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Human Gaze Stabilization During Active Head Translations

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Medendorp, W. P., J.A.M. Van Gisbergen, and C.C.A.M. Gielen. Human gaze stabilization during active head translations. *J Neurophysiol* 87: 295–304, 2002; 10.1152/jn.00892.2000. This study investigated how binocular gaze is controlled to compensate for self-generated translational movements of the head where geometric requirements dictate that the ideal gaze signal needs to be modulated by the inverse of target distance. Binocular gaze (eye plus head) was measured for visual and remembered targets at various distances in six human subjects during active head translations at frequencies of 0.25, 0.5, 1.0, and 1.5 Hz. We found that, during head translations, gaze changes were achieved by a combination of eye and head rotations. Accordingly, stabilization performance was characterized by the gaze response parameters sensitivity and phase, where sensitivity is defined as the ratio of gaze velocity and translational eye velocity and where phase refers to the phase delay of gaze velocity relative to translational eye velocity. In the analysis, we used a binocular coordinate system yielding a version and a vergence component. We examined how frequency and target distance, estimated from the vergence angle, affected sensitivity and phase of the version component of the gaze signal and compared the results to the requirements for ideal performance. The relation between gaze sensitivity and the inverse of distance was characterized by a linear regression analysis. The ratio of the slope of the linear regression and the slope required for ideal stabilization provided a measure for the degree of "distance compensation." The results show that distance compensation was better for a visual target than for remembered targets in darkness, and behaved according to low-pass characteristics in both target conditions. It declined from 1.00 to 0.84 for visual targets and from 0.87 to 0.57 for remembered targets in the frequency range 0.25–1.5 Hz. The intercept obtained from the regression yielded the gaze response at zero vergence and specified a "default sensitivity" of gaze compensation. Default sensitivity increased with frequency from 0.02 at 0.25 Hz to 0.10°/cm at 1.5 Hz for visual targets and from 0.04 to 0.16°/cm in darkness. The phase delays of the gaze response increased on average from 2 to 7° in the frequency range 0.25–1.5 Hz. In comparison with earlier passive studies, active translation compensation in the dark is superior at all frequencies where comparison was possible. We conclude that a nonvestibular signal with low-pass characteristics contributes to gaze during active head translations.

INTRODUCTION

An important issue in the realm of eye-head coordination is how retinal images can be held stable during movements of the head. Obviously, the vestibuloocular reflex (VOR) plays an important role by producing eye movements to compensate for head movements. The VOR is mediated by two types of specialized vestibular receptors. The semicircular canals respond to the angular acceleration of the head, and the peripheral otolith organs detect linear acceleration of the head, caused by translational movements and by the pull of gravity.

This paper reports how binocular gaze is controlled to compensate for self-generated translational head motion. Under these conditions, complex geometric requirements have to be met by the control system, reflecting the fact that compensatory eye movements, ideally, should depend not only on head translation but also on the spatial location of the object to be fixated relative to each eye (Angelaki 1998; Paige and Tomko 1991a,b; Paige et al. 1998; Schwarz and Miles 1991; Schwarz et al. 1989; Telford et al. 1997). When the head moves orthogonally to the line of sight, the ideal gaze response should be inversely related to target distance.

Another complicating factor for the control of gaze during head translations stems from the peripheral otolith organs. They produce ambiguous information in the sense that they respond to both gravity and translational accelerations. Therefore it is essential for the CNS to distinguish head translation from head tilt relative to gravity even though the otoliths cannot make this distinction. In the light, the visual system can help to distinguish between gravitational and translation components due to its ability to detect translations out of optic flow information caused by egomotion, at least for low-frequency movements. In the absence of visual input, it is well-known that the disambiguation process takes place at a central level in the nervous system. The literature presents two models for this disambiguation process. The "frequency parsing" model proposes that the distinction is made by filtering the otolith signal differently in two pathways (Paige and Seidman 1999; Telford et al. 1997). According to this hypothesis the brain interprets low-frequency otolith input as tilt, whereas high-frequency accelerations are interpreted as due to translations. An alternative model, the so-called "multisensory integration" hypothesis, combines information from the canals and the otoliths to differentiate between head tilt and translation (Angelaki et al. 1999; Merfeld et al. 1999). Study of the translational VOR may provide valuable data to resolve these issues.

Until now, all studies focusing on gaze control for image stabilization used passive stimulus conditions, where subjects were translated in a moving chair. These studies have shown a far from optimal performance in the dark, especially for low-frequency movements. As far as we know, there are no data about the performance of humans during *active* (i.e., self-generated) translational movements. In active movement conditions, performance might be better since additional sources of information about the movement, e.g., proprioception, ef-

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ference copies, or any other source of nonvestibular information, are potentially available to generate the appropriate eye movement responses. To fill this gap, this paper investigates the ability of human subjects to maintain binocular fixation on near targets during active lateral head translations to examine whether additional signals present during active movement conditions allow the system to optimize retinal image stabilization.

METHODS

Subjects

Six male subjects, between 20 and 29 yr of age, gave informed consent to participate in the experiments. One subject (*PM*) was familiar with the purpose of the experiment. His results were not different from those of the other subjects. All subjects had normal or corrected-to-normal (*subject MZ*) visual acuity. All subjects were free of any known sensory, perceptual, or motor disorders. Details about the setup and methods used to measure and analyze eye and head kinematics as well as the general paradigm have been described extensively in Medendorp et al. (2000). Here we provide only a brief summary and specify the response parameters that were used to analyze the data.

Measurement of head and eye motion

Location and orientation of the head as well as the locations of the ears and eyes in space were recorded using an OPTOTRAK 3020 motion analysis system (Northern Digital). This device tracks infrared-emitting diodes (ireds), attached to a moving object within a precalibrated space of ~1.5 m^3. To determine the location of the head, the subject wore a helmet ($<$0.25 kg) with four ireds at the top and two ireds at the backside. Prior to the experiment, the locations of the eyes and ears were calibrated with respect to the ireds on the helmet. During this calibration procedure, the subject faced the OPTOTRAK camera while wearing the helmet with four additional temporary ireds, one near the auditory meatus and one on each closed eyelid. The three-dimensional (3-D) locations of these ireds, which uniquely defined the location of the ears and eyes relative to the helmet, were recorded together with the ireds on the helmet. After the temporary ireds were removed, we ensured that the helmet remained stable on the head during the entire experiment. During the experiment, data were collected using a sample frequency of 100 Hz and stored on hard disk for off-line analysis. The coordinates of the ireds were transformed to a right-handed body-fixed coordinate system, as specified in Medendorp et al. (2000). The *x-y* plane was aligned with the subject's horizontal plane. The positive *x*-axis pointed forward, the positive *y*-axis was directed to the left (i.e., along the shoulder line), seen from the subject, and the *z*-axis pointed upward. The origin of the coordinate system coincided with the center of the interaural axis when the subject was looking straight ahead. From the helmet data the positions of the ears and eyes in space were computed for each instantaneous head posture on the basis of the calibration data. The orientation and location of the head were determined with respect to the stationary head-reference posture adopted when the subject was fixating straight-ahead (Veldpaus et al. 1988). Head orientations and locations could be determined with an accuracy $<0.2°$ and <0.2 mm, respectively. Binocular horizontal and vertical eye-in-space orientations (i.e., gaze) were measured using the search coil technique in a large magnetic field system (3.3 × 3.3 × 3.3 m) with alternating orthogonal magnetic fields at frequencies of 48, 60, and 80 kHz. After demodulation, the signals from the eye coils were amplified and low-pass filtered (150 Hz) and sampled at 500 Hz per channel. Data were stored on hard disk for off-line analysis. The resolution of this recording technique was $<0.04°$ in all directions. For both eye and head, leftward and downward rotations were taken positive.

Experimental paradigm

Subjects were instructed to make sinusoidal horizontal head translations (amplitude ~5 cm) while standing in a completely darkened room. Head translations were made along the horizontal shoulder *y*-axis of the coordinate system. During these movements the subject's feet did not move, since subjects made translational head movements by movements in the hip and the trunk. Head translation along the other axes was discernable but small, i.e., peak amplitudes <1.5 cm for forward-backward motion (*x*-axis) and <0.5 cm for upward-downward motion (*z*-axis). The movements were carried out at four different frequencies (0.25, 0.5, 1.0, and 1.5 Hz) indicated by a metronome. Since movements were made actively, the exact frequencies could vary slightly. Before the actual measurements, subjects practiced a few trials to become familiar with the task for each movement frequency. No feedback was given during the actual experiment.

During the head translations, subjects were instructed to maintain gaze on an earth-fixed visual target (a horizontal/vertical array of 4 small light-emitting diodes, size 0.5 cm), which was at eye level in front of the subject's cyclopean eye when the head was in the reference position (as defined above). In the first half of each trial, the target remained visible to the subject. Thereafter, the target was extinguished and the subject was instructed to keep gaze on the remembered target. In separate runs, the target was presented at four different viewing distances of approximately 1.5, 1, 0.5, and 0.2 m. A brief rest period was provided between trials. The complete experiment consisted of 16 different conditions (4 frequencies × 4 target distances) and lasted for about 30 min.

Kinematic constraints for ideal gaze stabilization

The requirements on gaze stabilization are completely determined by the geometric relationship between the position of the eyes and the target. When the target is far away, no compensatory eye movements are required to maintain a stable retinal image. When the target comes closer, it can be shown that the magnitude of the required compensatory eye movement has a nonlinear relation with target distance and target eccentricity (Angelaki 1998; Paige and Tomko 1991a,b; Paige et al. 1998; Schwarz and Miles 1991; Schwarz et al. 1989; Telford et al. 1997). In case the head moves orthogonally to the line of sight, geometry requires that the compensatory angular eye velocity ($-\dot{E}_R$) is related to the translational head velocity ($\dot{H}_T$) by $-\dot{E}_R = \dot{H}_T/D$ with D the distance of the target relative to the eye and the minus sign indicating that the movement is compensatory. Of course, when the two eyes are directed to a single near target, the head cannot move orthogonally to the line of sight of both eyes simultaneously. This implies that both eyes need to move slightly differently, which will be explored in more detail in RESULTS (Fig. 3). Although we instructed our subjects to generate only translational head motion, their head movements typically also had a small rotational component (see Fig. 1). It can be shown that in that case gaze (eye-in-space) velocity should equal translational velocity of the eye in space multiplied by $1/D$.

Data analysis

Data analysis was performed using Matlab software (The Mathworks). After low-pass filtering with a cutoff frequency of 25 Hz, the OPTOTRAK data were interpolated linearly to match the 500-Hz sampling rate of the search coil system. Calibrated eye-in-space orientation signals were low-pass filtered at 75 Hz (FIR filter, Matlab). Eye-in-head orientation was calculated by subtracting head orienta-

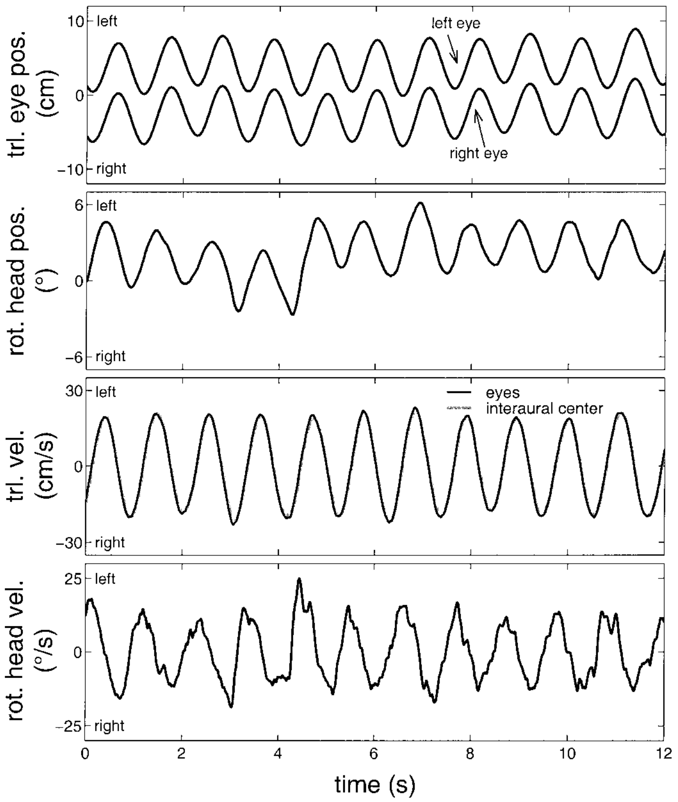

FIG. 1. Head kinematics of *subject AB* instructed to generate sinusoidal horizontal head translations of 1 Hz. The *top panel* shows the translation of the eyes in time, having a peak-to-peak amplitude of ~8 cm. The sinusoidal traces of the 2 eyes are separated by ~6.5 cm, which equals the interpupilar distance. The *2nd panel* shows that the movements involved also small horizontal head rotations. The *3rd panel* depicts both the translational eye velocity and the translational velocity of the interaural center. Both velocities are very similar, indicating that the effect of the head rotations on the translation of the eyes is small. Finally, the *bottom panel* shows that angular head velocity has a maximum amplitude of ~15°/s.

tion from eye-in-space orientation. Saccade detection was performed as described in Medendorp et al. (2000).

The signals required for optimal gaze stabilization were determined using the instantaneous locations of both eyes with respect to the target (using OPTOTRAK data), from which the ideal eye-in-space orientation, and in combination with head orientation in space, the ideal eye-in-head orientation signals could be calculated.

To describe the eye movements, we used a binocular coordinate system that distinguishes eye movements in direction (version) from eye movements in depth (vergence). Version angle (conjugate part) was computed from left (L) and right (R) eye-in-head orientation data as $(L + R)/2$; vergence angle was calculated as $(L - R)$. The vergence signal, the angle between the gaze directions of the two eyes intersecting at the target, was used to determine the fixation distance of the subject. Ideal version and vergence angles were computed based on the OPTOTRAK data, which provided information about the location of the head, the eyes, and the target. While drawing a clear distinction between version and vergence, we do not wish to imply that they are totally independent subsystems.

For the binocular analysis, eye and head orientation signals were digitally differentiated using a two-point differentiation technique to obtain velocity signals. In similar fashion, eye and head translational velocity signals were determined from their location signals. Using the velocity signals, we performed the same analysis as described in Paige et al. (1998). Individual cycles in the response traces were identified on the basis of zero-crossings in the translational eye velocity. We excluded cycles starting in the first second of the trial and those ending in the last second of the trial. Also cycles that started within 250 ms after target switch-off were discarded from further analysis. In the remaining cycles, saccadic epochs were identified in the eye angular velocity data and excluded from subsequent harmonic analysis. A least-squares sinusoidal fit to the fundamental frequency, performed on each cycle excluding the saccades, served to obtain the response parameters sensitivity and phase.

Since vertical eye and head movements were small, response parameters were only determined for the horizontal component. The data show that besides eye rotations, also head rotations were generated during the task. To quantify their effect, we computed the response parameters, sensitivity and phase, for each of them. For the head, sensitivity was defined as the ratio of peak angular head velocity (°/s) and peak translational eye velocity (cm/s), and phase was taken as the phase of the angular head velocity relative to the phase of the translational eye velocity. For the analysis of eye-in-head signals, sensitivity and phase were computed in similar fashion except that conjugate eye-in-head velocity and translational eye velocity were used. Finally, gaze response parameters were determined using gaze velocity and translational eye velocity. It is usual in the literature to define gaze sensitivity as the ratio of gaze velocity and translational head velocity. However, since head rotations also contribute to eye translation (Medendorp et al. 1998) and since for optimal gaze control the actual eye position in space is relevant, rather than head position, we have defined sensitivity as the ratio of gaze velocity and translational eye velocity. The response parameters of the measured signals were compared with the ideal response parameters (using OPTOTRAK data), to obtain a measure for the performance of each subject. We investigated the effect of the fixation distance on the response parameters for each cycle, by relating them to vergence angle expressed in meter-angles (MA; units m^{-1}) (see Telford et al. 1997).

RESULTS

Qualitative observations

TASK EXECUTION. Figure 1 shows a 12-s record from a subject asked to make sinusoidal horizontal head translations of 1 Hz with peak-to-peak amplitude of ~8 cm while fixating a near target at about 20 cm. The *top panel* depicts the translational movement of the two eyes as a function of time. Both eye signals differ by about 6.5 cm, which equals the interpupilar distance. Although we instructed the subject to make purely translational head movements, the *second panel*, showing the horizontal rotation of the head, indicates that the movements also contained small head rotations (amplitude <2°). Since head rotations induce eye translations equal to $r \cdot H_R$, where r refers to the distance of the eye to the head rotation axis, head rotations with an amplitude of 2° at a frequency of 1 Hz would induce translational eye velocities <2 cm/s (peak), which is small relative to the translational eye velocity due to head translations (~20 cm/s peak velocity). This can also be appreciated from the *third panel*, which illustrates that the translational velocities of the two eyes along the (horizontal) y-axis direction are almost indistinguishable from the translational velocity of the interaural center (i.e., the location midway between the 2 ears). If head rotations were substantial, eyes and interaural center would have different translational velocities due to their different distances to the head's rotation axis. Finally, the *bottom panel* depicts the angular velocity of the head, which reaches maximum amplitudes of about 25°/s. The involvement of head rotations was predominantly observed during the high-frequency movements (1.0 and 1.5 Hz) that we have been testing. In the section *Quantitative analysis of gaze*

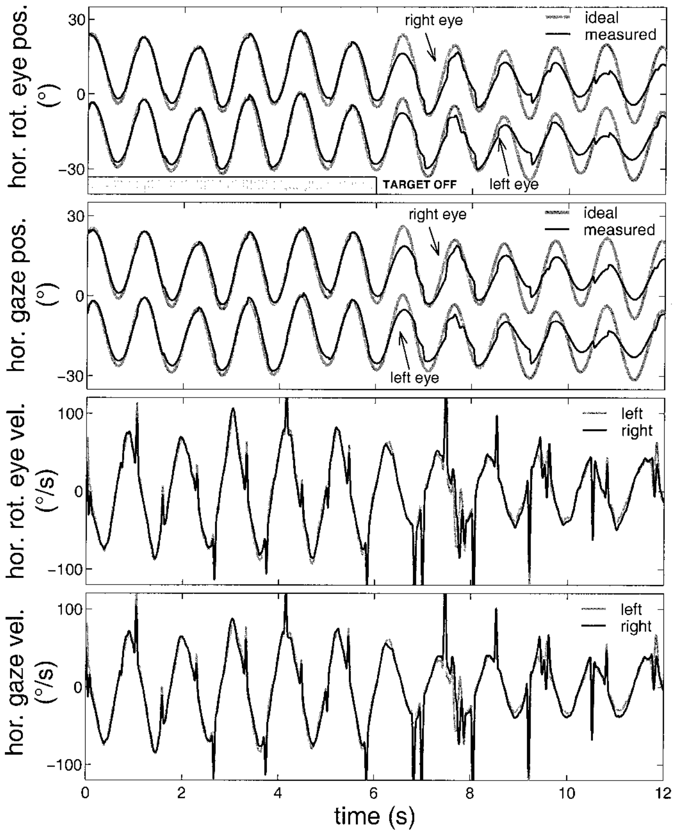

FIG. 2. Horizontal eye responses for the head motion in Fig. 1 while the subject (*AB)* was fixating a target at ~20 cm. The 1st 6 s show data for the visual target condition; the last 6 s present data after target offset. Vertical eye rotations (not shown) were small and are not analyzed. The *top panel* shows the measured eye-in-head orientation signals of the right and left eye (black) superimposed on the ideal eye orientation signals (gray, based on OPTOTRAK data). During the remembered target period, performance deteriorates, and several saccades can be identified. Horizontal gaze (eye in space) excursions in *panel 2* reveal a strong similarity with the corresponding eye-in-head orientation signals. The *3rd* and *bottom panels,* showing the compensatory velocity signals of each eye (eye-in-head and gaze, respectively), demonstrate that differences between left and right eye angular velocity are minor. These panels also show more clearly the presence of small saccades or quick phases after target offset.

signal we describe how to deal with the effect of head rotations. Similar task kinematics (i.e., translational and rotational motion) were found in all subjects.

MONOCULAR SIGNALS. Figure 2 illustrates the horizontal eye movements for the head movements characterized in Fig. 1. The first 6 s present the data for a visual target, followed by another 6 s when the subject was trying to fixate the remembered target location, i.e., after the target was switched off. The *top panel* shows the measured horizontal orientations of the two eyes relative to the head (eye-in-head) during the movement (black traces) superimposed on the signals required for perfect gaze stabilization (gray traces) which were computed on the basis of the OPTOTRAK data. During the visual target period, measured and required eye orientation signals match nicely, although small quick phases can be seen in the data. Performance deteriorates clearly during the remembered target period as indicated by more numerous and prominent small saccades or quick phases and a generally smaller amplitude of the smooth eye movements. Nevertheless, the eye excursions realize a substantial amount of what is necessary to keep gaze fixated on the remembered target location. The *second panel* illustrates the measured gaze signals of each eye (eye in space, in black) together with the optimal gaze signals (gray traces). In the case of perfectly linear motion, i.e., no head rotation, eye-in-space signals are equal to eye-in-head signals. Since the motion also entailed small head rotations (see Fig. 1), eye-in-head and eye-in-space signals are not exactly identical. The *two bottom panels* show the angular eye velocity and gaze velocity, respectively, again demonstrating a strong resemblance. These panels also show more clearly the appearance of small saccades or quick phases after target offset. While left and right eye tend to have similar velocity profiles, close inspection reveals subtle differences, which most likely occur because of their different locations with respect to the target.

BINOCULAR SIGNALS. For further analysis, we converted the data into a binocular coordinate system by making a distinction between the conjugate component (version) and the disconjugate component (vergence) in the movements of the two eyes (see METHODS). Figure 3 shows the data of Fig. 2 in this coordinate system. The *top panel* shows the actual version component of the eyes, which is superimposed on

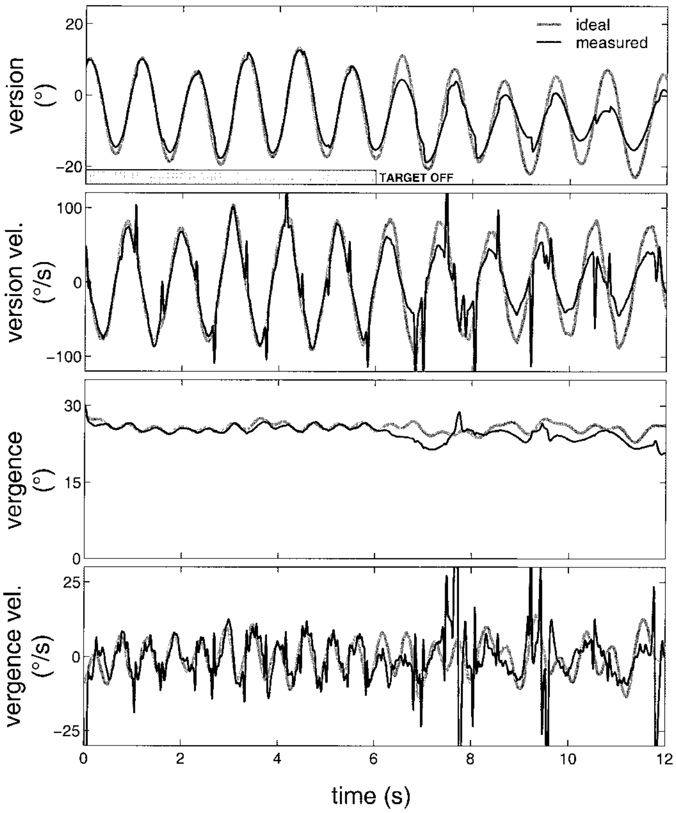

FIG. 3. Binocular signals. Same data as in Fig. 2, now presented in binocular coordinates. For all panels, the ideal trace is given in gray and the measured trace in black. The *top panel* shows actual version (conjugate part) superimposed on required version, computed from the OPTOTRAK data. The conjugate movement of the eyes within the head is in close correspondence to the required signal when the target is visible but reveals deviations after target offset. The *2nd panel* shows version velocity signals superimposed on the required velocity. The modulations in the measured vergence signal (disconjugate part; *panel 3*) match the required modulation for a visual target quite well, but deviate from the required modulation after target offset. The fact that vergence velocity follows required vergence velocity (*4th panel*), at least when the target is visible, indicates that both eyes move differently.

the ideal conjugate response, computed from the OPTOTRAK data. There is a good match between measured and ideal version signals in the visual target condition, but performance decays considerably after target offset. The *second panel* shows measured version velocity both for a visible target and after target offset. The degree of compensation for the head movement is clearly different in the two conditions. The *third panel* illustrates the vergence state of the two eyes. Measured vergence shows double-FMs that nicely correspond to required vergence in the visual target condition. During the sinusoidal movement of the eyes, target distance varies during both the leftward and the rightward parts of the head movement, which necessitates a double-FM of the vergence component, and thus a nonzero vergence velocity (see *bottom panel*). After target offset, this panel shows a less ideal behavior and a clear vergence drift. The *bottom panel* shows that vergence velocity nicely follows the required velocity when the target is visible, indicating that left and right eye move differently. Furthermore, vergence velocity declines after target offset, although its modulations do not completely fade away.

Quantitative analysis of gaze signal

As noticed earlier, subjects produced both eye and head rotations during the task (see Fig. 1). To visualize their contribution to gaze stabilization, Fig. 4 shows sensitivity and phase for head orientation in space, eye-in-head en gaze (eye-in-space) for 1.5-Hz motion for *subject AB*. *A* and *D* show response sensitivity and phase of angular head velocity as a function of fixation distance. Sensitivity of the head is defined here as peak angular head velocity divided by peak translational eye velocity (see METHODS). Phase is defined as the phase difference between angular head velocity and translational eye velocity. Gray circles represent visual target data, whereas filled circles correspond to data collected after target offset. Figure 4*A* clearly shows that head rotations are not negligible and that their contribution increases for more nearby targets. In the extreme case that the head would fully compensate for the translation of the body, its behavior would follow the dashed line. As becomes evident from the linear regressions quantifying the head's sensitivity-vergence relationship (solid lines), the actual head rotations realize $<$20% of what is required for complete stabilization in both target conditions (visual/remem-

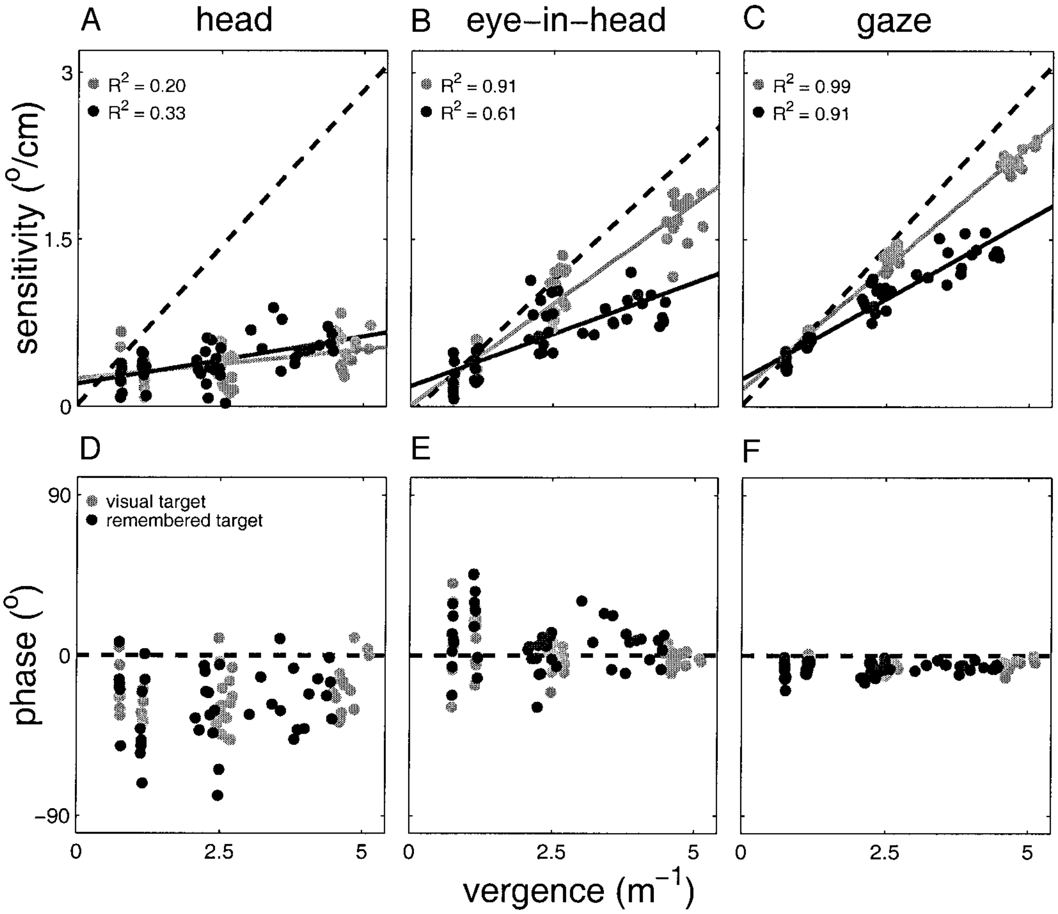

FIG. 4. Sensivity (*A–C*) and phase (*D–F*) of the head responses, the eye-in-head response, and the gaze (eye + head) response, plotted as a function of inverse fixation distance for both visual (gray circles) and remembered (filled circles) target fixations. Subject: *AB*. To obtain fixation distance we expressed vergence angle in m^{-1}. The sensitivity data scatter along a straight fit line with a positive slope, indicating a larger sensitivity for nearer targets. The dashed lines represent the ideal sensitivity. These lines were obtained using data from the OPTOTRAK system, which made it possible to determine the locations of subject's eyes in space with respect to the location of the target. Accordingly the ideal eye-in-space orientation was computed, and, in combination with head orientation, the ideal eye-in-head orientation. From these signals the ideal sensitivity values for that particular fixation distance could be determined. The phase plots show the least scatter for the gaze signals.

bered). The phase plot (Fig. 4*D*) shows that the head rotates in compensatory direction at all times, i.e., in the direction of the target, be it with considerable and rather variable phase delays of $\leq$90°. Eye-in-head rotation behavior is depicted in Fig. 4, *B* and *E*. Sensitivity and phase are now computed using angular eye-in-head velocity and translational eye velocity (see METHODS). Figure 4*B* shows an increase in the eye's sensitivity for more nearby targets, as required for optimal gaze stabilization. The amount of compensation for the remembered target condition is clearly less than optimal. The data remain well below the dashed lines representing the ideal sensitivity in the visual target condition. The phase plot (Fig. 4*E*) shows quite variable phase delays, both lags and leads, for both target conditions (visual/remembered). Finally, Fig. 4, *C* and *F*, depicts the gaze response parameters, sensitivity, and phase, by computing the ratio between gaze velocity and translational eye velocity. Notice the emergence of improved response characteristics, both for sensitivity and phase, indicating that, due to the head movement, gaze provides better stabilization than eye-in-head alone. There is less scatter in sensitivity for the gaze response than in the eye-in-head velocity signals, which becomes evident from the linear regressions quantifying the sensitivity-vergence relationship. The R^2 values of these fits are significantly higher for the gaze sensitivity (Fig. 4*C*) than for eye-in-head velocity based sensitivities (Fig. 4*B*; $P \ll 0.001$ for both target conditions). Gaze sensitivity increases for more nearby targets as required for optimal gaze control. Compensation in the remembered target condition is clearly less than in the visual target condition. In both conditions, sensitivity remains below the dashed line, representing ideal compensation. Also with regard to phase, the scatter is significantly reduced when considering the gaze signal (*t*-test; $P \ll 0.001$, for both target conditions). Across subjects, we found a significantly higher correlation for gaze sensitivities than for eye-in-head–based sensitivities (paired *t*-test; $P < 0.05$ for visual targets, $P < 0.001$ for remembered targets). Similarly, the scatter in phase was significantly smaller for the gaze signal ($P \ll 0.001$ for both target conditions). For the remainder of this paper, we therefore pursue the analysis of gaze velocity, illustrated in Fig. 4*C*, to characterize fixation performance.

Figure 5 shows sensitivity and phase of gaze as a function of vergence for all movement frequencies tested in *subject AB*. The solid lines in the *top panels* represent the sensitivity-vergence regressions. Since our response analysis was done on a cycle-to-cycle basis, the number of data points in the regression is dependent on the movement frequency, with higher frequencies yielding more data points during the same recording time. As a consequence, the smaller data set for the 0.25-Hz movement frequency renders the computation of the sensitivity-vergence relationship for this frequency less reliable. The slope of the fitted line represents the change in sensitivity as a function of vergence and characterizes the gaze compensation for the linear eye translation with respect to the target. For all frequencies, the slope of the fitted line is significantly steeper for fixation of visual targets than after target offset (paired *t*-test; $P < 0.02$), indicating better geometry correction in the visual target condition than in the remembered target condition. Furthermore, for both target conditions sensitivity decreases significantly for higher frequencies [ANOVA: visual targets $F(3,93) = 529$, $P \ll 0.001$; remembered targets $F(3,92) = 337$, $P \ll 0.001$]. Also, the scatter of the data along the fitted line is larger for the remembered target condition as compared with the visual target condition (paired *t*-test; $P < 0.02$).

The intercept of the sensitivity-vergence relationship corresponds to gaze sensitivity for a target at infinity. As such, it represents a geometry-independent default sensitivity and should be equal to zero in the ideal case on the basis of geometric considerations (see METHODS). As shown by the regression lines in Fig. 5, the intercept is close to zero for visual targets, except for the 1.5-Hz movement frequency. For the 1.5-Hz movement frequency, the intercept for subject *AB* is

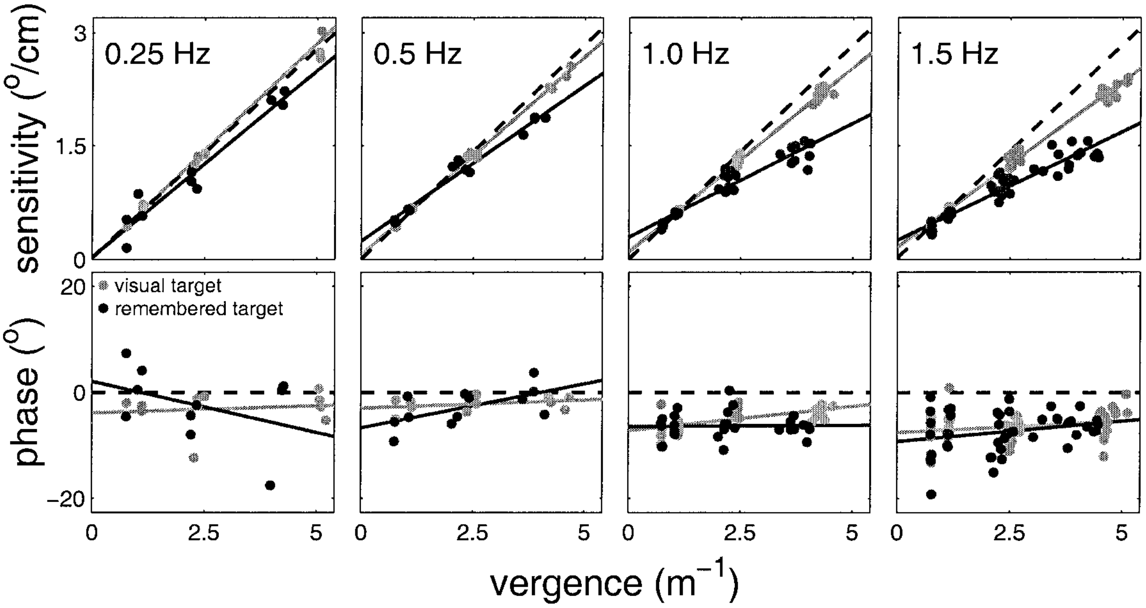

FIG. 5. Sensitivity (*top panels*) and phase (*bottom panels*) during voluntary horizontal head translations at various frequencies, plotted as a function of vergence for both visual (gray circles) and remembered (filled circles) target fixations. Subject: *AB*. For both target conditions the slope of the sensitivity-vergence regression lines decreases for higher frequencies (*top panels*). The phase plots show small lags, which increase with movement frequency.

0.16 ± 0.02°/cm (mean ± SD), which is significantly different from zero (*t*-test; $P < 0.001$). In his remembered target condition we found a statistically significant positive intercept value of 0.27 ± 0.03°/cm for frequencies ≥0.5 Hz.

The *bottom panels,* showing the phase, demonstrate that gaze velocity *lags* translational eye velocity by a small amount in both target conditions (range 2–20°). Note that ideally, the phase angle should be zero. We also examined the relationship between phase and vergence by performing a regression analysis. The correlation between phase and vergence was only significant for the 1.0-Hz visual target condition ($r = 0.57$, $P < 0.05$, $n = 28$) and the 0.5-Hz remembered target condition ($r = 0.61$, $P < 0.05$, $n = 12$). Generally, in none of the subjects, a significant relationship between phase and vergence across *all* movement frequencies could be detected. This has led us to simply characterize response phase by its average across vergence and across subjects for each movement frequency. For *subject AB,* the differences in phase between the visual and remembered target condition are not significant (paired *t*-test; $P = 0.30$). For both target conditions, phase lag increases significantly for higher frequencies in this subject [ANOVA visual targets: $F(3,93) = 11.1$, $P < 0.001$; remembered targets $F(3,92) = 7.9$, $P < 0.001$].

To express how actual performance compares with ideal performance, we computed the ratio of measured slope and ideal slope for both target conditions. This ratio, to be denoted as *distance compensation,* shows how well gaze control is modulated by the fixation distance. Accordingly, for optimal performance, distance compensation equals 1.0. The intercept of the sensitivity-vergence relationship corresponds to the sensitivity for a target at infinity and will be called *default sensitivity*. Note that it should be zero in the ideal case on the basis of geometric considerations (see METHODS).

Figure 6 summarizes all three response parameters averaged across all subjects. The *top panel* shows the degree of distance compensation. Generally, in all subjects distance compensation is better for visual than for remembered targets. Furthermore, distance compensation tends to deteriorate with increasing movement frequency in each target condition. Its value is near one for the 0.25- and 0.5-Hz movement frequency, indicating near-ideal gaze stabilization on visual targets in this frequency range. It ranges from 1.00 ± 0.06 at 0.25 Hz to 0.84 ± 0.06 at 1.5 Hz, with an overall mean value of 0.93 ± 0.07. An ANOVA revealed a significant effect of movement frequency on the degree of distance compensation [$F(3,15) = 22.4$, $P < 0.001$] for the visual target condition. For the remembered target condition, the mean distance compensation (across all frequencies) is 0.69 ± 0.13. This value is far from ideal but still demonstrates a clear amount of compensation for the translation of the eyes relative to the target. As in the visual target condition, there is a significant effect of movement frequency with regard to distance compensation for the remembered target condition [ANOVA $F(3,15) = 8.2$, $P < 0.01$]. The differences between the data in the visual target and remembered target condition appeared to be highly significant [ANOVA $F(1,23) = 38.5$, $P \ll 0.001$].

The *middle panel* plots the default sensitivity (and its SD) as a function of movement frequency for both visual and remembered target conditions. Across subjects, the default sensitivity ranges from 0.02 to 0.10°/cm in the visual target condition and varies between 0.04 and 0.16°/cm for the remembered target condition. Across frequencies, this difference between the visual and remembered target condition appeared to be significant in an ANOVA [$F(1,23) = 8.3$, $P < 0.01$]. Furthermore, an ANOVA revealed also a significant relationship between default sensitivity and movement frequency in both target conditions [visual targets: $F(3,15) = 9.0$, $P < 0.01$; remembered targets: $F(3,15) = 3.8$, $P = 0.03$].

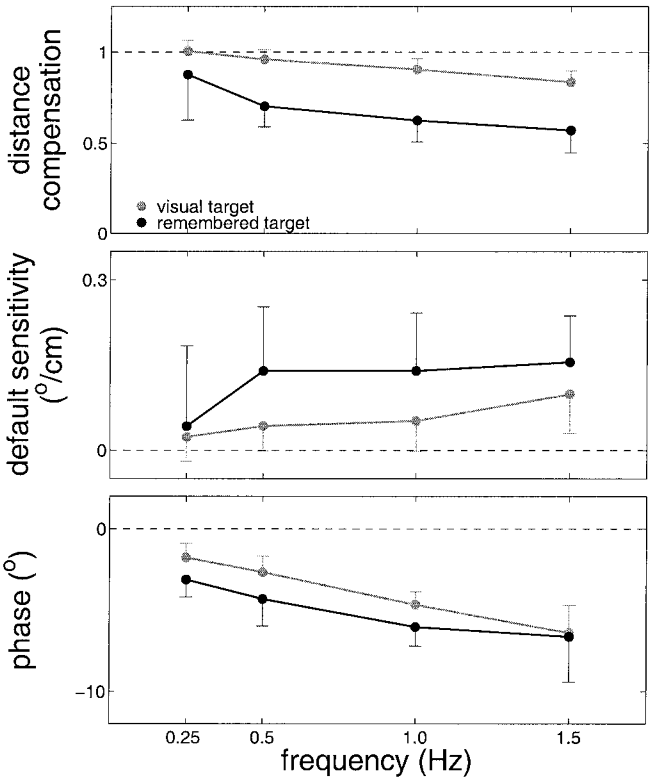

FIG. 6. Gaze stabilization performance for voluntary horizontal head translations. Distance compensation, default sensitivity, and phase (averaged across 6 subjects) plotted as function of movement frequency for both visual and remembered target conditions. Error bars represent SD between subjects. Ideal performance would require distance compensation 1.0, a default sensitivity of 0°/cm, and a phase angle of 0° (dashed lines).

The *bottom panel* depicts the average phase (the average across vergence and across subjects) for each frequency and stimulus condition (visual/remembered target). We found a significant increase in phase lag for higher movement frequencies, both in the visual target condition [$F(3,15) = 18.0$, $P < 0.001$] and in the remembered target condition [$F(3,15) = 5.1$, $P = 0.01$]. The differences between the phase in the visual and remembered target condition were significant ≤1.0-Hz movement frequency (*t*-test; $P < 0.05$). For the highest movement frequency, phase differences in the two target conditions were not significant (*t*-test, $P = 0.62$).

DISCUSSION

In this study we investigated the contribution of eye and head movements, as well as gaze, to near-target stabilization during active head translations. Examination of head movement kinematics (see Fig. 1) revealed that subjects also made small head rotations during active translational body movements. Eye and head contributions taken together (i.e., gaze) yielded better compensation characteristics than eye contributions alone (see Fig. 4). Therefore stabilization performance was characterized by the gaze response parameters (sensitivity and phase), which were determined by relating gaze velocity to translational eye velocity. These gaze response parameters were computed in a binocular coordinate system and were used to quantify the effects of target distance and the availability of visual feedback on the sensitivity and phase for various movement frequencies.

The results demonstrate that, for frequencies ≤1.5 Hz, gaze control is better with visual feedback than in its absence, indicating the importance of a visual component. As expected on the basis of geometric considerations, gaze sensitivity appears to be linearly related to the inverse of fixation distance. A linear regression on the sensitivity-vergence relationship yielded a positive slope, indicating that gaze sensitivity increased with target proximity. Relating this slope to the slope required for ideal stabilization provided a measure for the degree of distance compensation. The results show that distance compensation deteriorated for increasing movement frequencies in each target condition. Averaged across the frequencies tested, the degree of distance compensation was 0.93 for visual targets and 0.69 for remembered targets.

The intercept obtained from the regression, the gaze response at zero vergence, specified a default sensitivity. The default sensitivity was different in the two target conditions (see Fig. 6), and significantly dependent on movement frequency. Averaged across subjects, it ranged from 0.02 to 0.10°/cm for visual targets and from 0.04 to 0.16°/cm in the remembered target condition.

Finally, we found a small phase lag of gaze velocity relative to translational eye velocity, which increased on average from 2 to 7° in the frequency range 0.25–1.5 Hz. In the next sections, we discuss the role of the observed head rotations, compare our results with previous work, and discuss their wider implications.

Possible role of rotational and translational VOR

Although we instructed subjects to generate pure head translations, the occurrence of head rotations was clear, especially for 1.0- and 1.5-Hz movement frequencies. Figure 4, documenting the head rotation behavior, indicates that the head rotations are target-directed and too systematic to be dismissed as noisy variations. The reason for these small head rotations is a matter of speculation. The first hypothesis is that these head rotations are part of the gaze compensation system, in the sense that gaze compensation for translation is achieved partly through eye and partly through head rotations. In the context of this hypothesis, the fact that the passive translational VOR (tVOR) is far from optimal might be explained by the suppression of head rotations in these head-fixed experiments. The idea of eye and head working in unison to compensate for body translation has two implications. One is that the rotational VOR (rVOR) should be suppressed (otherwise the contribution to the desired gaze change would be zero). The second is that eye and head are driven by a common signal. Although we are not aware of any evidence in the literature to support the idea of rVOR suppression during translation, there is plenty evidence during head-free gaze shifts and smooth-pursuit (Guitton and Volle 1987; Laurutis and Robinson 1986; Pélisson et al. 1988; Tabak et al. 1996; Tomlinson and Bahra 1986; Waterston and Barnes 1991). As to the second point, if eye and head rotation would stem from a common source signal, then their different phase characteristics, as shown Fig. 4, *D* and *E*, can only be interpreted by temporally different processing streams for the eye and head.

An alternative hypothesis entails that the head rotations merely serve to keep eye eccentricity within comfortable limits without a particular role in translation stabilization per se. This would imply that their contribution to gaze is canceled by the rVOR. The latter assumption seems reasonable considering the results of Medendorp et al. (2000), who showed that the active rVOR almost ideally compensates for head rotations, even in the absence of visual feedback. Although head rotations are in the direction of the target, their variable nature (see Fig. 4, *A* and *D*) may argue against a gaze compensation contribution, as explained above. According to the present hypothesis, the fact that eye-in-head shows a larger scatter than eye-in-space (gaze) may reflect compensation of the highly variable head rotations by the rotational VOR. Thus the quite variable head rotations, by activating the rotational VOR, partly obscure the eye-in-head movement due to the translational VOR. If we correct for this by subtracting the putative rVOR contribution from the eye-in-head movements, we retain the part of the eye-in-head movement that compensates for the translation of the eye. It can be shown that the putative tVOR, obtained in this fashion, is fully equivalent with the eye-in-space (gaze) signal shown in Fig. 4, *C* and *F*. In other words, in terms of the second hypothesis, the gaze responses in our data are seen as pure oculomotor responses, that correspond to the active translational VOR response. Clearly, more work is necessary to evaluate these conflicting hypotheses further.

Relation to previous studies

As far as we are aware, no other studies have investigated human gaze control for stabilization of near targets during active head translations. The study of Crane and Demer (1997) on gaze stabilization during natural activities involving head translations (like walking and running) did not focus on the specific characteristics of the translation compensation. Therefore we can only compare our results with those of corresponding passive studies. Unfortunately, the proper *head-free* passive control experiment (i.e., passive translation allowing both head and eye rotations) has not yet been done. A further difficulty in making comparisons is that we were forced to use a slightly different measure of sensitivity than has been used in the literature (see METHODS section). When making a comparison with these reservations, we have to consider all three measures: distance compensation, default sensitivity, and phase.

Telford et al. (1997) and Paige et al. (1998) measured tVOR responses in squirrel monkeys and humans for passive linear motion of the whole body in a range between 0.5 and 4.0 Hz and performed the same analysis as the present study. They found that humans and monkeys share the same overall characteristics. With visual feedback, their results are qualitatively and quantitatively in correspondence with the present results for all three measures. This indicates that active and passive gaze compensation is similar in the presence of visual feedback. In the dark, however, the active and passive conditions differ strikingly with regard to the degree of distance compensation, as well as its frequency dependence and its phase behavior.

During passive motion in the dark, the degree of distance compensation is clearly worse at all frequencies where comparison is possible. A further striking difference with active results is that passive distance compensation (as shown by Paige et al. 1998) *improves* with increasing frequency from ~0.25 at 0.5 Hz to ~0.40 at 4 Hz. During active translations, distance compensation is better, but *declines* from 0.87 to 0.57 in the frequency range tested (0.25–1.5 Hz). These differences suggest that during active head translations apparently additional nonvestibular signals come into play to improve distance compensation in the tVOR substantially, especially at low frequencies. With regard to phase, further differences are noticeable. Paige et al. (1998) observed a phase *lead* of ~15°, whereas we found a phase *lag* $<7°$ for frequencies <1.5 Hz. This difference raises further questions about the relative involvement of vestibular and nonvestibular signals in active gaze control (see section *Modeling implications*).

In contrast, the results obtained for the default sensitivity had similar values (~0.15°/cm) in the active and passive condition in the frequency range <1.5 Hz. Various other studies found corresponding values for the default sensitivity (Angelaki 1998; Busettini et al. 1994; Paige and Tomko 1991b). Note that ideal geometry does not require translation compensation for targets at infinity. Paige and Tomko (1991b) argued that a positive intercept might be functionally useful, because it confers enhanced image stabilization at a broader range of vergence angles than if it were zero. The intercept adds a fixed value to the response sensitivity at the cost of a small retinal slip for distant targets but to allow better performance for nearer targets. Taking as an example the data of *subject AB* in Fig. 5, at 1.5 Hz the regression line of the data in the dark intersects the line of ideal performance at ~0.6 m^{-1}, which corresponds to an optimal viewing distance of ~1.6 m. Averaged across subjects, we found the optimal viewing distance of ~0.8 m for visual targets and ~1.8 m for remembered targets in the frequency range 0.5–1.5 Hz. This indicates that with vision translation compensation seems optimized for targets near 80 cm, which is within the subject's haptic space (Telford et al. 1997). Also monkeys tend to optimize their translational VOR at a distance of about 1 m (Angelaki 1998).

It is often assumed that the tVOR is also induced during off-centric head rotations to support the rotational VOR during near-target viewing (Crane and Demer 1999; Crane et al. 1997; Paige and Tomko 1991a; Paige et al. 1998; Telford et al. 1997; Viirre and Demer 1996; Viirre et al. 1986). Also active head movements often induce both a rotation and a translation of the eyes due to an off-centric location of the head rotation axis relative to the eyes (see Medendorp et al. 1998). In Medendorp et al. (2000) we have shown that during such movements the VOR in the dark compensates for about 60–80% of eye translation with respect to the target, dependent on movement frequency. This amount of compensation and its frequency dependence is in close correspondence with the results of the present study.

In conclusion, active and passive translation compensation perform similarly in the presence of visual feedback. In the dark, active translation compensation is clearly better in terms of distance compensation. Yet, in contrast to passive translation compensation, distance compensation decreases with increasing frequency in the active condition. Furthermore, active gaze control shows a phase lag, while most passive studies reported phase leads (at least for the movement frequencies tested in our study). Finally, active and passive translation compensation both show a default sensitivity.

Modeling implications

During passive translational movements, the reflexive eye responses must be vestibularly mediated, since additional sources of information about the movement (e.g., efference copies, proprioception) are not available in these conditions. Recently, several models have been put forward to account for the observed dynamics during passive translation compensation (Green and Galiana 1998; Musallam and Tomlinson 1999; Telford et al. 1997). Furthermore, different hypotheses have been proposed to resolve the otolith ambiguity in this condition (see INTRODUCTION) (Angelaki et al. 1999; Merfeld et al. 1999; Paige and Seidman 1999; Telford et al. 1997). The important point, from the viewpoint of this study, is that the translation-related VOR can be characterized by high-pass filter dynamics. These high-pass dynamics correspond to the observation that the passive tVOR in the dark demonstrates an increase in sensitivity with increasing frequency and, in addition, shows a phase lead of eye velocity relative to head velocity for low frequencies.

To explain our results we suggest that during active, voluntary movements the brain has a much better estimate of head translation due to the availability of nonvestibular signals. As to the nature of this nonvestibular signal, the role of neck proprioceptive inputs to central VOR pathways is controversial (Dichgans et al. 1973; Gdowski and McCrea 2000; Mergner et al. 1998; Roy and Cullen 2001). There is evidence that head movement efference copy signals arrive in the vestibular nuclei to combine with other sensory and motor estimates of head movement (McCrea et al. 1999). Although the nature of the nonvestibular signal (efference copy, proprioception, or any other sensory or motor signal) cannot be established from the present results, its apparent availability supports the multisensory hypothesis in the sense that it may help the CNS to improve gaze stabilization (Merfeld 1995).

If this hypothesis is accepted, we must assume that the additional nonvestibular signal was helpful primarily at low frequencies. If the frequency dependence of this nonvestibular contribution to the self-translation signal has the characteristics of a low-pass filter, our data can be understood qualitatively. Despite the contribution of the nonvestibular signal, active gaze compensation in the dark still accounts only for about 70% of the translation of the eyes relative to the target (see Fig. 6). We must conclude that the gain of the nonvestibular signal is <1.0.

In this context, it is interesting to note a striking parallel with the outcome of perceptual studies, which raises the question whether the putative nonvestibular signals may also play a role in the perception of egotranslation in actively moving subjects. In Medendorp et al. (1999) we found that subjects, when pointing to a remembered target in darkness after a self-made step, estimate their step by ~70% of the actual step displacement. This value is in the same range found for active gaze compensation in the dark, perhaps suggesting that the same information source is underlying egomotion perception and gaze stabilization. Several other studies in humans have also shown that subjects underestimate their walking distance when walking to a previously seen target in the dark (Amorim et al. 1997; Glasauer et al. 1994; Philbeck and Loomis 1997). Glasauer et al. (1994) argued that the vestibular system does not play a major role in the judgment of active displacements and indicated that nonvestibular signals are apparently more important. It seems plausible that such a nonvestibular signal also contributes to the active translation compensation.

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