RESEARCH ARTICLES

C. C. A. M. Gielen · S. F. Gabel · J. Duysens

Retinal slip during active head motion and stimulus motion

Abstract Gaze control in various conditions is important, since retinal slip deteriorates the perception of 3-D shape of visual stimuli. Several studies have shown that visual perception of 3-D shape is better for actively moving observers than for passive observers watching a moving object. However, it is not clear to what extent the improved percept of 3-D shape for active observers has to be attributed to corollary discharges to higher visual centers or whether the improved percept might be due to improved gaze stabilization during active head movements. The aim of this study was to measure binocular eye movements and to make a quantitative comparison of retinal slip for subjects instructed to fixate a visual stimulus in an active condition (subject makes an active head movement, object is stationary) and in a passive condition (the stimulus moves, the subject is stationary) for various movement frequencies, viewing distances, and stimulus diameters. Retinal slip remains below the "acuity threshold" of about 4 deg/s in active conditions, except for the highest frequency tested in this study (1.5 Hz) for nearby targets (0.25 cm). Retinal slip exceeds this threshold for most passive conditions. These results suggest that the enhanced performance in the visual perception of 3-D shape during active head movements can, at least partly, be explained by better fixation by actively moving observers.

Keywords Gaze · Retinal slip · Vision · Eye movement

Introduction

The stabilization of gaze during head movements is important, since human visual acuity is tolerant of retinal

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image motion up to 2–4 deg/s (Barnes and Smith 1981; Demer et al. 1994) and deteriorates rapidly for higher retinal slip velocities. Most studies in the past have investigated gaze for subjects that did not move while fixating moving stimuli, or for subjects that are passively rotated or translated in a chair. These experiments have shown that the control of gaze is good for low movement frequencies but deteriorates for higher frequencies. Recent experiments, where subjects were instructed to make voluntary head rotations (Medendorp et al. 2000) or head translations (Medendorp et al. 2002), have indicated that gaze stabilization is much better for actively moving observers than for passively moving observers.

The fact that fixation of gaze is better for actively moving observers is important for the visual perception of 3-D shape. Several studies have shown that perception of 3-D shape requires relative motion between an object and an observer (Braunstein 1962; Johansson 1973). In addition, Rogers and Graham (1979) demonstrated that perceived depth of 3-D shape is more pronounced for active observers moving in an environment with stationary objects than in the condition of a passive observer in an environment with moving objects. This observation has been reproduced many times since then (see, e.g. Cornilleau-Peres and Droulez 1994; Dijkstra et al. 1995) and stresses the importance of *active perception*.

The observation that active observers have a better percept of 3-D structure than passive observers has been explained in the literature by postulating the availability of extraretinal information about the observer's own movements to higher centers of visual information processing. The extraretinal information is postulated to be used in the visual pathways at a high stage in the structure-from-motion process to improve the perception of 3-D shape (see, e.g. van Damme and van de Grind 1996). However, Dijkstra et al. (1995) demonstrated that 3-D shape perception is equally good for subjects making active head movements and for subjects fixating a scene, which does not translate but does rotate as it would with perfect fixation in the active condition. Moreover, 3-D shape perception was considerably deteriorated in the condition

when the scene moves relative to the passive observer. Based on these results Dijkstra et al. (1995) suggested that active perception of 3-D shape may be better because fixation is better (and retinal slip smaller) during active movements than in conditions where the visual stimulus moves relative to a passive observer.

Only few studies have tested gaze control and retinal image motion during active head movements. Grossman et al. (1989) reported that retinal image slip was below 4 deg/s during standing and walking and about 9 deg/s during running for targets at optical infinity. Crane and Demer (1997) reported that the horizontal and vertical velocity of images on the retina was below 4 deg/s for a visible target located beyond 4 m. Image velocity significantly increased to values exceeding 4 deg/s during self-generated pitch and yaw movements at a frequency of 0.8 Hz while fixating targets at a distance of 1 m. Medendorp et al. (2000) found that retinal slip for head rotations along a vertical axis is typically below 2 deg/s for targets at 1 m or more. However, retinal slip could increase up to 5 deg/s for 1.5 Hz movements for near targets at about 20 cm.

This overview illustrates that a systematic comparison of retinal slip for active and passive observers in various stimulus conditions is lacking. The aim of the present experiments was, therefore, to provide a quantitative comparison between retinal slip for subjects making active head movements and for passive observers fixating moving targets, for targets of various sizes, at various distances relative to the observer, and for various frequencies of relative motion. For this purpose, we have asked subjects to fixate and track a small red target spot (0.5 deg diameter), while we monitored gaze. Either the subject was making rhythmic upper body horizontal translations parallel to the stimulus screen while the stimulus remained stationary, or the subject was standing still while the stimulus moved sinusoidally along a horizontal line. A cloud of random dots with a diameter of either 20 or 70 deg could surround the red fixation target. We varied both the target distance (25–75 cm) and the motion frequency (0.5–1.5 Hz). The results demonstrate that retinal slip is considerably smaller in most conditions for active observers, well below the acuity threshold of 4 deg/s.

Materials and methods

Subjects

Five normal human volunteers (ages 26–48 years) gave informed consent to participate in the experiments. The experiments were approved by the Ethics Committee of the University of Nijmegen in accordance with the ethical standards in the 1964 Declaration of Helsinki.

One subject (CG) 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 CG) visual acuity and all subjects were free of any known sensory, perceptual, or motor disorders. Details about the experimental set-up and methods have been described in great detail before (see

Medendorp et al. 2000, 2002). Here we provide only a brief summary of the experimental design and protocol.

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 infra-red emitting diodes (ireds) within a pre-calibrated space of about 1.5 m³. It does so by multiplexing the currents through a series of predefined ireds. For each ired, the current increases until the signal-to-noise ratio of the signals from the three detectors is sufficient for accurate detection. The 3-D resolution at a distance of 2.25 m is 0.01 mm. The sensor resolution is 1:200,000 and the maximal marker sample rate is 3,500 Hz. For further information, see http://www.ndigital.com/optotrak_technical.html).

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 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. We ensured that the helmet remained stable on the head throughout the entire experiment by comparing the position of the ireds on the helmet with that of the ireds near the auditory meatus before and after the experiment. During the experiment, data were collected using a sample frequency of 100 Hz and stored on hard disk for off-line analysis. From the helmet data the positions of the ears and eyes in space were computed for each instantaneous head posture. The orientation and location of the head were determined with respect to the stationary head-reference posture for fixation straight-ahead (Veldpaus et al. 1988). Head orientations and head locations could be determined with an accuracy <0.2º 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 (Remmel Labs). 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 with calibration errors typically smaller than 0.5 deg. Data acquisition of head movement data by the Optotrak and of eye movement data was synchronized to assure a correct alignment of types of data.

Experimental paradigm

Subjects were standing in a completely darkened room, and were instructed to fixate a red fixation target (diameter 0.5 deg). The visual stimulus consisted of this red fixation target, which could be surrounded by a circular random dot pattern with a diameter of 20 or 70 deg with bright white dots (diameter 0.2 mm; n=100). Fixation target and random dot pattern were either stationary or moved as one single stimulus with exactly the same velocity at all times. The stimulus was projected on a translucent screen in front of the subject with the fixation target at eye level of the subject using a Philips LCD projection system (ProScreen 4750).

Subjects were tested in two conditions. In the Passive condition subjects were standing upright and were instructed not to move while fixating the target spot, which was moving sinusoidally along a horizontal line on the screen at 0.5, 1.0 or 1.5 Hz with a peak-peak amplitude of 12 cm centered around the straight-ahead position for the subject. In the Active condition, subjects were instructed to move their head along a horizontal line parallel to the screen with an amplitude of about 6 cm left from the resting position to 6 cm right

from the resting position by movements in the hip and spine and to keep gaze fixated on the red target spot. Although subjects were instructed to make head translations only, small head rotations did occur. However, they were small. Information about head rotations and their implications for the interpretation of the data is provided in the "Results" section. The target spot and the random dot pattern did not move in this condition. A metronome guided subjects in order to obtain head movements at one of three different frequencies (0.5, 1.0 and 1.5 Hz). Before each combination of movement frequency and target distance, subjects familiarized themselves with the movement task by practicing several trials. During the practice trials subjects received feedback about direction and amplitude of head movements. When subjects were moving with the proper amplitude and frequency and in the proper direction, data collection began.

Both in the passive and active condition, the visual stimulus was presented at three different viewing distances (75, 50 and 25 cm). Because of the different viewing distances, the diameter of the white dots of the random dot pattern varied from 0.15, 0.21 and 0.42 deg for the 75 cm, 50 cm and 25 cm viewing distance, respectively. Since subjects inevitably made small head movements related to postural sway in forward/backward direction (Brandt et al. 1986; Dijkstra et al. 1992), the actual viewing distance could vary slightly. Typically, viewing distance varied by about 1 cm relative to the mean viewing distance of 25, 50 or 75 cm. The complete experiment consisted of 54 different conditions [3 frequencies (0.5, 1, 1.5 Hz) × 3 distances (25, 50, 75 cm) × 3 stimulus sizes (diameter 0.5, 20, 70 deg) × 2 conditions (active/passive)]. Each condition lasted for 12 s (excluding the practice trials) such that eye and head movements were measured for at least six complete movement cycles.

The constant amplitudes of object motion and ego motion imply that corresponding changes in gaze amplitude increase for decreasing viewing distance. We also tested two of the five subjects (subjects PM and VC) in conditions where movement amplitude was scaled inversely with viewing distance such that amplitude of gaze shifts was approximately the same for all viewing distances. The conclusions from the results of these experiments did not differ from those in the other experiment.

Data analysis

The eye coil signals were demodulated, amplified and low-pass filtered at 75 Hz (finite-impulse-response filter; this mainly reduced noise; any effects on phase were less than 1 ms), and resampled from 500 Hz to 100 Hz to match the Optotrak sampling rate. Eye-in-head orientation was calculated by subtracting head orientation from eye-in-space orientation. We will describe binocular gaze stabilization in a coordinate system that distinguishes eye movements in direction (version) from eye movements in depth (vergence). Version (conjugate part) was computed from left (L) and right (R) eye-in-space orientation as (L+R)/2; vergence angle was calculated as (L−R). Ideal version and ideal vergence angles were computed based on the Optotrak data, which provided information about the location of the head, the eyes and the target.

In order to make sure that the different recording techniques and data analysis of the head and eye movement data did not introduce undesired phase delays, we have measured movements of an ired simultaneously with the Optotrak and eye-recording system. An ired was attached to the mirror of a rotating mirror, driven by an optical scanner (G300-PDT, General Scanning) controlled by a driver amplifier (CCX-102-T, General Scanning). The mirror made small step-like displacements of 30 deg amplitude with a duration of 8 ms or 40 ms. The latter is a typical duration of a saccade. Any differences in the signals recorded by the Optotrak and the eye-measurement system were less than 1 ms for the 8 ms "saccade" and less than 0.5 ms for the 40 ms "saccade". These phase delays were much smaller than the phase delays between head and eye movements, as recorded in our subjects (see "Results" section).

For the binocular analysis, eye and head orientations were digitally differentiated to obtain velocity signals. Individual cycles in the response traces were identified on the basis of the zero crossings in the eye velocity signal. We excluded cycles starting in the first second of the trial and those ending in the last second of the trial. In the remaining cycles, saccadic epochs were identified in the eye velocity data, before the data was subjected to harmonic analysis. A least squares sinusoidal fit to the fundamental frequency, performed on each cycle excluding the saccades, served as the basis to obtain the response parameters gain and phase. A detailed analysis showed that vertical head displacements and up/down head

Fig. 1 Measured (*thick line*) and ideal gaze (version) traces while fixating a red target spot (0.5 deg diameter) at 25 cm distance for 0.5 Hz (*left panels*) and 1.5 Hz (*right panels*). *Upper panels* Gaze for stimulus translation with head stationary; *lower panels* gaze for active sinusoidal head translations. Data from subject CG
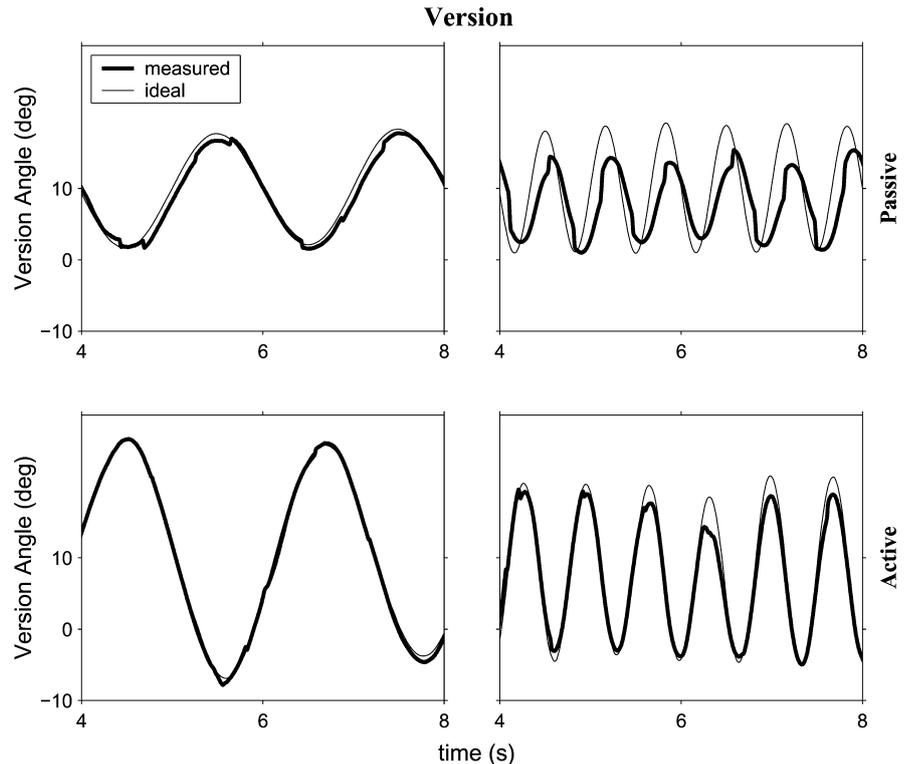
rotations in this study were small (typically less than 0.5 cm and 1.5 deg, respectively). Corresponding vertical eye-in-head movements were smaller than 2 deg. The effect of vertical head translations and head rotations on retinal slip appeared to be less than 1 deg/s for all subjects. Therefore, response parameters were only shown for the horizontal component. Response gain was defined as the ratio of amplitude of measured and ideal gaze velocity for the passive condition. For the active condition, gain was defined as the ratio of amplitudes of measured and ideal eye-in-space velocity. Response phase was taken as the phase of the measured gaze velocity relative to the phase of ideal gaze velocity. To calculate the amount of retinal slip during each trial, we subtracted the actual gaze velocity signals from the ideal gaze velocity signals. The resulting signal was low-pass filtered at 10 Hz (FIR filter, Matlab; filtering in two directions in order to eliminate any phase changes) before taking the root mean square (RMS) velocity of image slip (Crane and Demer 1997).

Results

Figure 1 shows gaze signals for subject CG while fixating the red fixation target (no surround) at a viewing distance of 25 cm. At 0.5 Hz (left panels) measured gaze and ideal gaze are almost the same for the active and passive condition. The delay in the passive condition is slightly larger than for the active condition [mean time delay 61 ms (SD=11 ms) versus 11 ms (SD=1 ms) equivalent to a mean phase delay of 11.0 deg (SD=2.0 deg) versus 2.0 deg (SD=0.2 deg)]. These differences become more prominent at 1.5 Hz (right panels), where gaze responses differ both in amplitude and phase delay, mainly for the passive condition. Moreover, for 1.5 Hz movements the delay of measured relative to ideal gaze is larger in the passive condition [mean phase delay 41.3 deg (SD=3.8 deg),

corresponding to a mean time lag of 76.5 ms] than in the active condition [mean phase delay 8.2 deg (SD=3.0 deg), mean time lag of 15.2 ms].

Any differences in velocity between measured and ideal version cause retinal slip of the fixated target. If vergence were perfect, the imperfect version in Fig. 1 would cause a retinal slip of 0.7 deg/s (4.3 deg/s) and 1.9 deg/s (12.7 deg/s) for the 0.5 Hz (1.5 Hz) movement in the active and passive conditions, respectively. The results shown in Fig. 1 are representative for all subjects and will be presented in more detail below for the various specific experimental conditions after presentation of the vergence data.

Figure 2 shows the vergence signal for the same data shown in Fig. 1. For 0.5 Hz movements the measured vergence signal does not follow the ideal vergence signal, neither for the passive, nor for the active condition. For the 1.5 Hz movements measured gaze follows the slow trends in the ideal vergence signal. If the subject is positioned precisely in front of the target (for the active condition) or in front of the center of the sinusoidal target trajectory (for the passive condition), the distance between subject and target is largest for the most extreme positions of the sinusoidal movement and is smallest when the subject is just in front of the target. Therefore, vergence changes twice from near to far during one movement cycle. When the subject is not positioned precisely in front of the central target position, the vergence signal consists of a superposition of a first and second harmonic of the movement frequency.

If retinal slip of target position is the result of incomplete vergence only (with perfect version!), the

Fig. 2 Measured and ideal vergence eye movements while fixating a red target spot (0.5 deg diameter) at 25 cm distance for the same data as shown in Fig. 1. Measured (*thick line*) and ideal vergence (*thin line*) for 0.5 Hz (*left panels*) and 1.5 Hz (*right panels*). *Upper panels* Vergence for stimulus translation with head stationary; *lower panels* vergence for active sinusoidal head translations. Data from subject CG
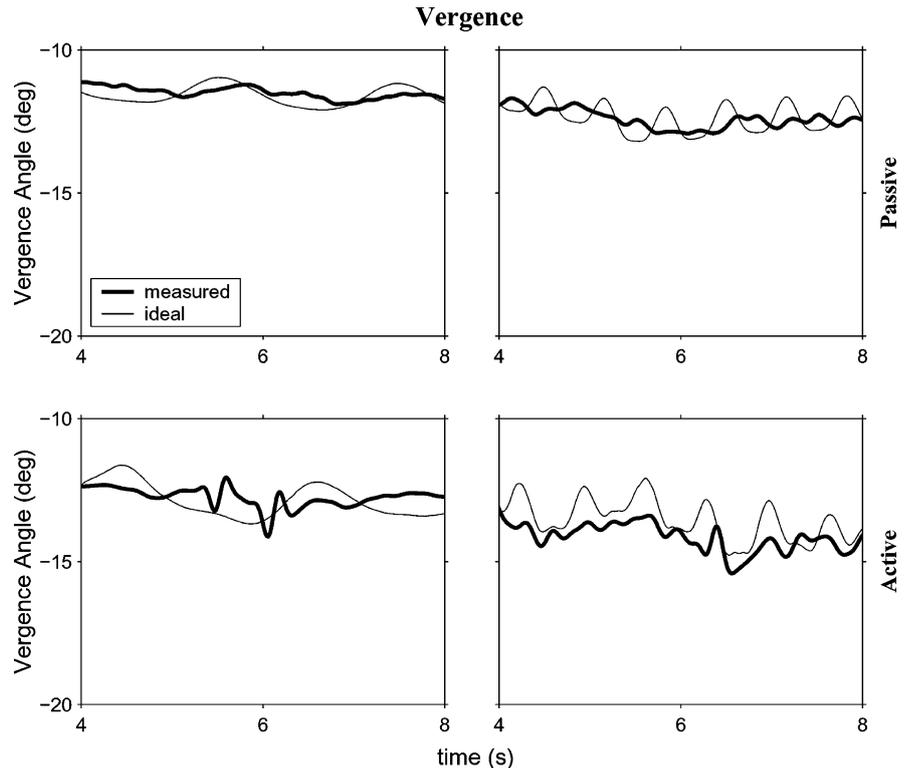
retinal slip varies between 0.1 and 0.3 deg/s for all subjects for the viewing distance of 25 cm. For viewer distances larger than 25 cm, vergence errors have even smaller effects on retinal slip. Based on the small effect of vergence on retinal slip and the much larger effect of version on retinal slip (see above), we will focus on version in the remainder of this manuscript.

The effects of movement frequency, viewing distance, and stimulus size on the gaze are illustrated in Figs. 3 and 4 for a single fixation target (no random dot pattern). Figure 3 shows gain (ratio of amplitudes of measured and ideal gaze velocity) for all subjects for the passive (upper panels) and active conditions (lower panels) for various frequencies and for various target distances. The gain is near unity for the active condition for all target distances. The intersubject variability is relatively small for 0.5 Hz in the active condition but increases for higher frequencies, especially for the smallest viewing distance, where some subjects tend to have a somewhat smaller gain. For the passive condition gain is significantly smaller than unity for most subjects, especially for the higher frequencies. An analysis of variance revealed that gain for the passive condition is significantly smaller than that for the active condition for each viewing distance for 1 Hz and 1.5 Hz, indicating that gaze stabilization is better in the active than in the passive condition. There is a significant effect of frequency on gaze gain, both for the active ($F_{(2,987)}$=86; p<0.001) and the passive condition ($F_{(2,1162)}$=398.5; p<0.001). Gaze gain also depended on viewing distance: both for the active and passive conditions gaze gain decreased slightly, but significantly for a smaller viewing distance [($F_{(2,231)}$=7.61, p<0.001) and ($F_{(2,231)}$=9.11, p<0.001), respectively].
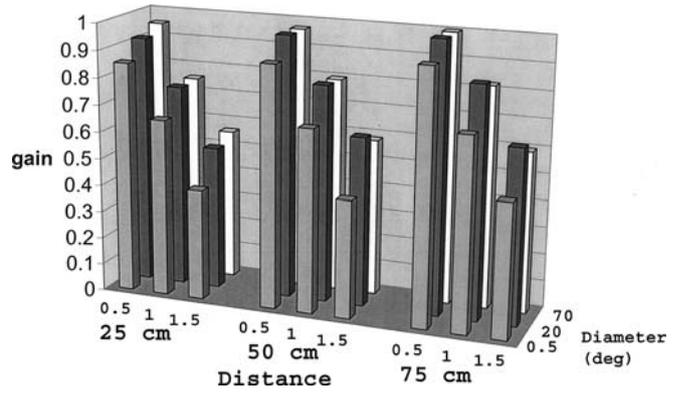

Fig. 4 Mean gaze gain for the passive condition. Mean values (averaged over all subjects) are shown for each of the three distances tested (25, 50 and 75 cm), for three frequencies (0.5, 1 and 1.5 Hz) and for three stimulus diameters

As pointed out in the "Introduction," gaze gain may also be affected by the size of the visual stimulus. For the active condition, gaze gain is close to one for most frequencies and target distances for a small fixation target of 0.5 deg (data shown in Fig. 3). Increasing the size of the stimulus did not lead to a significant increase in gain ($F_{(2,231)}$=0.754, p>0.4) for the active condition. For the passive conditions the effect of stimulus diameter was more obvious.

Figure 4 shows the mean results of five subjects for various frequencies, distances and stimulus sizes for the passive viewing condition. The mean gain decreases with frequency for each of the target distances for all stimulus diameters. Gain increased with stimulus diameter for each frequency at any of the three target distances. The increase of gain for larger stimulus diameters is most pronounced at

Fig. 3 Mean gaze gain (± standard deviation) for stimulus translations (stationary subject, *upper panels*) and active head translations (*lower panels*) for all subjects (see *inset*), plotted as a function of viewing distance. Gains are averaged over all stimulus sizes (0.5, 20 and 70 deg). Gain decreases with decreasing viewing distance and with increasing motion frequency, in active and (more explicitly) in passive conditions
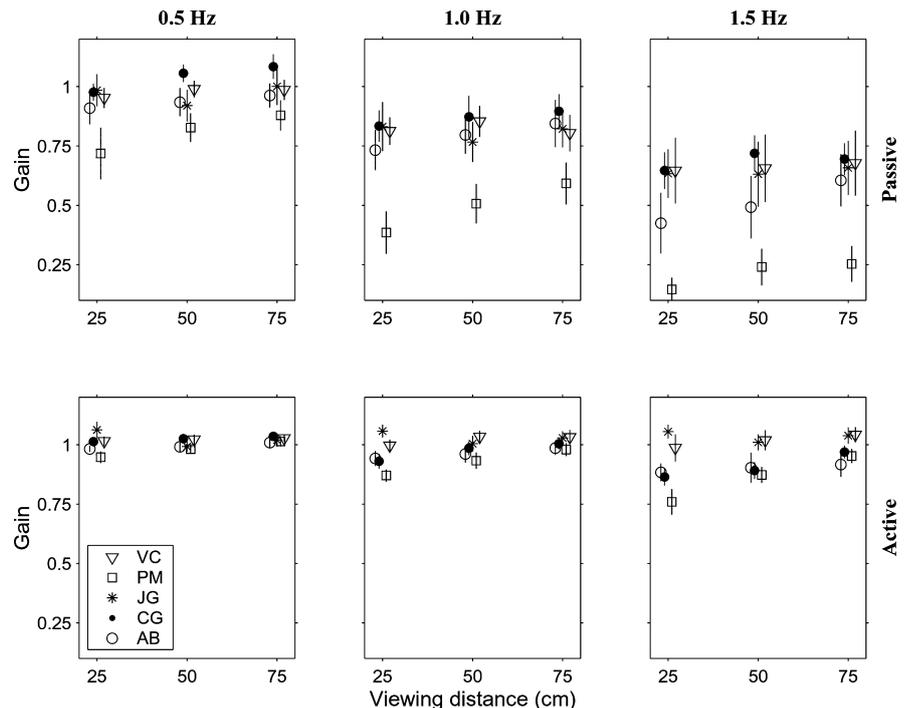
1.5 Hz. For this (passive) condition, we found a significant effect of stimulus size on gaze gain ($F_{(2,231)}$=17.08, $p<0.0001$).

The quality of fixation depends both on the gain and phase of the eye movements in space. Therefore, phase is just as important for minimization of retinal slip as gain. The differences in phase for the measured responses are close to the ideal of zero delay in the active condition for all frequencies (lower panels of Fig. 5). The mean phase delay in the active condition is small (mean delay 3.5 deg; SD=1.0 deg), which is in agreement with results in previous studies for the translational VOR (Medendorp et al. 2002). For the passive condition the mean phase delay across subjects increases with frequency from 8.7 deg (SD=3.2 deg) (corresponding to a mean time delay of 48 ms) at 0.5 Hz to about 43.8 deg (SD=10.0 deg) (corresponding to a mean time delay of 81 ms) at 1.5 Hz (upper panels in Fig. 5). This effect was significant ($F_{(2,1162)}$=1,663; $p<0.0001$). Corresponding phase delays were 0.9 deg (SD=0.5 deg) and 4.8 deg (SD=1.8 deg) for frequencies 0.5 and 1.5 Hz in the active condition. Data from different subjects were very consistent and reproducible in both conditions. Changes in stimulus diameter did not appear to have a significant effect on phase delay, neither in the active nor in the passive condition.

The amplitude of the sinusoidal target movements was 6 cm (12 cm peak-peak amplitude) in the passive condition for all viewing distances and the amplitude of positional shifts by the observer's head was about 6 cm for the active movement condition. The constant amplitudes of object motion and ego motion imply that the corresponding changes in gaze amplitude increase for decreasing viewing distance. We have tested two of the five subjects (subjects PM and VC) in conditions where

movement amplitude was 6 cm for the viewing distance of 75 cm and where movement amplitude was scaled inversely with viewing distance such that amplitude of gaze shifts was approximately the same for all viewing distances. The results were the same in both conditions. Similarly, we have tested two subjects with two different amplitudes (3 and 6 cm) with the same results. These results indicate that amplitude of stimulus motion or subject motion did not affect the results for the range of movement amplitudes in this study.

Figure 6 shows retinal slip for each of the five subjects while looking at a small fixation target (diameter 0.5 deg) for various frequencies and target distances. For the active condition, retinal slip is in the range between 2 and 5 deg/s at 0.5 Hz for all subjects, between 2 and 9 deg/s for 1.0 Hz, and between 3 and 16 deg/s at 1.5 Hz. In agreement with the earlier observation that larger stimuli did not lead to higher gain or smaller phase delay in the active condition, the effect of stimulus diameter was not significant for the active condition. For the passive condition retinal slip is slightly larger than in the active condition for 0.5 Hz. However, for 1 Hz and 1.5 Hz, retinal slip is considerably larger in the passive condition than in the corresponding active conditions. For the passive condition retinal slip increases significantly both as a function of frequency ($F_{(2,1162)}$=1984; $p<0.0001$) and as a function of the inverse of target distance ($F_{(2,1162)}$=935; $p<0.0001$). Since gain of gaze increases with stimulus diameter for the passive condition (Fig. 4), one would expect a smaller retinal slip for larger stimulus diameters for the passive condition. This was confirmed in a statistical analysis, where a paired-samples t-test demonstrated a significantly smaller retinal slip for a 70 deg

Fig. 5 Mean and standard deviation of phase delay between measured and ideal gaze during passive (*upper panels*) and active condition (*lower panels*) for all subjects (see legend) for three movement frequencies and three viewing distances. Phase is averaged over all stimulus sizes used (0.5, 20 and 70 deg). Positive values indicate that measured gaze lags ideal gaze. Phase delays increase with frequency
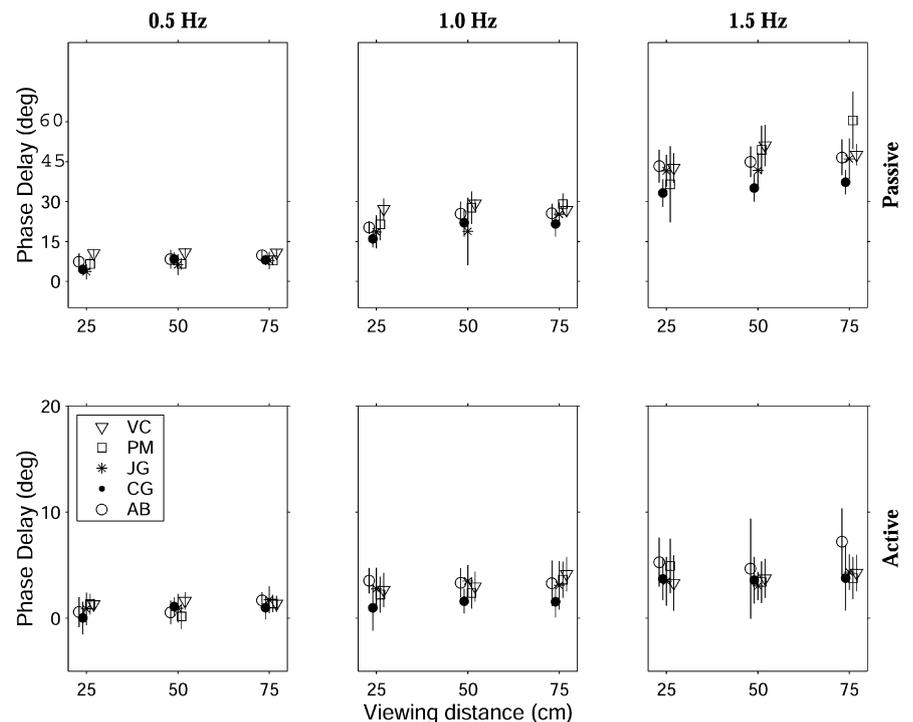
Fig. 6 Mean and standard deviation of retinal slip (deg/s) for passive (*upper panels*) and active (*lower panels*) condition for all subjects (see *inset*) for three movement frequencies, plotted as a function of viewing distance. Retinal slip is averaged over all stimulus sizes used (0.5, 20 and 70 deg). Retinal slip increases with decreasing viewing distance and with increasing frequency
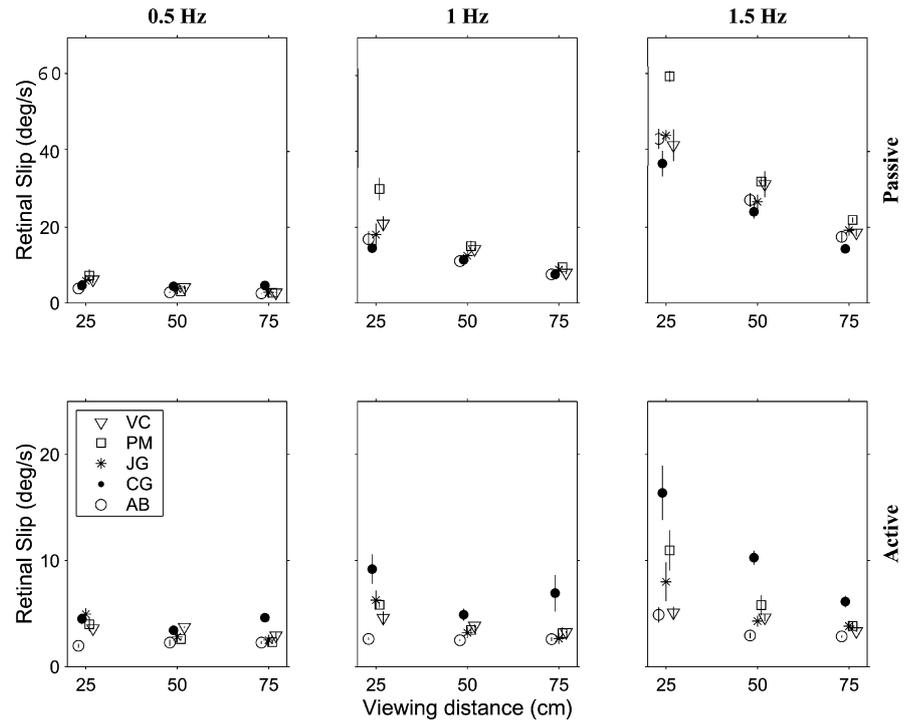
diameter stimulus than for a 20 deg diameter stimulus ($t=2.7$; $p<0.01$).

A statistical analysis revealed that retinal slip is significantly larger in the passive condition for each combination of frequency, distance and target size than in the corresponding active condition. It is much larger in the passive condition at the higher frequencies (from 3 deg/s to 7 deg/s at 0.5 Hz to 13–60 deg/s at 1.5 Hz), and increases for smaller distances and higher motion frequencies. These results indicate that gaze stabilization in the active condition is superior to that in the passive condition, especially at small distances and high frequencies.

Discussion

The main result of this study is that fixation of gaze is significantly better in conditions where subjects make voluntary movements relative to a non-moving stimulus than in conditions in which the stimulus moves relative to a passive subject. Retinal slip due to ego-motion increases for higher movement frequencies, especially for nearby targets, but not as fast as for a passive observer fixating a moving stimulus. For active movements gaze stabilization is such that retinal slip is almost within the range where perception is not seriously affected (approximately below 4 deg/s), except for small viewer distances (25 cm) and high movement frequencies (1.5 Hz). For a passive observer, retinal slip exceeds the threshold of 4 deg/s for almost all stimulus conditions.

Methodological considerations

In this study differences between actual gaze and ideal gaze were used to calculate retinal slip. However, retinal slip can also be the consequence of torsional eye movements, which were not measured in this study, where we used 2-D coils. In a previous study Crane and Demer (1997) used 3-D search coils to measure eye movements in three orthogonal directions. Their results demonstrated that for walking, running and active yaw/pitch head movements, any torsional eye movements were small such that ignoring torsion did not produce significant differences in any of the measured values. Therefore, ignoring torsion does not significantly affect the data on retinal slip shown in this paper.

Tweed (1997) recently demonstrated that in eye-head movements to targets in 3-D the eye is driven toward a 3-D orientation in space so that Listings' law of the eye in head will hold. This implies that when gaze moves repeatedly to the same target with varying contributions of eye and head, torsion of the eye in space varies depending on the contribution of head and eye to gaze. Taking into account Listings' law for the eye in head and Donders' law for the head (Theeuwen et al. 1993; Medendorp et al. 1999), cyclotorsion of the eye in space results in rather small values for cyclotorsion velocity (<2 deg/s). Cyclotorsion would not induce retinal slip of a small target when fixation is right on target. However, for large stimuli with a diameter of 70 deg, cyclotorsion related to head rotations of 15 deg/s would give rise to RMS values for retinal slip velocities of 1 deg/s for the pixels at the extreme border of the 70 deg diameter stimulus. This agrees with the experimental data by Crane and Demer, who reported that torsional eye movements during natural head move-

ments are small and that their contribution to retinal image motion can be neglected.

Mechanisms underlying gaze control

Normal head movements involve both rotation and translation of the head in space (Crane and Demer 1997; Medendorp et al. 1998). Therefore, perfect gaze stabilization requires compensation for these angular rotations and linear translations of the head. In a recent study Collewijn and Smeets (2001) have shown that in general the rotational VOR is far from adequate for perfect fixation, since its gain in complete darkness is between 0.8 and 0.9. Based on this result, they conclude that the otoliths also contribute to the rotational VOR. With regard to the translation-related VOR most studies postulate that it is mainly otolith-driven with high-pass filter characteristics. These high-pass characteristics were hypothesized based on the observation that the tVOR for passively moving subjects 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 (Angelaki et al. 1999; Merfeld et al. 1999; Paige and Seidman 1999; Telford et al. 1997). In active observers, these systems complement the smooth pursuit system (Barnes 1993) and other ocular-following responses that are elicited by motion of large-field visual patterns and which explicitly incorporate perceived distance of an object relative to the observer (see, e.g. Busettini et al. 1996). The latter two mechanisms have low-pass characteristics with phase delays.

Relation to previous studies

Very few studies have investigated gaze control for subjects who made voluntary head translations (for an overview, see Medendorp et al. 2002). Most of these studies have focused on gaze stabilization for head rotations and some studies have tested gaze control in walking or running subjects.

Crane and Demer (1997) studied gaze stabilization during natural activities (such as locomotion on a treadmill) and reported that retinal slip was less than 4 deg/s for visual targets beyond 4 m. Since most frequency components of head movements are below 1.5 Hz during walking (Crane and Demer 1997), these results are well in agreement with the data in our study. For running, these authors reported that retinal slip increases from about 5 deg/s or less for targets at 5 m distance to 20 deg/s for running while fixating targets at a distance of 1 m. The larger retinal slip during running is most likely due to the higher frequency components in head movements during running.

In another locomotion study, Moore et al. (1999) reported that gain and phase characteristics of observed eye velocity for near and far targets (range 0.25–2 m) were close to ideal for the stabilization of gaze in space, but not perfectly the same. In their experimental paradigm, walking induced vertical head movements in a narrow frequency range centered around 2 Hz. The root-mean-square retinal slip varied between 14 deg/s at 0.25 m viewing distance to about 7 deg/s at 2 m viewing distance, in agreement with previous studies (Grossman et al. 1989; Crane and Demer 1997). These values for retinal slip are slightly larger than the values found in our study. It is not clear whether these differences have to be attributed to vertical head movements in the study by Moore et al. versus the horizontal head movements in our study and that by Medendorp et al. (2002), or whether these differences have to be attributed to different experimental paradigms used in these studies.

Gaze stability and perception

Dijkstra et al. (1995) investigated the detection of 3-D shape in subjects for three conditions. In the first two conditions, either the subject or the stimulus was translating horizontally in the fronto-parallel plane while the subject tried to maintain fixation on the stimulus. In the third condition, both subject and stimulus remained in place while the stimulus rotated. The latter condition created the same retinal image as would have been obtained in the other two conditions if fixation had been perfect. For a small stimulus (8 deg diameter), the best performance was obtained in the third condition. This result is compatible with the hypothesis that gaze stabilization is the major factor in explaining the superior perceptual performance for 3-D shape detection in the active condition. For large stimuli (90 deg diameter) Dijkstra et al. observed no differences in performance for the detection of curvature for movements at 0.33 Hz at a viewing distance of 72 cm in any of the three conditions. Based on our data, the difference between performance for small and large stimulus diameters can be explained by the better fixation for larger visual stimuli at low movement frequencies in the passive conditions of this study (see Figs. 4, 6).

Summarizing, the present study is the first study which gives a systematic comparison between retinal slip for passive observers fixating moving stimuli and for observers, making active head movements, for various frequencies, stimulus diameters, and viewer distances. The results demonstrate that retinal slip is well below the "acuity threshold" of about 4 deg/s for active head movements, but exceeds this threshold for most stimulus conditions for a passive observer. The reduced retinal slip in actively moving subjects may, at least partly, explain why the detection of 3-D shape is better for actively moving observers than for passive observers fixating similarly moving stimuli.

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