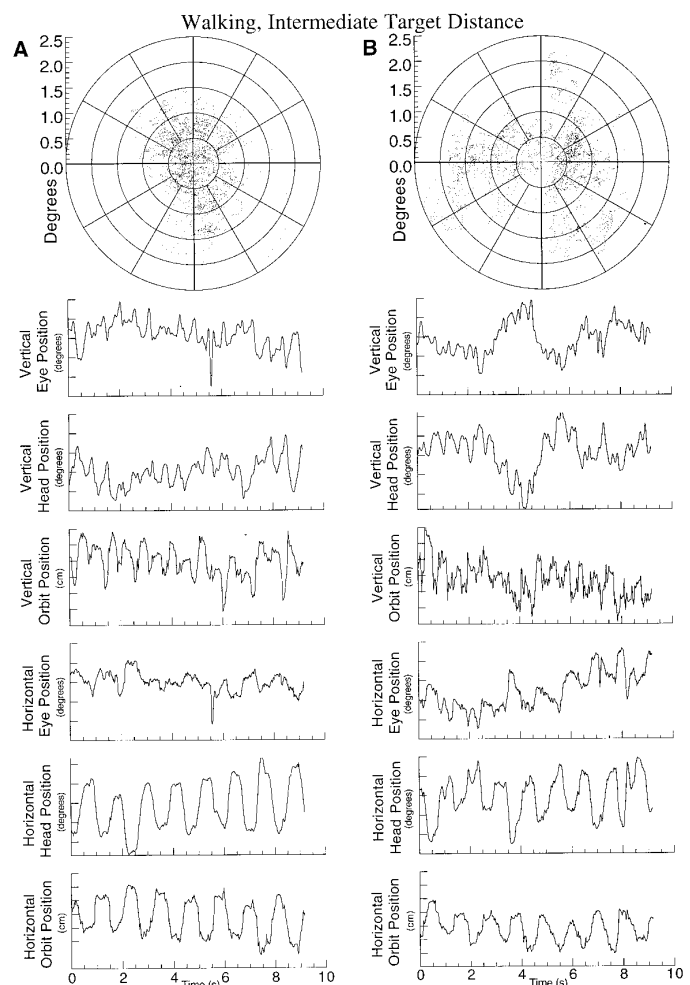


FIG. 1. Stabilization of gaze position of representative subject in light (A) and darkness (B). Subject walked on a treadmill at 0.9 m/s with a target located 150 cm from flux gate magnetometer sensor (FGM) transmitter (~ 90 cm from eye). Polar plots (*top*) show 400-Hz time sampled gaze position in target plane calibrated in units of retinal angle. Time plots (*below*) show position in each of 6 df. Note inverse phase behavior between angular eye position and linear orbit position. Inverse phase behavior also was observed between angular head position and linear head position.

brief duration of each trial imposed a limited precision in determination of phase at any given frequency, and phase only could be determined at those frequencies where the spectrum of head motion contained significant amplitude. Antiphase behavior was observed only at predominate frequencies <4 Hz and not observed when predominate frequencies exceeded 4 Hz (Fig. 3). Because only the lower frequency data were informative, Fig. 3 plots the range 0–10 Hz. No effect of target distance or visual feedback was detected in head-movement spectra. In the horizontal plane, head rotation and translation usually occurred with the same peak frequency (Table 1, Fig. 3, *D* and *E*). In the vertical plane, the peak frequency was often lower for head rotation than for head translation due to slow drift in head position that often occurred during the course of a trial. However, there was also significant spectral content at higher frequency; this matched the predominate head translation frequency (Fig. 3*A*). Spectral analysis of gaze position exhibited a number of frequencies <3 Hz with significant amplitude (Fig. 3, *C* and *F*). In darkness, the peak frequency of gaze was usually much lower because gaze error was dominated by the slow drift in the absence of visual feedback. The predominate frequency in the presence

of visual feedback was <1 Hz in all conditions except during running, where it was ~ 2.5 Hz in the vertical direction. When translation was neglected in gaze calculations, retinal image slip velocity appeared greater than when translation was considered, as shown in Fig. 4. Effects on head motion of target location and activity are considered in detail below.

Stability of gaze during various activities

Despite attainment of retinal image stability under all conditions, AVOR gain varied significantly according to activity (ANOVA $P < 0.05$), approximating unity only during self-generated head motion. During the natural activities of standing, walking, and running, gains were significantly less than unity (Fig. 5), occasionally as low as 0.55. Gains differed significantly among activities. Clarification of this apparent paradox is provided by examination of the relationship of orbital translation to rotation (Fig. 6). For self-generated pitch, the ratio of RMS translational velocity (bandwidth 0–8 Hz) to rotational velocity was $0.021 \pm 0.001 \text{ cm} \cdot \text{s}^{-1} \text{ per deg} \cdot \text{s}^{-1}$ (mean $\pm$ SE) in the vertical plane. Similarly during active yaw movements the ratio was $0.108 \pm 0.005 \text{ cm} \cdot \text{s}^{-1}$

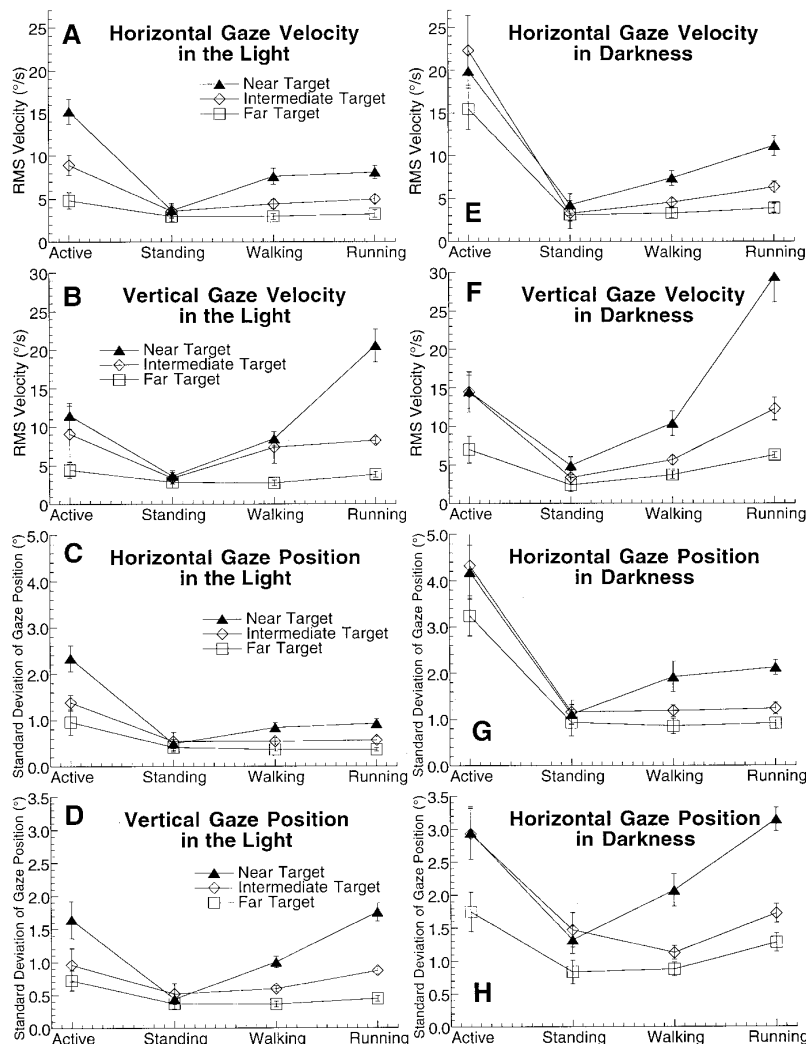


FIG. 2. Stabilization of gaze velocity (A, B, E, and F) and image position on the retina (C, D, G, and H). Data shown for all activities and target distances with unaided vision averaged over 14 subjects. A–D: recorded with target visible. E–H: recorded in darkness immediately after corresponding trials on left. Active trials refer to self-generated 0.8-Hz sinusoidal motion in either horizontal or vertical plane, as stated. Velocities are root-mean-square (RMS) values over the range 0–8 Hz. Far target was located 500 cm from FGM, intermediate target located 150 cm from FGM, and near target was located 100 cm from FGM. Error bars $\pm$ SE. A: horizontal gaze velocity in light. Minimum image slip velocity occurred for natural activities with far target. Active movements produced greater image motion as compared with natural movements at every target distance. B: vertical gaze velocity in light. As with horizontal axis, lowest image slip occurred for far target. Greater image slip velocities were observed during running with near target when compared with active condition and with running in horizontal axis. C: horizontal gaze position dispersion in light. Standard deviation of gaze position was least for most distant targets. Gaze position was less localized for self-generated motion than natural movements. D: vertical gaze position dispersion in light. As with image slip velocity, standard deviation of gaze position was higher in the vertical plane. Running produced greater errors than self-generated head rotation. E: horizontal gaze velocity in darkness. Same trends as seen during lit conditions, except image slip velocities were higher for each condition. F: vertical gaze velocity in darkness. Similar to trend seen with visible target except image slip velocities were greater for each condition. G: horizontal gaze position in darkness. Gaze position was less localized than in light. There was a disproportionately large increase during self-generated head rotation in comparison with natural activities. H: horizontal gaze position in darkness. Standard deviation of gaze position increased in darkness. Increase with active movement was similar to that with natural activities.

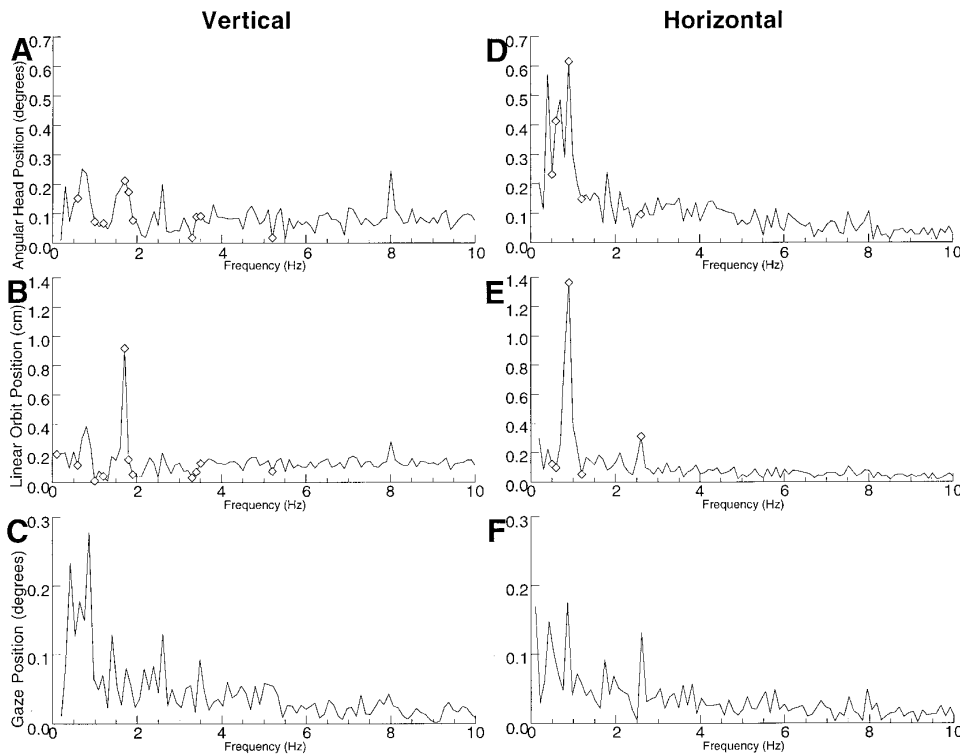


FIG. 3. Frequency domain analysis of a subject walking while viewing a target at intermediate distance. Same trial shown in Fig. 1A. —, amplitude spectrum; $\diamond$, frequencies with antiphase relationship ($180 \pm 45^\circ$) between head rotation and translation of the eye in corresponding plane. A–C: represent vertical head rotation, eye translation, and angular gaze position. D–F: represent horizontal head rotation, eye translation, and angular gaze position.

per $\text{deg} \cdot \text{s}^{-1}$. These figures indicate negligible orbital translation in comparison with the large rotation, making a gain near unity ideal for self-generated motion. The ratios of translation to rotation velocity were significantly higher during the natural activities of standing, walking, and running in both the pitch and yaw axes (Fig. 6). During standing, consideration of translation in gaze computations was found to have no significant effect or to slightly increase retinal slip velocity. However, orbital translation played a key role in image stabilization during running and walking, as demonstrated by significant drops in image slip velocity when translation is considered for these activities (Fig. 4). Vertical translation, as indicated by the standard deviation of orbit position, ranged from means of 1.2 to 3.2 cm between subjects during running.

In the horizontal direction, both image velocity and gaze position dispersion (SD) were lower during natural than

during self-generated head movement, although for the vertical direction, running often was associated with more image motion than during active head movement (Fig. 2). For a distant, visible target, both horizontal and vertical retinal image slip was found to be $<4^\circ/\text{s}$ across standing, walking, and running, independent of the specific activity ($P > 0.1$) (Fig. 2, A and B). Image slip was significantly greater in the direction of motion during self-generated pitch ($4.5 \pm 1.0^\circ/\text{s}$) and yaw ($10 \pm 4^\circ/\text{s}$) with the distant, visible target.

In the light, subjects easily maintained body position on the moving treadmill. However, in darkness and while wearing telescopic spectacles, subjects fell out of position within a few steps. For this reason, when the treadmill was moving subjects were instructed to grasp a rail for tactile reference except in the trials where vision was not compromised either by spectacles or darkness. To quantify any effects of tactile reference, each free-standing, walking, and running trial was preceded by a identical trial where the subject grasped the rail. No significant differences in linear or angular movement were present in the vertical plane. There was significantly greater medial-lateral translation velocity during free movement than during tactile reference trials (Fig. 7A). For running with a distant target, this difference was $1.7 \pm 0.5 \text{ cm/s}$; similar differences occurred during other conditions. Yaw head velocity also significantly decreased with tactile reference, but only at the near and intermediate target distances (Fig. 7B). Despite lower velocity head movements, the retinal slip velocity was not significantly influenced by tactile reference for any target condition. Yaw AVOR gain, which ranged from 0.55 to 0.80, was in all cases greater during tactile reference than without it, although this difference was only significant for the near target during running and the intermediate target during walking (Fig. 7C).

TABLE 1. Mean peak frequencies of head movement

	Standing	Walking	Running
Pitch	0.15 ± 0.01	0.53 ± 0.06	1.1 ± 0.1
Vertical translation	0.30 ± 0.05	1.43 ± 0.06	2.53 ± 0.03
Yaw	0.14 ± 0.01	0.60 ± 0.03	0.67 ± 0.05
Horizontal translation	0.17 ± 0.01	0.54 ± 0.03	0.78 ± 0.05
Horizontal gaze	0.40 ± 0.06	0.58 ± 0.05	0.69 ± 0.07
Vertical gaze	0.34 ± 0.07	0.34 ± 0.05	1.5 ± 0.1

Mean peak frequency (in Hz, $\pm$ SE) of the maximum Fourier component over the range 0.1–20 Hz of head position and image position on the retina. Peak frequencies of head position were independent of visual feedback and target distance and represent averages of all trials with unmagnified vision. Peak frequency of retinal image position is given for trials with visual feedback.

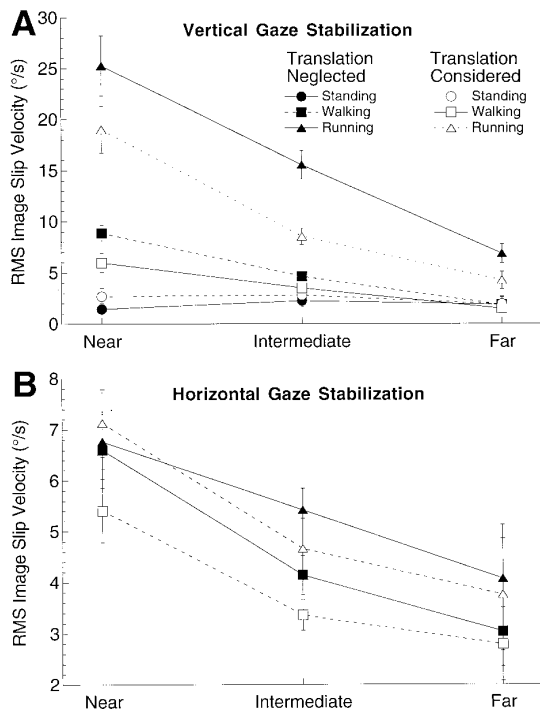


FIG. 4. Effect of translation on gaze stabilization for 3 target distances. Open symbols represent complete calculations considering eye translation. Solid symbols represent the same data but assume that the eye remains fixed in space 60 cm from the FGM. Data averaged across all 6 subjects where binocular search coils were used. Standing data are omitted for clarity because it shows no significant trend with either target distance or translation consideration. Error bars $\pm$ SE. A: vertical, B: horizontal.

Individual variation

Under identical testing conditions, AVOR gain values varied significantly among subjects during natural activities. During walking while viewing the distant target with unaided vision, gain values varied by subject from 0.73 to 0.95 (mean 0.86) in pitch and from 0.56 to 0.93 (mean 0.77) in yaw

(Fig. 8, C and D). Similar variation in AVOR gain also was observed during other conditions. The degree of gaze stabilization during this same set of tests was also variable among subjects. Vertical RMS image slip velocity (0–8 Hz) varied from 0.95 to 6.5°/s (mean 2.7°/s) and horizontal image slip varied from 1.3 to 6.6°/s (mean 2.9°/s). We plotted AVOR gain and image slip velocity for individual trials in Fig. 8. Surprisingly, a lower image slip velocity did not correspond to higher AVOR gain for natural viewing conditions except with the extremely low gains seen during running (Figs. 8, C–F). Although much smaller variations in gain occurred during self-generated movements, only for self-generated yaw was there a significant inverse correlation between gain and image slip velocity (R^2 for linear fit = 0.87, Fig. 8B).

Effects of target distance

The distance to the target varied continuously because subjects moved about. Mean distance from the far target to the eye was 441.3 ± 0.6 cm (mean $\pm$ SE). Mean distance of the intermediate target averaged 89.0 ± 0.5 cm, whereas mean near target distance was 40.6 ± 0.5 cm.

As target distance decreases, a given eye translation will cause a greater geometric error in gaze position. The observed effect of target distance on retinal slip velocity is plotted in Fig. 9, A and B, for natural activities. As expected, ambulatory activities associated with large orbit translations showed the greatest increase in image slip for nearer targets. This increase in image slip is consistent with oscillopsia of the near target reported by some subjects while running. During standing, there was only a small, nonsignificant ($P > 0.1$) increase in horizontal and vertical slip velocity due to target proximity. This may be attributed to the low linear RMS orbit velocity during distant target viewing while standing, averaging 2.1 ± 0.6 cm/s dorsal-ventrally and 1.6 ± 0.3 cm/s medial-laterally (Fig. 10, B and C). There was a significant increase in

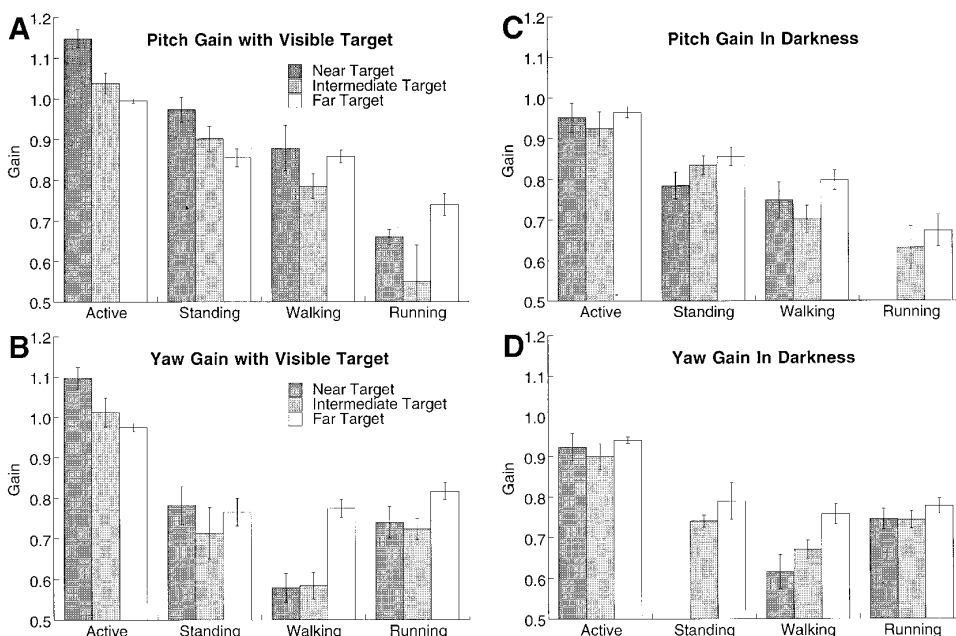


FIG. 5. Effects of activity on mean angular vestibulo-ocular reflex (AVOR) and visually enhanced VOR (VVOR) gain of 14 subjects. Near target (100 cm from FGM) data are shown by darkest bar, intermediate target (150 cm from FGM) by lightly shaded bar, and far target (500 cm from FGM) by unshaded bar. "Active" represents self-generated 0.8-Hz sinusoidal head movement. For trials in darkness (C and D), subjects remembered the previously visible target. No data shown for conditions where adequate data existed for <2 subjects. Error bars $\pm$ SE. A: pitch gain with visible target. Near unity gains occurred only with active head movements. B: yaw gain with visible target. As with pitch axis, near unity gain occurred only with active movement. C: pitch gain in darkness. A decrease in gain was observed as compared with lit conditions across all activities and target distances. D: yaw gain in darkness. When compared with lit conditions, a decrease in gain was observed during active head rotation. During natural movements, no clear trend was present.

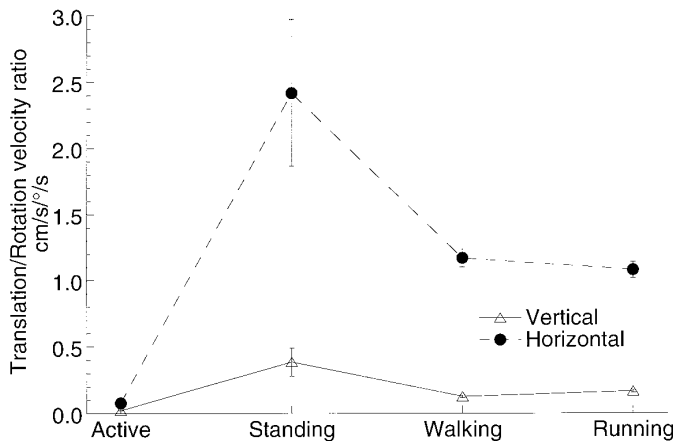


FIG. 6. Mean ratios of orbital translation to rotation in 14 subjects. Ratio of RMS velocity of orbital translation (cm/s) to RMS velocity of head rotation (deg/s) is plotted on the ordinate. Active refers to self-generated movement in either the vertical (Δ) or horizontal plane ($\bullet$). Data collected with a lit target located 500 cm from FGM. Error bars $\pm$ SE.

retinal slip velocity for more proximal targets during running and walking ($P < 0.05$). During walking, dorsal-ventral and medial-lateral linear velocities were 9.3 ± 0.5 and 5.5 ± 0.2 cm/s, respectively. For running, a further increase in linear velocity was observed to 28.5 ± 0.8 cm/s dorsal-ventrally and 7.8 ± 0.3 cm/s medial-laterally (Fig. 10, B and C).

Although retinal image motion during natural activities increased with increasing target proximity, compensatory phenomena appeared to be acting to minimize slip for closer targets. From the distant to the closest target, translational orbit velocity decreased significantly in both the medial-lateral (Fig. 10B) and dorsal-ventral (Fig. 10C) directions. Dorsal-ventral RMS translational velocity decreased with target proximity by 0.7 ± 0.6 , 0.9 ± 0.5 , and 3 ± 1 cm/s for standing, walking, and running, respectively. Medial-lateral RMS translational velocities decreased by 0.6 ± 0.3 , 0.4 ± 0.3 , and 1.1 ± 0.3 cm/s for standing, walking, and running, respectively. Along anterior-posterior axes there were no significant ($P > 0.1$) variations in translation velocity with target distance (Fig. 10A). Changes in rotational velocity of the orbit with target distance were only significant in yaw, and in that axis only during walking and running where the velocity increased with target proximity by 1.6 ± 0.3 and $1.1 \pm 0.3^\circ/\text{s}$, respectively. This decrease in translation and increase in orbit rotation minimized the effect of target distance on retinal image stability. Despite these compensatory effects, at the two closer target distances RMS image slip exceeded $4^\circ/\text{s}$ for all activities except standing still (Fig. 9, A and B).

We sought to observe a physiological indicator of the target distance estimated by the oculomotor system. This estimate was deduced from convergence in trials employing binocular search coils and with the parallax method for all trials. Convergence and parallax target distance estimates differed from one another and varied over the course of each 10-s trial conducted with visible targets. Examples of the instantaneous variation in target distance estimate are shown in Fig. 11. In darkness, these indicators

of the target distance estimate varied more from the actual target distance and often grew progressively less accurate during the course of the trial. Aggregate target distance estimate data averaged across all trials are shown in Fig. 12. The convergence estimate of target distance was generally more accurate than the parallax estimate. Compared with trials conducted in the light, both methods of target distance estimation indicated systematic oculomotor underestimation in darkness of all but the nearest target distance, which was systematically overestimated.

Effects of visual feedback

In general, gaze position was controlled more precisely in light than in darkness. The type of activity did not signifi-

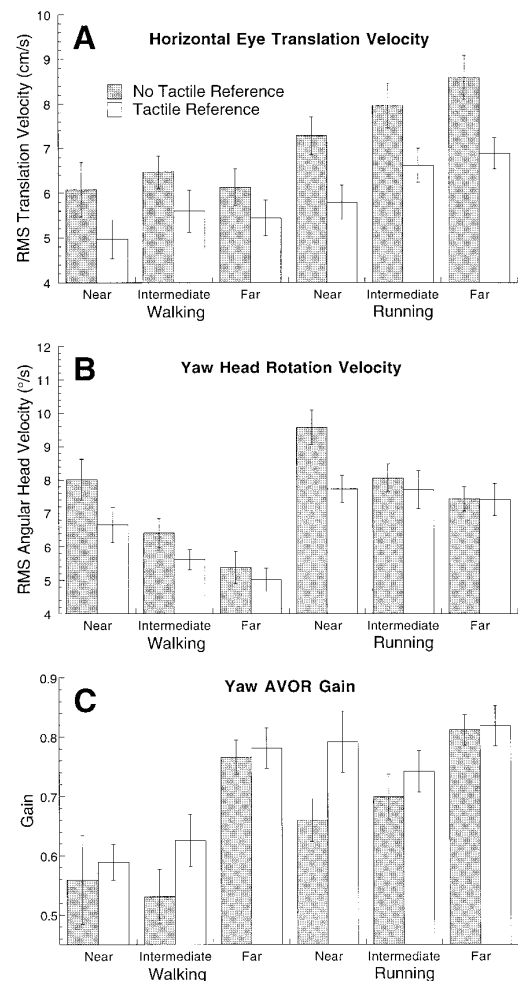


FIG. 7. Effect on horizontal head motion and yaw AVOR gain of tactile reference as compared with free movement. Data shown for horizontal plane. Error bars $\pm$ SE. A: effects of tactile reference on eye translation velocity. During free movement, translation velocities were greater for both modes of locomotion and at all target distances when compared with tactile reference. B: effects of tactile reference on yaw velocity. Velocity of head rotation was greater during free movements than with tactile reference. Although this trend was observed across all conditions, it was only significant for near target conditions. C: effects of tactile reference on yaw AVOR gain. AVOR gain was higher with tactile reference under all conditions, although this difference was only significant for near targets while running and at the intermediate target distance while walking.

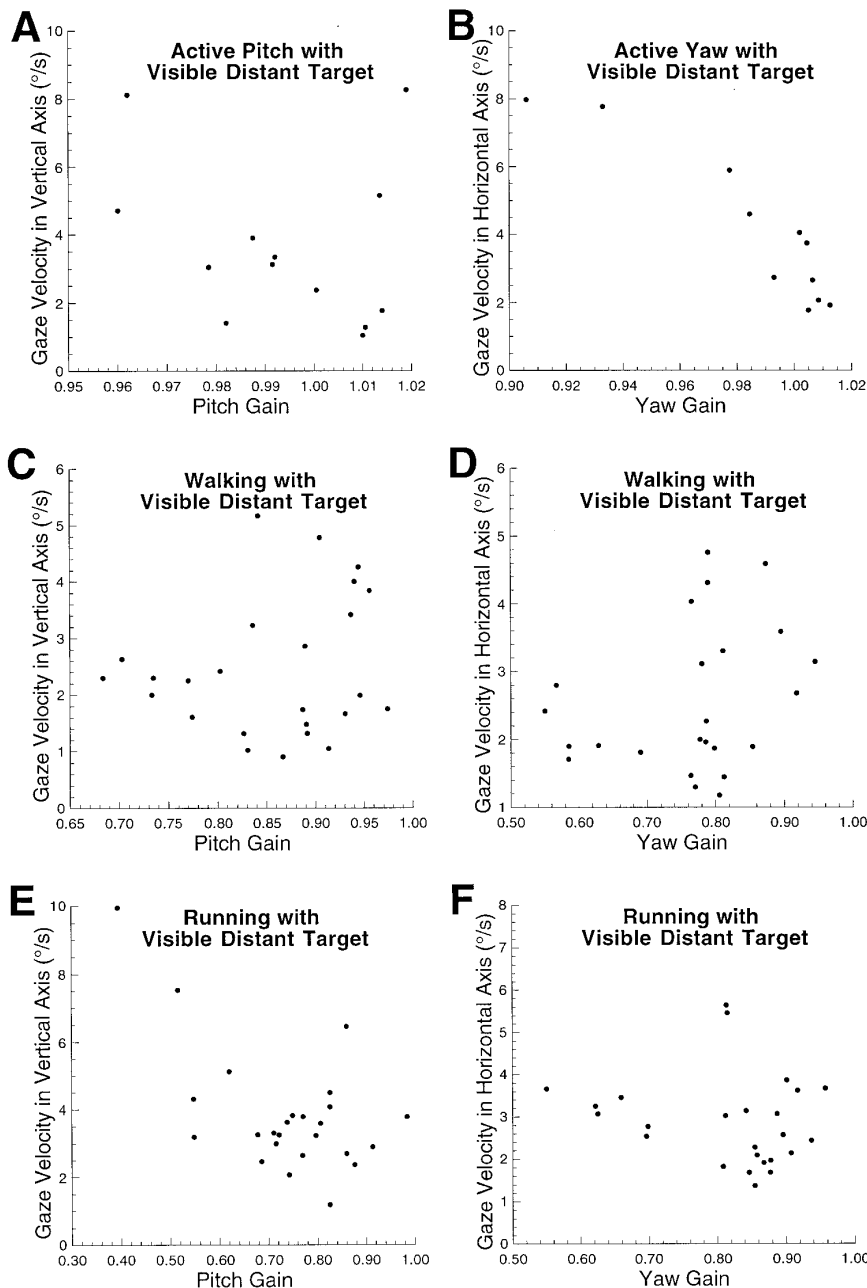


FIG. 8. Weak relationship between AVOR gain and image slip velocity. Each data point represents an individual trial. Data shown from every trial in 14 subjects. Data were collected with visible target located 500 cm from FGM. More data points are present for walking and running (C–F) because these trials were done in duplicate with and without tactile reference. A: self-generated movements in pitch. Although there were outlying points, a decrease in image slip velocity was observed for gains closest to unity. Gain varied by only 0.07. R^2 for linear fit = 0.05. B: self-generated movements in yaw. As with self-generated movement in pitch, velocity of image slip decreased as gain approached unity. Gains varied over narrow range. R^2 for linear fit = 0.87. C: vertical data for walking. Gains were more variable than during active head movements. No significant relationship between gain and gaze velocity was observed. R^2 for linear fit = 0.04. D: horizontal data for walking. Gain values clustered near 0.8 with many outliers. Significant increase in image slip velocity occurred with higher gain values. R^2 for linear fit = 0.16. E: vertical data for running. Gains varied over an octave, yet no correlation between gain and gaze stability was observed, except for increased slip velocity for very low AVOR gains. R^2 for linear fit = 0.31. F: horizontal data for running. Despite large variation in gain there was no relationship between AVOR gain and gaze stability. R^2 for linear fit = 0.01.

cantly influence the dispersion of horizontal gaze position. Vertical gaze dispersion was significantly greater during running. However, the percent increase in gaze dispersion in darkness as compared with lit conditions remained similar across natural activities. Averaging across all activities with a far target for the unmagnified viewing condition, the dispersion (SD) of horizontal gaze position was 2.4 ± 0.2 times greater and vertical gaze position 2.5 ± 0.4 times greater in darkness as compared with light (Fig. 2, C, D, G, and H). Much of the increase in gaze dispersion can be explained by slow drift observed in all subjects. Gaze velocity error varied less between darkness and light than did gaze position error, but did vary by activity (Fig. 2, A, B, E, and F). For the unmagnified distant viewing condition, the presence of

vision had no significant effect on image slip velocity during standing ($P > 0.1$). However, there were significant effects during walking where slip velocity was 1.4 ± 0.1 times greater in darkness and during running when slip was found to be greater by a factor of 1.6 ± 0.1 . Gain of the AVOR tended to be greater for visible as compared with remembered targets, but this difference was only significant ($P < 0.05$) during active pitch and yaw movements in their respective axes and walking in pitch (Fig. 5).

The latency between angular eye and head movements was <10 ms (the presumed latency of the VOR) across all activities and target distances independent of the presence of visual feedback (Fig. 9, C and D). In the case of standing, eye movement was found to precede head movement by as

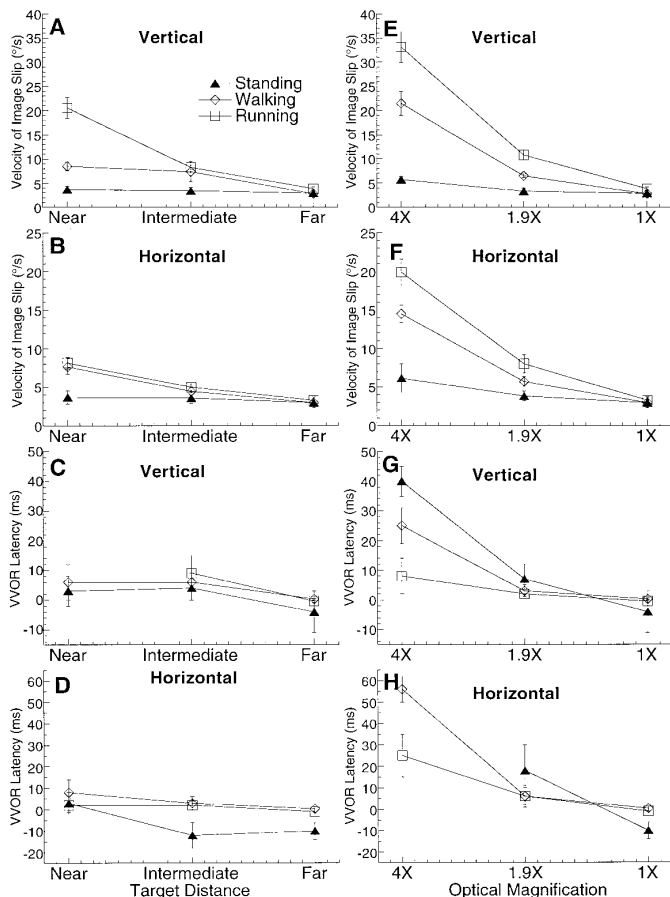


FIG. 9. Effects of target distance and magnification on image slip velocity and VVOR latency. Average data from 14 subjects shown during standing, walking, and running. Only points where data from multiple subjects was available are shown. Error bars $\pm$ SE. A: vertical image slip velocity increased with closer targets most prominently during running. B: horizontal image slip velocity increased with closer targets mainly during walking and running. C: vertical angular VVOR latency was <10 ms. D: horizontal angular VVOR latency. Lag was <10 ms. E: velocity of vertical image slip with $\times 1.9$ and $\times 4$ telescope spectacles increased most during running and walking. F: velocity of horizontal image slip with $\times 1.9$ and $\times 4$ telescopic spectacles was less than vertical for each activity. G: pitch VVOR latency increased with telescopic magnification of vision. Latency was greater during conditions where image slip velocity was lower. H: angular VVOR latency was greater in yaw than it pitch (G) and increased with telescope magnification.

much as 10 ms during intermediate and far target conditions (Fig. 9, C and D). The latency between linear and angular head movements was not significantly different from zero. In darkness, target distance did not have any significant effect ($P > 0.1$) in either axis on latency. In the light, close target distances slightly but significantly ($P < 0.05$) increased latency for both pitch and yaw although latency remained <10 ms (Fig. 9, C and D).

Magnified vision

Telescopic spectacles magnify the visual consequences of angular head movements. Retinal image slip velocity was increased with telescopic spectacles under all conditions tested (Fig. 9, E and F). Although significant increases in

VVOR gain were observed with magnified vision during all activities, this gain increase did not match the telescopic magnification (Fig. 13). Gain enhancements were larger for voluntary head rotation than during natural activities. During voluntary movements, VVOR gain was not significantly less than unity during unmagnified vision. In pitch, VVOR gain during voluntary rotation was increased to 1.51 ± 0.05 with $\times 1.9$ magnification and to 2.2 ± 0.2 with $\times 4$ magnification (Fig. 13A). Even greater gain enhancement was achieved during voluntary yaw at 1.60 ± 0.08 for $\times 1.9$ and 3.2 ± 0.2 for $\times 4$ telescopes (Fig. 13B). More modest VVOR gain increases were observed under natural motion conditions. During walking, pitch VVOR gain increased from 0.86 ± 0.02 with unmagnified vision to 1.06 ± 0.03 and 1.25 ± 0.08 with $\times 1.9$ and $\times 4$ magnification, respectively (Fig. 13A). Similarly, yaw VVOR gains during walking were 0.77 ± 0.02 , 0.99 ± 0.04 , and 1.27 ± 0.09 for unmagnified, $\times 1.9$, and $\times 4$ conditions, respectively (Fig. 13B).

Changes in patterns of head movement occurred with telescopic spectacles. As with decreased target distance, a decrease in eye translation was observed with increased magnification. In contrast to the effect seen with near targets, magnification also decreased rotational orbit velocity (Fig. 10).

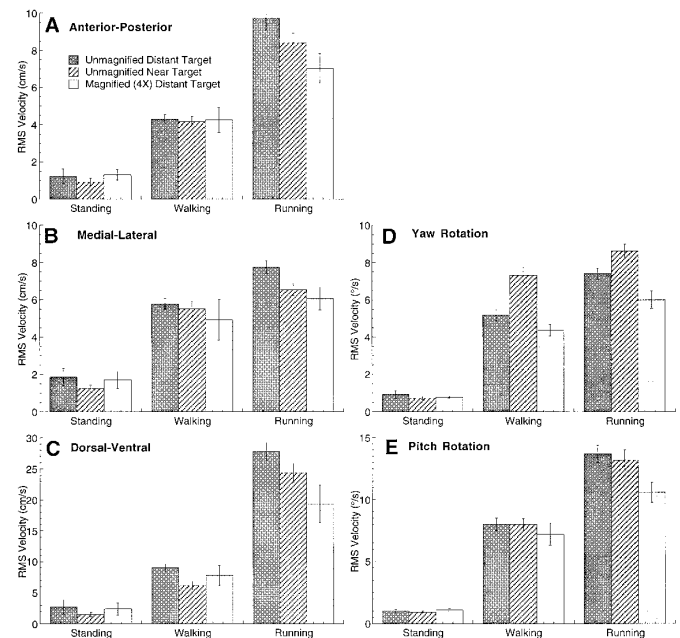


FIG. 10. Mean RMS translational and rotational head velocities during natural movements with visible target. Data are shown for distant (500 cm from FGM) and near (100 cm from FGM) targets with unaided vision and distant target while wearing $\times 4$ telescopic spectacles. For each condition and type of motion, velocities decreased from running to walking to standing. Bandwidth was 0–8 Hz, error bars $\pm$ SE. A: antero-posterior translation velocity. During running, translation velocity decreased with closer targets and magnification. B: medial-lateral translation velocity. As with anterior-posterior direction, RMS velocity decreased for near targets and with magnification. C: dorsal-ventral translation velocity. Translation velocity decreased with near targets for all activities. Decrease with magnification occurred only during running. D: yaw head velocity increased with near targets. Yaw velocity was less with telescopic spectacles than for viewing of unmagnified, distant target. E: pitch head velocity was similar for near and distant targets. With magnified target, there was a significant decrease in pitch velocity during running.

These changes in head movement were significant ($P < 0.05$) during running and walking but not during standing. During self-generated movements, orbit velocities decreased, possibly due to the narrow field of the telescopic spectacles, which allowed the target to remain in view only for small angular head movements. Medial-lateral RMS orbit velocity decreased by 0.8 ± 1.0 (SE) and 1.3 ± 0.8 cm/s for walking and running, respectively, comparing unaided vision with $\times 4$ magnification. Dorsal-ventral RMS translational velocity decreased by 2.3 ± 1.6 and 10 ± 3 cm/s for walking and running, respectively. Unlike effects of decreased target distance, there was also a significant decrease in anterior-posterior translation of 3.1 ± 0.8 cm/s during running, even though translation in this direction has a negligible effect on image stability. Pitch RMS orbit velocity also decreased by 0.8 ± 0.9 and $3.2 \pm 0.8^\circ/\text{s}$ during walking and running, respectively. Yaw orbit velocity with $\times 4$ telescopes was reduced by 0.8 ± 0.3 and $1.4 \pm 0.5^\circ/\text{s}$ during walking and running, respectively.

With increasing magnification, there was a significantly longer latency between rotational orbit movements and the ocular response; this effect was greater than the effect of target proximity (Fig. 9, *G* and *H*). Type of activity had a significant effect on latency in both pitch and yaw with magnification. With unaided vision, VVOR latency tended toward zero with only a slight delay or even a lead in the case of standing still. Latency increased monotonically with magnification for each of the three natural activities.

DISCUSSION

By simultaneously accounting for both ocular translation and rotation, images of a remote target on the retina were found to be stabilized during natural activities to $<4^\circ/\text{s}$, a value that would permit clear vision. The evidence here

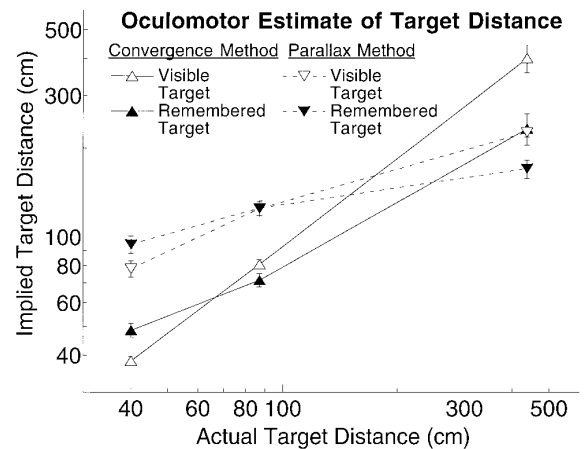


FIG. 12. Estimated target distances derived from parallax and convergence techniques. Parallax data ($\blacktriangledown$) averaged over 14 subjects. Convergence data ($\blacktriangle$) averaged from a subset of 6 subjects who wore binocular search coils. Targets were located 100, 150, or 500 cm away from FGM transmitter located ~ 60 cm behind subject's eye. Error bars represent $\pm$ SE but are smaller than plotting symbols for actual target distance.

suggests that stabilization of gaze is achieved by a precise dynamic interplay among orbit rotation, orbit translation, and eye rotation. Orbit translation is an important factor in gaze stabilization because neglecting it significantly exaggerates slip velocity (Fig. 4). Although substantial loss of visual acuity is likely for motion $>4^\circ/\text{s}$, some loss of visual acuity is likely to occur with motion as slow as $2^\circ/\text{s}$ (Demer and Amjadi 1993; Demer et al. 1994). Some of our subjects did limit far target image motion to $<2^\circ/\text{s}$ during walking and even running, but the mean value was $2\text{--}4^\circ/\text{s}$. Targets used in this experiment were large, making them easy to view even with less than optimal visual acuity. This may have affected the cognitive state of some of the subjects, causing them not to attain maximum image stabilization potential (Crane and Demer 1997). For targets closer than 100 cm from the eye, retinal slip frequently exceeded $4^\circ/\text{s}$, consistent with oscillopsia reported at these distances.

Gaze stabilization during natural movements

Function of the AVOR traditionally has been described in terms of gain—defined as angular eye velocity divided by angular head velocity. However, both eye translation and target distance are required to determine ideal AVOR gain (Crane et al. 1997; Viirre and Demer 1996; Viirre et al. 1986). Gain of the AVOR is informative only when head movement and eye movement are considered in a single plane. This simplification is reasonable under many laboratory conditions when a subject is rotated about a fixed axis or accelerated along a track. However, under natural conditions, head movement is multiplanar. The AVOR gain still can be calculated by arbitrarily choosing planes with respect to which gains can be determined.

The amount of translation and the relationship of orbit translation to rotation are key factors in gaze stabilization. For infinitely distant targets, translation can be neglected. However, even for the most distant target used in this study (~ 440 cm), translation played a significant role in gaze

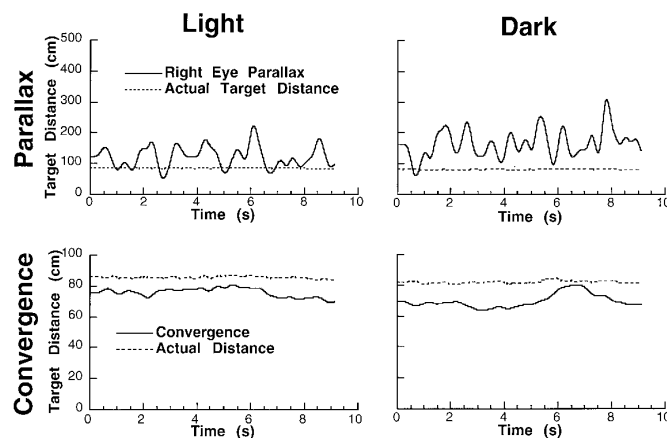


FIG. 11. Changes in oculomotor estimate of target distance during course of representative 10-s trial. Subject walked at 0.9 m/s while viewing target located 150 cm from FGM. Actual target distance as measured from eye ($---$) varied between 80 and 90 cm. Data in left column were collected in light with target visible. Data on right were collected in darkness immediately after trial shown on left. Top: parallax estimate of target distance ($—$) as implied from right eye position (for clarity, left eye is not shown but was similar). Notice that parallax target distance varied more from actual target distance in darkness. Bottom: vergence estimate of target distance ($—$) as calculated from binocular eye positions. Data filtered to $0\text{--}2$ Hz.

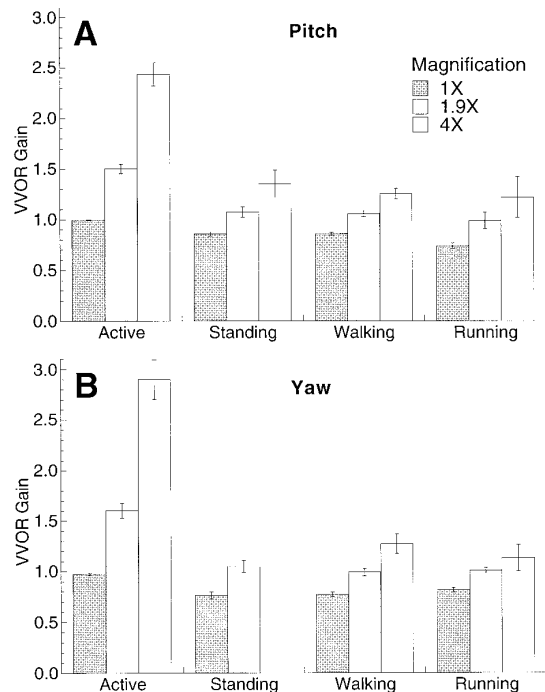


FIG. 13. Effects of telescopic spectacle magnification on mean VVOR gain of 14 subjects during several activities. Dark shaded bars, unaided ($\times 1$) magnified vision; lightly shaded bars, $\times 1.9$ magnifying spectacles worn; unshaded bars, $\times 4$ magnifying telescopic spectacles worn. Data omitted for conditions where fewer than 2 subjects met inclusion criteria. Gain enhancement with magnification was greatest during self-generated (active) head movement. Error bars $\pm$ SE. A, pitch; B, yaw.

stabilization during running (Fig. 4). In everyday life, it is frequently necessary to view targets (i.e., faces and signs) at distances of ≤ 4 m with a high degree of visual acuity.

Repeatable AVOR gains were observed from trial to trial within individual subjects. However, AVOR gains varied substantially among subjects during natural movements without reliable correlation between AVOR gain and image slip velocity (Fig. 8). Experimental error in determining AVOR gain was at most a few percent, making this factor unlikely to account for the wide variation. The most plausible explanation for variation in AVOR gain is individual variation in the relative magnitudes and relationships between orbit translation and rotation. Only by accounting for all six degrees of freedom in orbit position can the degree of image stability can be determined during natural activities. Because AVOR gain values are highly variable and have little predictive value for retinal slip during ambulatory conditions, it is doubtful that measuring AVOR gain alone is a fair measure of ability to stabilize images.

Eye movement recording techniques

All results presented were calculated from data collected with dual winding ocular search coils able to record all three rotational degrees of freedom (Tweed and Vilis 1990). However, these coils also present a disadvantage in that they are bulkier and more expensive than single winding coils. For small eye movements, the direction of gaze can be approximated closely without taking eye torsion into account.

We repeated our analysis ignoring eye torsion and found no significant differences in any of the values. This suggests that future experiments done with a similar protocol need not employ three-dimensional ocular recording.

Gaze stabilization during active movements

During self-generated sinusoidal head movements, position and velocity stabilization of images on the retina were worse than for head movements under natural motion conditions. This was true regardless of viewing distance, presence of visual feedback, or magnification of vision. This finding is consistent with previous work showing AVOR gain to be less than unity for either self-generated (Hine and Thorn 1987; Steinman and Collewyn 1980) or passive (Demer 1992; Gresty et al. 1987) sinusoidal rotation. Based on studies made during self-generated rotation about these fixed axes, it might have been anticipated that large values of retinal slip also would occur during natural movements. This has proven not to be the case. There are several possible explanations for this observation. There is plasticity in the VOR such that its gain can be modified during extended periods of training (Demer et al. 1989; Lisberger and Fuchs 1978; Paige and Sargent 1991; Tiliket et al. 1993). During natural movement, as the orbit translates in one direction it rotates in the other so that a lower AVOR gain is needed than would be required for a purely rotational movement (Demer and Viirre 1996). The AVOR might adapt to this lower level of gain during everyday movements. When self-generated, sinusoidal motion is undertaken, the VOR may continue to use this lower gain. A second hypothesis is that the behavioral context during running, walking, and standing also may enhance image stabilization. This idea is supported by recent single-unit recordings made in the vestibular nuclei that show different neuron firing patterns depending on whether a head movement was self-generated or externally applied (McCrea et al. 1996). During standing, walking, and running, gaze stabilization occurred seemingly unconsciously in all subjects, although the degree of gaze stabilization often varied between subjects and even within the same subject. This variation may have been due to the level of concentration subjects had on the target (Collewyn 1989a,b).

Different effects of magnification and target distance

At a superficial level, the effects of magnification with telescopic spectacles are similar to those observed with target proximity. As shown in Fig. 9, increased retinal image slip during natural activities occurs with both near targets and with magnification. Because telescopes were put on immediately before trials, there was no time for the VOR to adapt to a higher gain. This put the burden on the visual pursuit system to stabilize gaze. Pursuit has a latency of 80–120 ms (Bronstein and Gresty 1988; Carl and Gellman 1987; Lisberger 1990), much longer than that of the VOR. When vision was magnified, the latency of the VVOR was prolonged (Fig. 9, G and H), consistent with a linear interaction of the VOR and pursuit systems (Demer 1992). There also may be a role for visual pursuit without magnification at close target distances, but the phase lag effect was more

subtle. This varied pursuit contribution may be due to inherent differences between viewing a close target and viewing a magnified distant target. While viewing a near target, translation of the viewer is the primary factor destabilizing images. For a near target, effects of rotation are no greater in terms of angle on the retina than they would be with a distant target. However, both rotational and translational errors are multiplied by the telescopes and hence become key sources of image motion.

Pursuit is likely to be the main mechanism for supplementing the VOR during magnified viewing, but the amount of gain augmentation depends on the activity. The VVOR latency, an indicator of pursuit activity, was found to be greater during lower velocity and lower frequency movements so the longest latency was during standing and the shortest during running. A similar effect can be seen when comparing latencies in the horizontal and vertical directions. Lower frequency and lower velocity head movements often were seen in the horizontal plane, where latencies were prolonged with magnification. It is likely that pursuit makes a minimal contribution to gaze stabilization during high-frequency motion such as that which occurs in the vertical direction during running because pursuit would not be fast enough to be effective in stabilizing gaze. This theory is further supported by the image slip velocity (Fig. 9, *E* and *F*), which increased only slightly with magnification during standing but increased by more than the magnification factor during running.

The VOR is much better able to adapt to near targets than to magnified vision. The effect of proximity would make the distant target appear 5 times larger at the intermediate target position and 11 times larger at the near target position. Despite this, the amount of retinal slip at the nearest target distance was still less than it was with $\times 4$ magnification of the distant target (Fig. 9, *A*, *B*, *E*, and *F*). There are several possible explanations for greater image slip velocity with magnification than with a comparable unmagnified target distance: First, when images on the retina are magnified telescopically, any given rotation of the head causes greater image motion than would be caused by the same head movement with unaided vision. Second, magnifying spectacles require a different eye or eye-head movement strategy to stabilize gaze. These two factors complicate the task of image stabilization for an unadapted VOR.

Head-movement strategies play an active role in gaze stabilization during both near target fixation and during magnification of vision. The movement pattern of the orbit has been described previously as acting to stabilize vision during locomotion (Demer and Viirre 1996) as well as to help correct for errors caused by near targets and inverting spectacles (Bloomberg et al. 1992). We also found that orbit translation velocity decreased concurrent with an increase in rotational velocity for more proximal targets. Although this strategy is appropriate for stabilizing gaze on near targets, it would be a poor one during magnified vision due to increased sensitivity to orbit rotation. With magnified vision, both orbit rotation and translation decreased. This seems to indicate a dynamic adjustment of strategy coordinating translation and rotation according to environmental circumstances. The reduction of orbit translation with magnification does help stabilize gaze, but to no greater degree than it would with

unmagnified vision. Further evidence that head movement strategy is the result of neural mechanisms and not just the result of mechanical linkage of the head to the trunk, is provided by the frequency spectra (Fig. 3), which show that antiphase head translation-rotation behavior only occurs at the peak frequency and some local maxima < 4 Hz.

Internal target distance estimates

Because appropriate image stabilization depends on target distance, the gaze stabilization system must estimate distance. The brain probably uses multiple cues such as vergence angle, accommodation, object size, and relationship to the surroundings to determine a single estimate of target distance. The angle of binocular convergence could be used as an estimate of target distance (Paige 1991; Snyder et al. 1992). However, in darkness, convergence is often not maintained although the low-frequency VOR gain required for a specific target distance is maintained (Viirre and Demer 1996). It is also likely that other cues such as accommodation, image size, and context contribute to estimation of target distance (Busetini et al. 1994). Vergence measured here in six subjects correlated very well with actual target distance in the light (Fig. 12). In darkness, the far and intermediate target distances were underestimated by vergence, whereas the nearest target distance was overestimated.

A parallax technique, using the lines of gaze from two temporally different eye positions, was developed as an alternative empiric means of assessing the oculomotor estimate of target distance; we do not suppose it to imply a different biological mechanism for determining target distance. However, the parallax estimate of target distance significantly differed the vergence estimate (Fig. 12). Parallax is expected to be less precise than the convergence technique because the translation of an eye in space over a short time was generally smaller than the interpupillary distance. There might also be temporal variation in the estimated target distance as the eye translated between positions. Despite its lower accuracy, the parallax technique offers some advantages in that only monocular eye position is required, and there is no requirement to define target distance during calibration. The trends obtained by the parallax method mirrored those of the convergence method. It seems plausible that both the convergence and parallax methods reflect to some degree the state of a target distance estimator mechanism in the brain.

APPENDIX

Coordinate system corrections

Experimental data were sampled from search coils on eyes and head as well as from the FGM sensor. Search coils were approximately centered on the eyes, and the head coil and flux sensor were mounted relative to the same axes. However, geometric corrections were made for possible coil slippage and alignment error in the coordinate systems of the sensors. To find central gaze position, calibration trials were executed repeatedly throughout the experiment. During calibration trials, the subject was asked to remain still and look directly at the target mounted at eye level. Measurements of three-dimensional angular positions of the eyes and head were taken using both the FGM sensor and the coil system with respect to the right-handed coordinate system with the *z* axis posi-

tive downward, the y axis positive to the subject's right, and the x axis positive forward. Angular eye position recorded by the

search coils was used to calculate the following rotation matrix (Haslwanter 1995)

$$\begin{bmatrix} \cos(\phi) \cos(\theta) & -\cos(\psi) \sin(\theta) + \sin(\psi) \sin(\phi) \cos(\theta) & \sin(\psi) \sin(\theta) + \cos(\psi) \sin(\phi) \cos(\theta) \\ \cos(\phi) \sin(\theta) & \cos(\psi) \cos(\theta) + \sin(\psi) \sin(\phi) \cos(\theta) & -\sin(\psi) \cos(\theta) + \cos(\psi) \sin(\phi) \sin(\theta) \\ -\sin(\phi) & \sin(\psi) \cos(\phi) & \cos(\psi) \cos(\phi) \end{bmatrix} \quad (A1)$$

This matrix can be used to describe the relationship between central gaze and the axis of a search coil. When the angular eye position is entered into this matrix, we will call it H , and using FGM angular data, we will call it F . We will use E' , H' , and F' to indicate the values of these parameters during central gaze. For the sake of further analysis, we transform the data to a coordinate system where at central gaze, θ , ϕ , and ψ are all zero. When data are given in this coordinate system, we denote it by E° , H° , and F° . If we take the inverse of the central gaze matrix (which for a rotation matrix is also the transpose) and multiply the rotation matrices of data collected during trial by it, the data then will be in relationship to the axes defined by central gaze

$$E'^\circ = E' E'^{-1} = 1 \quad (A2)$$

Thus the eye position in the transformed coordinate system is

$$E^\circ = E E'^{-1} \quad (A3)$$

and head position in the transformed coordinate system is

$$H^\circ = H H'^{-1} \quad (A4)$$

We do not assume the FGM coordinate system is the same as the search coil system because the transmitter or receiver could be misaligned slightly relative to the magnetic search coil system. Ideally the FGM and the head coils should give the same values for any position of the head. Creating a separate rotation matrix ensures that this will be the case

$$F^\circ = F F'^{-1} \quad (A5)$$

Rotation matrices also can be used to correct for translation in space. We define two vectors: e_r , the vector from the FGM receiver to the eye, necessary to obtain orbital translation, and e_t , the vector from the FGM transmitter (defined as the origin of our coordinate system) to the eye. The vector from the transmitter to the receiver is r . The vector is measured in the coordinate system defined by the orientation of the FGM sensor relative to the head. This vector is converted to the coordinate system defined by central gaze using

$$e_r^\circ = F'^{-1} e_r \quad (A6)$$

$$r^\circ = F'^{-1} r \quad (A7)$$

$$e_t^\circ = r^\circ + e_r^\circ F^\circ \quad (A8)$$

In the subsequent derivation, positions will be given without superscripts and should be assumed to be in reference to the axes defined by central gaze, with the origin being the position of the FGM transmitter.

Calculation of gaze position

First we will define a unit vector, n , that is parallel to the line of gaze

$$n = \begin{bmatrix} \cos \theta \cos \phi \\ \sin \theta \cos \phi \\ -\sin \phi \end{bmatrix} \quad (A9)$$

This allows us to find define parametric equations for the line of gaze knowing that the center of the eye is located at position (e_x, e_y, e_z)

$$x = e_x + \alpha \cos \theta \cos \phi$$

$$y = e_y + \alpha \sin \theta \cos \phi$$

$$z = e_z - \alpha \sin \phi \quad (A10)$$

We assure that the target screen is always perpendicular to the floor and are also careful to align the target on the screen to eye level during the experiment so line of central gaze is also parallel to the floor. Although our screen was always perpendicular to the line of sight in the current experiments, we will generalize equations for the screen so that we can account for a screen tilted in the yaw axis by an angle, γ . The unit vector normal to the screen is given by

$$\begin{bmatrix} \cos \gamma \\ \sin \gamma \\ 0 \end{bmatrix} \quad (A11)$$

If is the distance to the screen, the equation defining the plane of the screen is

$$x \cos \gamma + y \sin \gamma = D \cos \gamma \quad (A12)$$

Substituting Eq. 10 into 12 allows us to solve for the parameter, α .

$$\alpha = \frac{D \cos \gamma - e_x \cos \gamma - e_y \sin \gamma}{\cos \gamma \cos \theta \cos \phi + \sin \gamma \sin \theta \cos \phi} \quad (A13)$$

Substituting back into Eq. 10, we can find the point in space where gaze intersects the screen

$$\begin{aligned} x &= \frac{e_x \sin \theta \sin \gamma - e_y \cos \theta \sin \gamma + D \cos \theta \cos \gamma}{\cos \theta \cos \gamma + \sin \theta \sin \gamma} \\ y &= \frac{e_y \cos \theta \cos \gamma - e_x \sin \theta \cos \gamma + D \sin \theta \cos \gamma}{\cos \theta \cos \gamma + \sin \theta \sin \gamma} \\ z &= e_z - \frac{\tan \phi (D \cos \gamma - e_x \cos \gamma - e_y \sin \gamma)}{\cos \theta \cos \gamma + \sin \theta \sin \gamma} \end{aligned} \quad (A14)$$

Parallax method

We can calculate the oculomotor estimate of target distance based on two lines of gaze as shown in Fig. 14. These lines of gaze can be determined by measuring the positions and angles of both eyes simultaneously or the position and angles of one eye at different times. Although ideally these two lines of gaze should intersect at the target, in fact real lines never exactly intersect in three-dimensional space. To avoid this problem, we assume that the intended position of gaze is at the segment defining the shortest distance between these two lines. We define the two lines of gaze in parametric form as follows

line 1: line 2:

$$x = x_1 + a_1 t_1 \quad x = x_2 + a_2 t_2$$

$$y = y_1 + b_1 t_1 \quad y = y_2 + b_2 t_2$$

$$z = z_1 + c_1 t_1 \quad z = z_2 + c_2 t_2 \quad (A15)$$

The starting point of the line of gaze is the position of the eye given by x_1, y_1 , and z_1 for line 1, and x_2, y_2 , and z_2 for line 2. The direction of gaze is given by vectors $\langle a_1, b_1, c_1 \rangle$ and $\langle a_2, b_2, c_2 \rangle$.

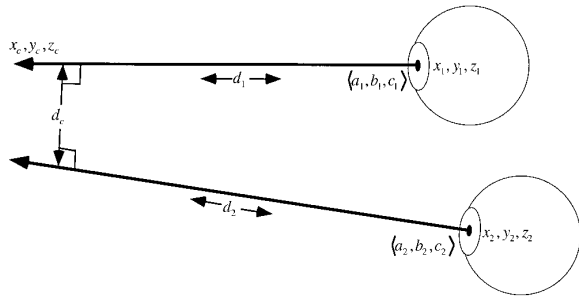


FIG. 14. Methods of target distance estimation. Two eye positions are required; these can either be for both eyes at a single point in time or for the same eye separated at different times. Positions of eyes in space (x_1, y_1, z_1 and x_2, y_2, z_2) and directions of lines of gaze ($\langle a_1, b_1, c_1 \rangle$ and $\langle a_2, b_2, c_2 \rangle$) are calculated as described in the APPENDIX. Point on the first line of gaze that is closest to the second line of gaze is defined as x_c, y_c, z_c . Shortest distance between these 2 lines of gaze (d_c) is along segment perpendicular to both lines of gaze. Distance from first eye position to x_c, y_c, z_c (d_1) is defined as the implied target distance. Distance from second eye position to the connecting segment is given by d_2 , which is not significantly different from d_1 when distance between the 2 eye positions is small relative to target distance.

The shortest distance between two lines is along a segment perpendicular to both lines. We can find a vector perpendicular to both lines by taking the cross product of the two gaze vectors

$$\begin{bmatrix} a_1 \\ b_1 \\ c_1 \end{bmatrix} \times \begin{bmatrix} a_2 \\ b_2 \\ c_2 \end{bmatrix} = \begin{bmatrix} b_1 c_2 - c_1 b_2 \\ c_1 a_2 - a_1 c_2 \\ a_1 b_2 - b_1 a_2 \end{bmatrix} \quad (A16)$$

We also define the starting point of our connecting line as being (x_c, y_c, z_c), which is also a point on line 1. Thus the equation of the line connecting these two vectors is

$$\begin{aligned} x &= x_c + (b_1 c_2 - c_1 b_2) t_c \\ y &= y_c + (c_1 a_2 - a_1 c_2) t_c \\ z &= z_c + (a_1 b_2 - b_1 a_2) t_c \end{aligned} \quad (A17)$$

Because we defined the starting point of this line to be on line 1 at distance d_1

$$\begin{aligned} x_c &= x_1 + a_1 d_1 \\ y_c &= y_1 + b_1 d_1 \\ z_c &= z_1 + c_1 d_1 \end{aligned} \quad (A18)$$

The connecting line will cross the second line of gaze after the distance d_c along the connecting line and at a distance from the eye, d_2 , along the second line of gaze

$$\begin{aligned} x_c &= x_2 + a_2 d_2 - (b_1 c_2 - c_1 b_2) d_c \\ y_c &= y_2 + b_2 d_2 - (c_1 a_2 - a_1 c_2) d_c \\ z_c &= z_2 + c_2 d_2 - (a_1 b_2 - b_1 a_2) d_c \end{aligned} \quad (A19)$$

Equations 18 and 19 can be combined to yield three equations with d_1, d_2 , and d_c unknowns

$$\begin{aligned} x_2 + a_2 d_2 - (b_1 c_2 - c_1 b_2) d_c &= x_1 + a_1 d_1 \\ y_2 + b_2 d_2 - (c_1 a_2 - a_1 c_2) d_c &= y_1 + b_1 d_1 \\ z_2 + c_2 d_2 - (a_1 b_2 - b_1 a_2) d_c &= z_1 + c_1 d_1 \end{aligned} \quad (A20)$$

Solving for d_1 we get the implied distance to the target

$$\begin{aligned} d_1 &= \{(a_1 b_2 - b_1 a_2)[a_2(y_1 - y_2) + b_2(x_2 - x_1)] \\ &+ (c_1 a_2 - a_1 c_2)[a_2(z_2 - z_1) + c_2(x_1 - x_2)] \} \end{aligned}$$

$$\begin{aligned} &+ (b_1 c_2 - c_1 b_2)[b_2(z_1 - z_2) + c_2(y_2 - y_1)] / [(a_1 b_2 - b_1 a_2)^2 \\ &+ (c_1 a_2 - a_1 c_2)^2 + (b_1 c_2 - c_1 b_2)^2] \end{aligned} \quad (A21)$$

The distance from the eye at the second location (d_2) is usually not calculated because in general targets are much further away than the distance between the two eye positions so that $d_1 \approx d_2$.

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REFERENCES

- BARNES, G. R. AND SMITH, R. The effect on visual discrimination of image movement across the stationary retina. *Aviat. Space Environ. Med.* 52: 466–472, 1981.
- BLOOMBERG, J. J., RESCHKE, M. F., HUEBNER, W. P., AND PETERS, B. T. The effects of target distance on eye and head movement during locomotion. *Ann. NY Acad. Sci.* 656: 699–707, 1992.
- BOYLE, R., BELTON, T., AND MCCREA, R. A. Responses of identified vestibulo-spinal neurons to voluntary eye and head movements in the squirrel monkey. *Ann. NY Acad. Sci.* 781: 244–263, 1996.
- BRONSTEIN, A. M. AND GREYSTY, M. A. Short latency compensatory eye movement responses to transient linear head acceleration: a specific function of the otolith-ocular reflex. *Exp. Brain Res.* 71: 406–410, 1988.
- BUSETTINI, C., MILES, F. A., SCHWARZ, U., AND CARL, J. R. Human ocular responses to translation of the observer and of the scene: dependence on viewing distance. *Exp. Brain Res.* 100: 484–494, 1994.
- BÜTTNER-ENNEVER, J. A. Patterns of connectivity in the vestibular nuclei. *Ann. NY Acad. Sci.* 656: 363–378, 1992.
- CARL, J. R. AND GELLMAN, R. S. Human smooth pursuit: stimulus-dependent responses. *J. Neurophysiol.* 57: 1446–1463, 1987.
- COLLEWIJN, H. The vestibulo-ocular reflex: an outdated concept? *Prog. Brain Res.* 80: 197–209, 1989.
- COLLEWIJN, H. The vestibulo-ocular reflex: is it an independent subsystem? *Rev. Neurol. (Paris)* 145: 502–512, 1989.
- COLLEWIJN, H., VAN DER MARK, F., AND JANSEN, T. C. Precise recording of human eye movements. *Vision Res.* 15: 447–450, 1975.
- CRANE, B., VIIRRE, E., AND DEMER, J. Effect of age on the vestibulo-ocular reflex (VOR) and visual-vestibular interactions during natural movements. *Soc. Neurosci. Abstr.* 22: 274, 1996.
- CRANE, B. T. AND DEMER, J. L. Gaze stabilization in six degrees of freedom during natural movements. In: *Vision Science and Its Applications*. Washington, DC: Optical Society of America, 1997, p. 182–185.
- CRANE, B. T., VIIRRE, E. S., AND DEMER, J. L. The human horizontal vestibulo-ocular reflex during combined linear and angular acceleration. *Exp. Brain Res.* 114: 304–320, 1997.
- DEMER, J. L. Mechanisms of human vertical visual-vestibular interaction. *J. Neurophysiol.* 68: 2128–2146, 1992.
- DEMER, J. L. AND AMJADI, F. Dynamic visual acuity of normal subjects during vertical optotype and head motion. *Invest. Ophthalmol. Vis. Sci.* 34: 1894–1906, 1993.
- DEMER, J. L., GOLDBERG, J., PORTER, F. I., JENKINS, H. A., AND SCHMIDT, K. Visual-vestibular interaction with telescopic spectacles. *J. Vestib. Res.* 1: 263–277, 1990.
- DEMER, J. L., HONRUBIA, V., AND BALOH, R. W. Dynamic visual acuity: a test for oscillopsia and vestibulo-ocular reflex function. *Am. J. Otol.* 15: 340–347, 1994.
- DEMER, J. L., PORTER, F. I., GOLDBERG, J., JENKINS, H. A., AND SCHMIDT, K. Adaptation to telescopic spectacles: vestibulo-ocular reflex plasticity. *Invest. Ophthalmol. Vis. Sci.* 30: 159–170, 1989.
- DEMER, J. L. AND VIIRRE, E. S. Visual-vestibular interaction during standing, walking, and running. *J. Vestib. Res.* 6: 295–313, 1996.
- GAGNON, J., ROTH, J., FINZER, B., HOFMANN, R., HAYCOCK, K., SIMPSON, J., AND FELDMAN, D. *SuperANOVA*. Berkeley, CA: Abacus Concepts, 1991.
- GREYSTY, M. A., BRONSTEIN, A. M., AND BARRATT, H. Eye movement re-

- sponses to combined linear and angular head movement. *Exp. Brain Res.* 65: 377–384, 1987.
- GROSSMAN, G. E. AND LEIGH, R. J. Instability of gaze during locomotion in patients with deficient vestibular function. *Ann. Neurol.* 27: 528–532, 1990.
- GROSSMAN, G. E., LEIGH, R. J., BRUCE, E. N., HUEBNER, W. P., AND LANSKA, D. J. Performance of the human vestibuloocular reflex during locomotion. *J. Neurophysiol.* 62: 264–272, 1989.
- HASLWANTER, T. Mathematics of three-dimensional eye rotations. *Vision Res.* 35: 1727–1739, 1995.
- HINE, T. AND THORN, F. Compensatory eye movements during active head rotation for near targets: effects of imagination, rapid head oscillation and vergence. *Vision Res.* 27: 1639–1657, 1987.
- LISBERGER, S. G. Visual tracking in monkeys: evidence for short-latency suppression of the vestibuloocular reflex. *J. Neurophysiol.* 63: 676–688, 1990.
- LISBERGER, S. G. AND FUCHS, A. F. Role of primate flocculus during rapid behavioral modification of vestibuloocular reflex. II. Mossy fiber firing patterns during horizontal head rotation and eye movement. *J. Neurophysiol.* 41: 764–777, 1978.
- MCCREA, R. A., CHEN-HUANG, C., BELTON, T., AND GDOWSKI, G. T. Behavior contingent processing of vestibular sensory signals in the vestibular nuclei. *Ann. NY Acad. Sci.* 781: 292–303, 1996.
- PAIGE, G. D. The influence of target distance on eye movement responses during vertical linear motion. *Exp. Brain Res.* 77: 585–593, 1989.
- PAIGE, G. D. Linear vestibulo-ocular reflex (LVOR) and modulation by vergence. *Acta Otolaryngol. Suppl. (Stockh.)* 481: 282–286, 1991.
- PAIGE, G. D. AND SARGENT, E. W. Visually-induced adaptive plasticity in the human vestibulo-ocular reflex. *Exp. Brain Res.* 84: 25–34, 1991.
- PAIGE, G. D. AND TOMKO, D. L. Eye movement responses to linear head motion in the squirrel monkey. I. Basic characteristics. *J. Neurophysiol.* 65: 1170–1182, 1991.
- POZZO, T., BERTHOZ, A., AND LEFORT, L. Head stabilization during various locomotor tasks in humans. I. Normal subjects. *Exp. Brain Res.* 82: 97–106, 1990.
- ROBINSON, D. A. A method of measuring eye movement using a scleral search coil in a magnetic field. *IEEE Trans. Biomed. Elect.* 10: 137–145, 1963.
- SCHWARZ, U., Busetini, C., AND MILES, F. A. Ocular responses to linear motion are inversely proportional to viewing distance. *Science* 245: 1394–1396, 1989.
- SCHWARZ, U. AND MILES, F. A. Ocular responses to translation and their dependence on viewing distance. I. Motion of the observer. *J. Neurophysiol.* 66: 851–864, 1991.
- SHIRADO, O., GIZZI, M., HARPER, H., AND WANG, W. Suppression of vestibular nystagmus by forced convergence in normal human subjects. *J. Pediatr. Ophthalmol. Strabismus* 34: 52–57, 1997.
- SNYDER, L. H. AND KING, W. M. Effect of viewing distance and location of the axis of head rotation on the monkey's vestibuloocular reflex. I. Eye movement responses. *J. Neurophysiol.* 67: 861–874, 1992.
- SNYDER, L. H., LAWRENCE, D. M., AND KING, W. M. Changes in vestibulo-ocular reflex (VOR) anticipate changes in vergence angle in monkey. *Vision Res.* 32: 569–575, 1992.
- STEINMAN, R. M. AND COLLEWIJN, H. Binocular retinal image motion during active head rotation. *Vision Res.* 20: 415–429, 1980.
- TAKEDA, N., IGARASHI, M., KOIZUKA, I., CHAE, S. Y., AND MATSUNAGA, T. Vestibulo-ocular reflex in eccentric rotation in squirrel monkeys. *Am. J. Otolaryngol.* 12: 185–190, 1991.
- TILIKET, C., SHELHAMER, M., TAN, H. S., AND ZEE, D. S. Adaptation of the vestibulo-ocular reflex with the head in different orientations and positions relative to the axis of body rotation. *J. Vestib. Res.* 3: 181–195, 1993.
- TWEED, D. AND VILIS, T. Geometric relations of eye position and velocity vectors during saccades. *Vision Res.* 30: 111–127, 1990.
- VIIRRE, E., TWEED, D., MILNER, K., AND VILIS, T. A reexamination of the gain of the vestibuloocular reflex. *J. Neurophysiol.* 56: 439–450, 1986.
- VIIRRE, E. S. AND DEMER, J. L. The human vertical vestibulo-ocular reflex during combined linear and angular acceleration with near target fixation. *Exp. Brain Res.* 112: 313–324, 1996.