RESEARCH ARTICLE

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Effect of viewing distance on the generation of vertical eye movements during locomotion

Abstract Vertical head and eye coordination was studied as a function of viewing distance during locomotion. Vertical head translation and pitch movements were measured using a video motion analysis system (Optotrak 3020). Vertical eye movements were recorded using a video-based pupil tracker (Iscan). Subjects (five) walked on a linear treadmill at a speed of 1.67 m/s (6 km/h) while viewing a target screen placed at distances ranging from 0.25 to 2.0 m at 0.25-m intervals. The predominant frequency of vertical head movement was 2 Hz. In accordance with previous studies, there was a small head pitch rotation, which was compensatory for vertical head translation. The magnitude of the vertical head movements and the phase relationship between head translation and pitch were little affected by viewing distance, and tended to orient the naso-occipital axis of the head at a point approximately 1 m in front of the subject (the head fixation distance or HFD). In contrast, eye velocity was significantly affected by viewing distance. When viewing a far (2-m) target, vertical eye velocity was 180° out of phase with head pitch velocity, with a gain of 0.8. This indicated that the angular vestibulo-ocular reflex (aVOR) was generating the eye movement response. The major finding was that, at a close viewing distance (0.25 m), eye velocity was in phase with head pitch and compensatory for vertical head translation, suggesting that activation of the linear vestibulo-ocular reflex (lVOR) was contributing to the eye movement response. There was also a threefold increase in the magnitude of eye velocity when viewing near targets, which

was consistent with the goal of maintaining gaze on target. The required vertical lVOR sensitivity to cancel an unmodified aVOR response and generate the observed eye velocity magnitude for near targets was almost 3 times that previously measured. Supplementary experiments were performed utilizing body-fixed active head pitch rotations at 1 and 2 Hz while viewing a head-fixed target. Results indicated that the interaction of smooth pursuit and the aVOR during visual suppression could modify both the gain and phase characteristics of the aVOR at frequencies encountered during locomotion. When walking, targets located closer than the HFD (1.0 m) would appear to move in the same direction as the head pitch, resulting in suppression of the aVOR. The results of the head-fixed target experiment suggest that phase modification of the aVOR during visual suppression could play a role in generating eye movements consistent with the goal of maintaining gaze on targets closer than the HFD, which would augment the lVOR response.

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Introduction

During both natural overground locomotion and while walking on a treadmill there is a significant vertical linear translation and pitch rotation of the head. The maximal vertical displacement of the head occurs in the single limb support phase, and displacement is minimal in the double limb support phase. Estimates for the peak amplitude of vertical head translation vary from 18 to 90 mm (Bloomberg et al. 1992, 1997; Hirasaki et al. 1993, 1999; Murray et al. 1964, 1966; Pozzo et al. 1990, 1991; Waters et al. 1973), with the predominant frequency ranging from 1.4 to 2.5 Hz and peak vertical accelerations ranging from 0.3 to 0.7 G. In conjunction with head translation, there is a compensatory rotation of the head. As the head translates up the head pitches down, and as

the head translates down the head pitches up (Bloomberg et al. 1992; Crane and Demer 1997; Demer and Viirre 1996; Hirasaki et al. 1993, 1999; Pozzo et al. 1990). The predominant frequency of head pitch is similar to that of vertical head translation, but there is a wide variation in the reported peak amplitude of head pitch from 1.5° to 7.5°, with peak velocities from 28° to 149°/s (Berthoz and Pozzo 1988; Bloomberg et al. 1992, 1997; Crane and Demer 1997; Hirasaki et al. 1993, 1999; Keshner et al. 1992; Keshner and Peterson 1992; Reschke et al. 1994; Kubo et al. 1997; Pozzo et al. 1989, 1990, 1991). The origin of the compensatory pitch head movement is not known.

When walking, pitching of the head stimulates the semicircular canals. The angular head movement, sensed by the semicircular canals, would generate compensatory eye velocity via the angular vestibulo-ocular reflex (aVOR). The head pitch would also activate the otoliths by a linear acceleration component proportional to the radial distance from the otoliths to the axis of head pitch rotation, and by variation of the orientation of the otoliths with respect to the gravitational field (Gresty et al. 1987; Telford et al. 1996, 1997). In addition, the otoliths would be stimulated by a large vertical linear acceleration generated by the head translation. This combination of linear accelerations would also contribute to the eye movement response via the linear vestibulo-ocular reflex (lVOR). To see targets clearly at various distances when walking, the central nervous system must generate appropriate eye movements in response to activation of the VOR and visual input (Crane and Demer 1997; Demer and Virre 1996). The gain of the aVOR (the ratio of eye to head pitch velocity) and the sensitivity of the lVOR (defined as the amount of eye movement generated per unit of head translation, i.e., °/cm) vary inversely with viewing distance (Busettini et al. 1994; Paige 1989; Paige et al. 1996; Viirre and Demer 1996). For far targets, the aVOR gain is close to 1.0, whereas the lVOR response is negligible (Busettini et al. 1994; Paige 1989; Paige et al. 1996). This implies that when viewing distant targets during locomotion compensatory eye movements should be generated almost entirely by the aVOR, while for near targets the lVOR would play a more significant role.

During "walking in place" while viewing far targets, vertical eye velocity is typical of an aVOR response (180° out of phase with head pitch velocity and with a close to unity gain) for targets at 6 m (Demer and Viirre 1996) and 100 m (Grossman et al. 1989). Little is known about eye movements during locomotion when fixating on near and intermediate targets. Due to the dramatic increase in the lVOR response for near targets (Busettini et al. 1994; Paige 1989; Paige et al. 1996), it would be expected that the lVOR would exert greater control over the generation of eye movements. Crane and Demer (1997) measured eye movements while fixating on near (0.4-m), intermediate (0.9-m) and far (4.4-m) targets during slow (0.9 m/s) treadmill locomotion. The vertical aVOR gain was found to be less than unity (0.8–0.9) at all target distances, but no change was reported in the compensatory phase relationship of vertical eye velocity to head pitch velocity. There was no clear indication, therefore, that the lVOR had contributed to the generation of eye movements for near targets. In contrast, during fast treadmill walking (1.78 m/s) vertical eye movements in a single subject had appropriate phase to compensate for vertical head movement for a near (0.3-m) target (Bloomberg et al. 1992), suggesting a contribution by the lVOR.

In a previous study we demonstrated that the magnitude and frequency of vertical head translation during locomotion were dependent on walking velocity and were sufficient to activate the lVOR (Hirasaki et al. 1999). The purpose of the present study was to determine the relative contributions of the angular and linear VOR in the generation of vertical eye movements during locomotion, while viewing targets over a range of distances.

Materials and methods

Five normal healthy subjects (four males and one female) with uncorrected vision and normal vestibular function participated in this experiment. The visual acuity of all subjects was verified as 20/20 or better. Their ages ranged from 17 to 33 years (mean 28.8 years) and heights from 1.55 to 1.85 m (mean 1.74 m). The Institutional Review Board (IRB) approved the experiment and subjects signed consent forms prior to participation. The experiment was divided into two components: locomotion and body-fixed active head pitch. Five subjects were tested for the locomotion protocol and four subjects participated in the active head pitch study.

Locomotion protocol

The locomotion study required subjects to walk on a linear treadmill (Quinton Q55) while viewing a target at varying distances from 0.25 m to 2.0 m. The treadmill speed was a moderate to fast walking pace of 1.67 m/s (100 m/min), which is close to natural adult walking speeds (Finley and Cody 1970; Imai et al. 1998; Perry 1992). It is also within the optimal range of treadmill walking velocities of 1.2–1.8 m/s where vertical head translation and pitch are the most highly correlated (Hirasaki et al. 1999). The subjects first practiced treadmill locomotion until they could walk comfortably without using the handrail. After a short rest, testing began. Subjects fixated on a 1.0×0.75-m white screen with a target at the center consisting of the word "focus" in black 90-point Times Roman font. Each character was 15 mm high, and presented a visual angle of 0.43° at a distance of 2.0 m. The screen was positioned vertically such that the target word was centered at eye level when standing. Head and eye movement data were acquired with the target screen placed 0.25, 0.5, 0.75, 1.0, 1.25, 1.5, 1.75 and 2.0 m from the subject's eye. Position on the treadmill was maintained by having the subject briefly touch a handrail in front of them with their arm outstretched prior to each trial, and the actual eye-target distance was continuously monitored. A rest period of 60 s was inserted between each target condition while the treadmill was stopped and the screen repositioned. A period of approximately 90 s was allowed for transient effects to dissipate after restarting the treadmill.

At each target distance three-dimensional (3D) head and left heel position data were acquired from three trials of 10 s duration using a motion analysis system. Monocular horizontal and vertical eye movements were acquired simultaneously using a video-based pupil tracker (see "Measurement apparatus" below). Torsional eye position was not measured, but a recent study has demonstrated that two-dimensional (2D) eye measurements are sufficient to

study pitch and yaw VOR parameters during locomotion (Crane and Demer 1997). Subjects were instructed to refrain from blinking during the 10-s data acquisition period. Video images of the subject's eye were continuously monitored, and if blinking occurred the trial was repeated.

Active head pitch protocol

To explore the relationship between target distance and the interaction of the aVOR and lVOR in producing eye movements during locomotion, we also investigated the eye velocity response to active head pitch in the absence of vertical linear translation. Subjects were comfortably seated with their trunk supported and asked to perform self-generated sinusoidal head pitch movements in time with a digital metronome at 1 or 2 Hz. Based on a previous study (Moore et al. 1997), the locations of the head pitch rotation axes in the stereotaxic sagittal plane were approximately 8 mm anterior to and 24 mm below the interaural axis at 1 Hz and 4 mm below the interaural axis at 2 Hz, consistent with the results of Medendorp et al. (1998). With the trunk supported, head movement was close to a pure pitch rotation about these axes.

Subjects viewed either a space-fixed target (the target screen used in the locomotion study) at a distance of 0.3 m and 2.0 m, or a head-fixed target at a distance of 0.3 m. The head-fixed target consisted of a 160×115-mm white screen with the same target word ("focus") centered on the display. The screen was fixed to a 0.3-m aluminum shaft (6 mm diameter) which was attached to a lightweight plastic headband (120 g) and rigidly fixed to the head. The movement of the head-fixed target relative to the head was measured by placing an Optotrak marker on the target and calculating its movement relative to the head rigid body (see "Measurement apparatus" below). The peak amplitude of vertical target movement at 1 Hz was 0.4 mm relative to the head, which was equivalent to a pitch angular movement of 0.05°, or 1.1% of the peak head pitch amplitude of 4.5°. At 2 Hz, the peak vertical translation of the target relative to the head was 0.7 mm, corresponding to a peak pitch movement of 0.09°, or 1.36% of the head movement amplitude. Decoupling of the target relative to the head was therefore unlikely to have influenced the results. In all conditions the target word was placed at the subject's eye level. Both 3D head and monocular 2D eye position data were acquired simultaneously (see "Measurement apparatus" below). Three trials of 10 s duration were performed at each frequency and target condition.

Measurement apparatus

Head movement was recorded using the Optotrak 3020 video motion analysis system (Northern Digital, Ontario, Canada) positioned 4 m from the treadmill. The sensor tracked the 3D position of ten infrared (IR) markers (diameter 8 mm, weight 5 g) attached to a lightweight (120-g) headband. Data were acquired at a sampling rate of 150 Hz. The ten IR markers were used to specify a rigid body model of the head and a head-fixed coordinate frame (see "Measurement coordinate system" below). The raw position data of the IR markers were processed after testing to yield rotation and translation of the head rigid body in 3D space. To measure the distance from the eye to the target, the 3D coordinates of the midpoint of the ridge of the left orbit in the head coordinate frame were determined using a digitizing probe (Northern Digital, Ontario, Canada). The Optotrak system provides the 3D position of the origin of the head rigid body in space, and from the relative position of the orbit in head coordinates it was possible to calculate the coordinates of the eye in space. This allowed an accurate calculation of the distance from the eye to the target screen. For the locomotion study an IR marker was also placed on the left heel to obtain stride information. We have previously validated the Optotrak system using a rigid body placed 4 m from the sensor (Hirasaki et al. 1999), demonstrating an accuracy and resolution in both pitch and yaw of 0.1°. The accuracy and resolution for trans-

lation measurement was 0.3 mm at a distance of 4 m (manufacturer's specifications).

Horizontal and vertical eye movements were recorded at a sampling rate of 60 Hz using a commercial video pupil tracker (Iscan, Cambridge, MA). A miniature video camera (Eyecam, Iscan, Cambridge, MA) was attached to lightweight goggles (combined weight 114 g), which tightly fitted the eye sockets and allowed minimal camera movement during treadmill walking. This was verified by placing an Optotrak IR marker on the camera and measuring the relative movement of the camera with regard to the head during locomotion. Camera movement was less than the resolution of the Optotrak system (0.3 mm). A small transient spike (0.2°) with a duration of one sampling point (1/60 s) was occasionally superimposed on the eye movement waveform at heel strike, which was removed by a median filter (see "Locomotion data processing").

Video images were acquired of the subject's left eye, which was illuminated by a single 940-nm IR light-emitting diode (LED). The image of the eye was reflected onto the camera charge-coupled device (CCD) by an IR-sensitive "hot" mirror, which was transparent to light in the visible frequency range and allowed the subject a clear view of the target screen. In order to obtain pupil center coordinates at a rate of 60 Hz, the Iscan system calculates eye position from the odd and even fields of one full video image, and therefore the resolution for vertical eye movements is usually half that of the horizontal direction. To optimize the measurement of vertical eye position, the video camera was rotated 90° to obtain the maximum resolution of 0.2° in the vertical direction. Video techniques for tracking the pupil center have been well documented, demonstrating an accuracy of 0.12° for horizontal and 0.16° for vertical position using an artificial eye (Moore et al. 1996). An *in vivo* validation of video pupil tracking during locomotion measured system noise with a standard deviation of less than 0.04°, and a performance superior to electro-oculography and comparable to scleral search coils (DiScenna et al. 1995). A simultaneous *in vivo* comparison of video eye movement recording and scleral search coils during centrifugation yielded a mean difference in eye position measured with the two techniques of 0.05±0.14° (Moore et al. 1996).

The monocular video signal was processed in real time to provide analog voltage signals of raw horizontal and vertical position of both the pupil and the corneal reflection of the IR illumination source. These signals were input to an analog to digital converter (Northern Digital, Ontario, Canada), which provided digital data synchronized to the Optotrak head position measurements at a sampling rate sufficient to prevent aliasing (150 Hz). Both head and eye raw data were stored on an IBM-compatible PC for later processing.

Eye position was calculated from the raw pupil data using a calibration file acquired prior to testing. The subject was seated and asked to fixate on horizontal and vertical targets at gaze angles of 2.86° and 5.71° on a calibration grid placed 2 m distant while maintaining a stationary head position. The center point of the grid was positioned directly in front of the subject at eye level. Multiple calibrations were performed for each subject and head movement data were analyzed to ensure the validity of the eye position data for the calibration file to be utilized.

Measurement coordinate system

The space- and head-fixed coordinate frames were specified during calibration of the Optotrak system. A right-handed space-fixed coordinate frame {X, Y, Z} was defined as follows. The positive X-axis was parallel to the forward direction of the treadmill (in the direction of locomotion) and normal to gravitational vertical. The Y-axis was positive to the subject's left and the positive Z-axis upward vertical. The Optotrak software has the capability to specify coordinate axes relative to the markers that define a rigid body (see Medendorp et al. 1998), which in our experiment were fixed to the head. A head-fixed coordinate frame $\{X_h, Y_h, Z_h\}$ was defined such that X_h was parallel to the naso-occipital axis (positive

forward), Y_h parallel to the interaural axis (positive left), and Z_h normal to the X_h–Y_h plane (positive upwards). The origin of the head coordinate frame was the intersection of these axes, located on the interaural axis at a point approximately midway between the vestibular labyrinths. Previous studies have demonstrated that rotation axes for small head pitch movements, such as those encountered during locomotion, are approximately coincident with the interaural (Y_h) axis (Moore et al. 1997; Medendorp et al. 1998). An eye-fixed coordinate frame $\{X_e, Y_e, Z_e\}$ was also defined with the origin at the center of the eye and X_e passing through the center of the pupil (positive forward) and normal to the Y_e–Z_e plane. When the subject fixated on the center point of the calibration grid $\{X_e, Y_e, Z_e\}$, $\{X_h, Y_h, Z_h\}$ and $\{X, Y, Z\}$ were approximately aligned. Vertical position of the head and left heel were measured in the space-fixed coordinate frame $\{X, Y, Z\}$. Rotation of the head rigid body in $\{X, Y, Z\}$ was given in terms of Euler angles around the head-fixed axes $\{X_h, Y_h, Z_h\}$ (*passive rotation* or *rotation of the coordinate frame*) using a Fick rotation sequence (yaw, pitch, roll) (Fick 1854; Moore et al. 1996). The eye was assumed to be a sphere exhibiting ideal *ball and socket* behavior. All eye movements were therefore considered pure rotations around the center of this sphere, with no translational component (Crawford and Villis 1991; Haslwanter and Moore 1995; Moore et al. 1996; Raphan 1998; Tweed and Villis 1987). Eye position in head-fixed coordinates $\{X_h, Y_h, Z_h\}$ was represented as yaw and pitch rotations about the eye-fixed axes Z_e and Y_e using a Fick rotation sequence. A simple 3D model of the eye, calculated from the calibration data, was used to obtain eye position from the raw pupil center coordinates acquired during testing (Moore et al. 1996). An advantage of using the Fick sequence to calculate eye position from a digitized video image is that the formula for deriving vertical eye position from the pupil center image coordinates is independent of horizontal eye position (Haslwanter and Moore 1995; Moore et al. 1996). According to the right-hand rule, eye and head rotations to the left, down, and clockwise (from the subject's point of view) were positive.

Locomotion data processing

After testing, the raw data were processed to provide calibrated eye position in head-fixed coordinates, and head position data in the space-fixed frame. Only head movements in the vertical (X–Z) plane and eye movements in the sagittal (X_h–Z_h) plane were considered in this study. There were no saccades present in the eye position data and it was unnecessary to desaccade the records before processing. From examination of the power spectra of the raw head and eye position data, the vast majority of the power was concentrated at the predominant frequency of head movements (approximately 2 Hz). Low-frequency drift was evident below 2 Hz. One subject exhibited low-power harmonics at twice the step frequency (4 Hz). The results of previous locomotion studies have demonstrated negligible power at frequencies above 6 Hz (Demer and Virre 1996; Hirasaki et al. 1999). On this basis, the raw eye and head rotation and translation data were filtered using a 3-point median (to remove single-point spikes) and a 7-point moving average filter. This filter combination did not affect the phase of the original waveform. This was confirmed experimentally by cross-correlation of the original raw waveform with the filtered data. No phase shift was observed. This filter had a gain of –3 dB at 10 Hz and a null gain at 18 Hz. The power spectrum of the filtered waveforms was compared with that of the original raw data to confirm that there was no alteration in the frequency characteristics of the signal below 10 Hz.

Eye and head pitch velocities were calculated by differentiation of the filtered position waveforms with a 2-point forward difference algorithm. Head vertical acceleration was calculated by applying the 2-point forward difference algorithm to the filtered head translation, then again to the vertical head linear velocity waveform. Finally, both the eye and head pitch velocity, and the head vertical linear acceleration, were filtered with an 11-point moving average filter with a gain of –3 dB at 7 Hz and a null gain

at 13 Hz. The filter bandwidths were similar to those used in previous locomotion studies (Bloomberg et al. 1997; Crane and Demer 1997). The gain and phase characteristics of the filters were determined from the input-output relationship of sinusoidal waveforms from 0.1 to 30 Hz.

Phase relationships between the various waveforms were calculated by cross-correlation. A Hamming window was applied to each 10-s data record, which was then cross-correlated with another waveform (e.g., eye velocity and head pitch velocity). The shift in the peak of the cross-correlation function closest to the origin provided an estimate of the shift between the two signals in the time domain. The predominant frequency of the waveforms was estimated from the peak of the power spectrum and was used to obtain the period. The time shift was then divided by the period to obtain the phase relationship between the two waveforms.

In order to obtain a robust estimate of the mean peak amplitude for eye and head pitch position and velocity, and vertical head translation and linear acceleration, each 10-s data record was subdivided into strides using the local minima of the heel vertical position (left heel-strike). Each stride waveform (approximate duration 1 s) was resampled to provide 200 data points following a cubic spline interpolation, and an average stride waveform calculated from these individual strides (typically 10 per trial). Peak eye and head pitch position and velocity, and peak vertical head translation and linear acceleration, were calculated for each trial by halving the peak to peak value of the relevant averaged stride waveform.

The results of the phase analysis and the peak position, velocity and acceleration values for all subjects were sorted into 25-cm-wide bins centered on the nominal target distances (0.25, 0.5, 0.75, 1.0, 1.25, 1.5, 1.75 and 2.0 m) based on the actual eye-target distance. The mean and 95% confidence intervals (CI) were calculated for each bin in order to compare data across subjects. Statistical analysis was performed using a one-dimensional analysis of variance (ANOVA) (Labview, National Instruments, Austin, TX). Results were considered significant for $P<0.05$.

Active head pitch data processing

For the space-fixed targets at 0.3 m and 2.0 m at both 1 Hz and 2 Hz and for the head-fixed target at 1 Hz, the aVOR gain was obtained for each 10-s trial from the slope of a linear least squares fit to the plot of eye versus head pitch velocity (see Demer and Viirre 1996). The phase relationship of eye to head pitch velocity was determined using cross correlation (see "Locomotion data processing" above). For the head-fixed target condition at 2 Hz the variable nature of the eye re head pitch velocity phase did not allow for conventional gain analysis. In this case the aVOR gain was estimated from the ratio of the average peak eye and head pitch velocity. The phase relationship between eye and head pitch velocity for the 2-Hz head-fixed target condition was further studied by calculating the phase for each cycle within a 10-s trial. The time delay between the positive peak of head velocity and the subsequent positive peak of the eye velocity waveform was measured for each cycle. The predominant frequency of the head pitch movement was determined from the power spectrum of the head pitch velocity waveform and used to provide an estimate of the period. The instantaneous phase for each cycle was then calculated from the time delay values and the period of the waveform.

Results

Locomotion

Vertical head and eye movements

Subjects were able to maintain a stable position on the treadmill relative to the target screen (Fig. 1A), with a

A

Eye - Target Distance

y = 0.001 + 1.01x   r = 0.999

B

Predominant Frequency

y = 4.67 - 1.50x   r = 0.949

- o   subject 1
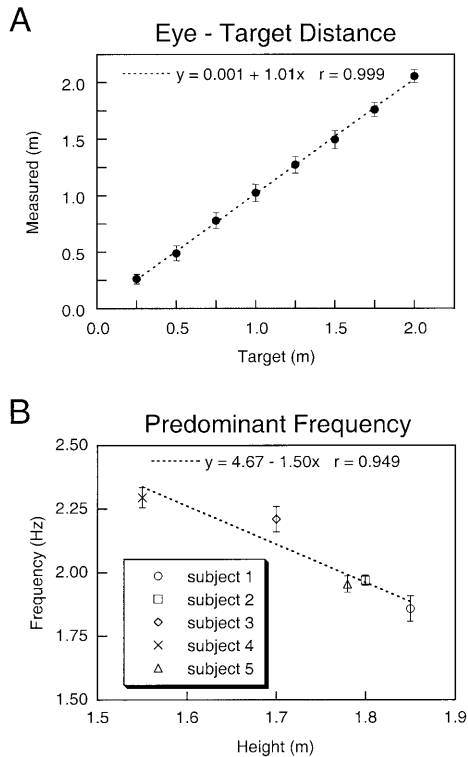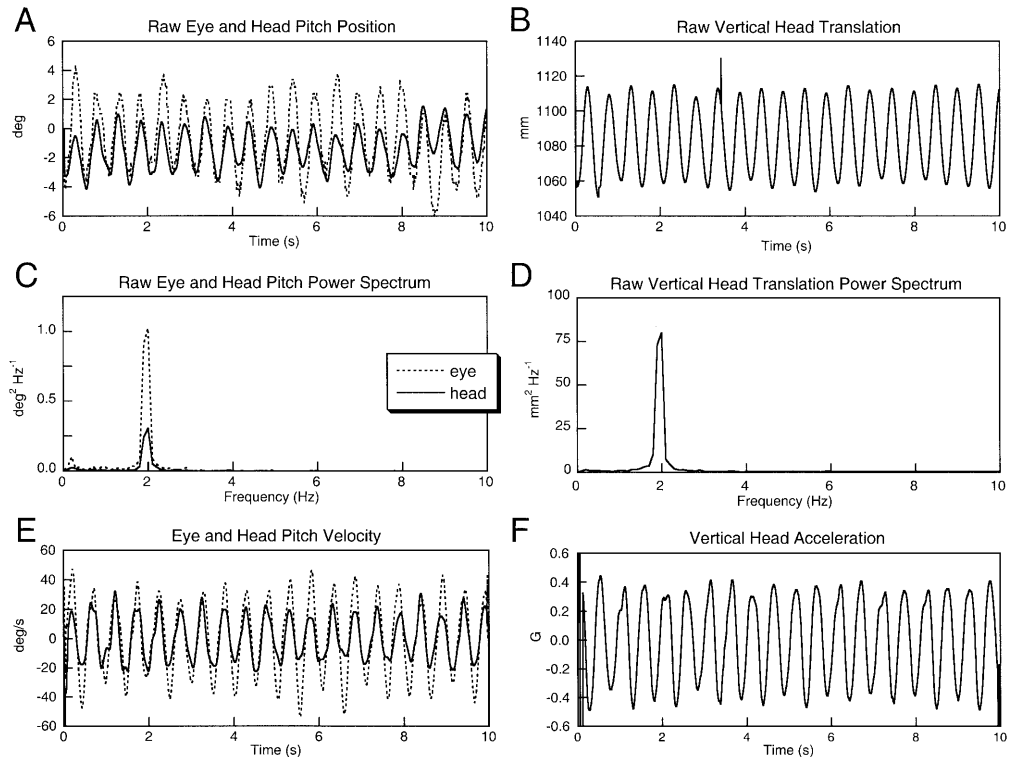- □   subject 2
- ◇   subject 3
- ×   subject 4
- △   subject 5

Fig. 1 A Measured distance from the eye to the target screen (mean and 95% CI of all subject trials at each target distance) plotted as a function of nominal target distance. Subjects were able to maintain their position on the treadmill with respect to the target screen during locomotion. **B** The predominant frequency of head movement for each of the five subjects in the locomotion protocol (mean and SD of all trials) plotted as a function of subject height. The frequency of head movement was inversely related to subject height in a linear manner

strong linear relationship between the measured distance from the eye to the target and the nominal target distance (slope=1.01, r=0.99). The predominant frequency of head movements over all subject trials was 2.06±0.17 Hz (mean±SD), and was not affected by target distance (P>0.2). The predominant frequency for each subject was finely tuned (Fig. 1B), and was inversely related to subject height in a linear fashion (slope=−1.5 Hz/m, r=0.95), ranging from 1.86 Hz to 2.30 Hz for subject heights of 1.85–1.55 m.

The raw eye and head position data exhibited little noise, as shown by data from a typical subject (5) for a near (0.25-m) target (Fig. 2A,B). The predominant frequency of both eye and head vertical movements was 1.96 Hz, which was twice the stride frequency of 0.98 Hz. The mean vertical eye position amplitude was 3.8° (Fig. 2A, dashed trace), which was significantly larger than the mean head pitch amplitude of 1.7° (Fig. 2A, solid trace). No saccadic eye movements or blinks were present, which was typical of most subject trials. Eye position was essentially in phase with the head pitch, with a small phase advance of 1.8°. Mean vertical head translation amplitude was 25.0 mm (Fig. 2B) and lagged the head pitch by −164.4°. The majority of the power spectra of eye and head pitch (Fig. 2C) and vertical head translation (Fig. 2D) were concentrated at the step frequency (1.96 Hz), with low-frequency drift evident below 2 Hz. The mean peak amplitude of vertical eye velocity (35.9°/s) was significantly greater than head pitch velocity (20.7°/s) (Fig. 2E), and vertical head linear acceleration reached amplitudes of up to 0.45 G (Fig. 2F).

Averaged stride data for the same subject (5) for a near (0.25-m), intermediate (1.0-m) and far (2.0-m)
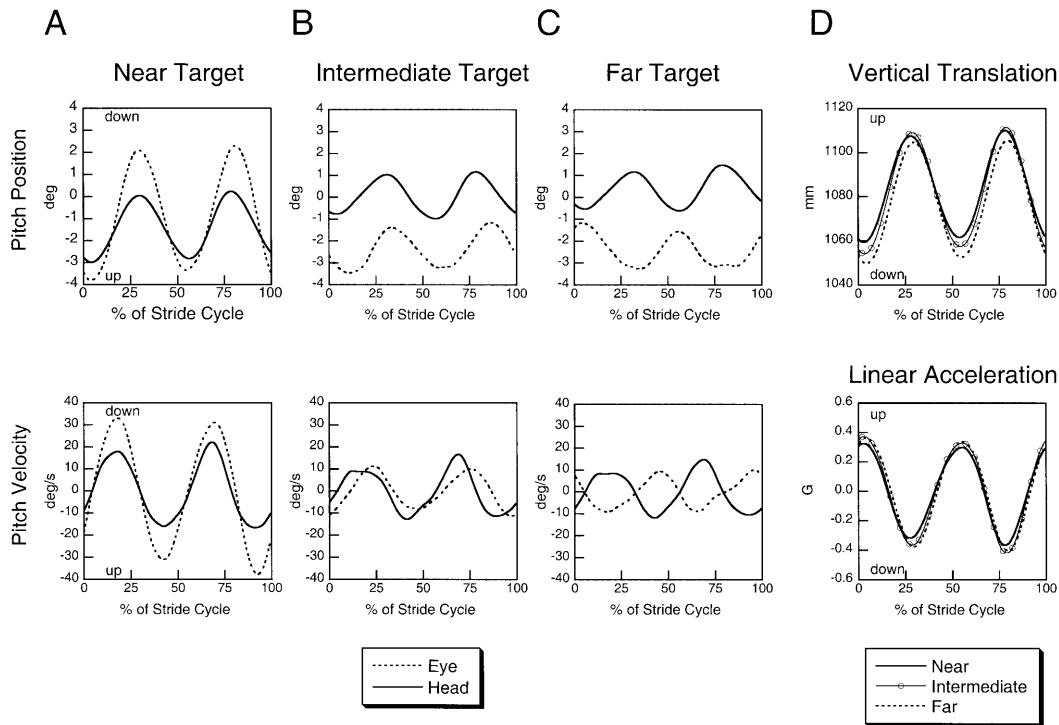
Fig. 2A–F Eye and head data from a typical subject (5) when viewing a 0.25-m target during locomotion. **A** Raw eye (*dashed trace*) and head pitch (*solid trace*) position. The magnitude of eye movement was larger than the head pitch, and the two waveforms were in phase. **B** Raw vertical head translation. **C** Power spectrum of the raw eye and head pitch and **D** raw vertical head translation waveforms (with the DC component removed). Power was concentrated at the step frequency of 1.96 Hz. **E** The raw data were filtered and differentiated (see "Materials and methods") to provide eye and head pitch velocity and **F** head vertical linear acceleration

A Raw Eye and Head Pitch Position

B Raw Vertical Head Translation

C Raw Eye and Head Pitch Power Spectrum

- ······· eye
- —— head

D Raw Vertical Head Translation Power Spectrum

E Eye and Head Pitch Velocity

F Vertical Head Acceleration

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Fig. 3 Averaged stride data for subject 5 while viewing **A** a near
(0.25-m), **B** intermediate (1.0-m) and **C** far (2.0-m) target. *Top
panel* shows vertical eye (*dashed trace*) and head pitch (*solid
trace*) position. *Lower panel* shows eye (*dashed trace*) and head
pitch (*solid trace*) velocity. There was a complete reversal in the
phase of the eye movements from near to far targets; eye move-
ments were compensatory for head pitch for the far target but in
phase with head pitch when viewing the near target. The magni-
tude of both eye and head pitch movements increased for near tar-
gets. **D** Target distance had little effect on the magnitude or timing
of vertical head translation (*upper panel*) and linear acceleration
(*lower panel*)

target condition exhibited a marked change in the magni-
tude and phase of eye velocity over the range of viewing
distance (Fig. 3A–C). For the far target condition (Fig.
3C), the peak amplitude of eye position (1.0°) and veloc-
ity (9.6°/s) were close to peak head pitch (1.1°) and ve-
locity (13.3°/s) amplitudes. The eye position and veloci-
ty waveforms were virtually compensatory for head
pitch position and velocity, with phase lags of –185.7°
and –191.9°, respectively. For the intermediate target
(Fig. 3B) there was little change in the amplitude of eye
position and velocity (1.2° and 11.2°/s) or head pitch po-
sition and velocity (1.1° and 14.7°/s). There was, how-
ever, a considerable shift in the phase of the eye move-
ment response, which was no longer compensatory for
head pitch. The eye position and velocity waveforms ex-
hibited a phase lag of –59.2° and –55.9°, respectively.
For the near target (Fig. 3A), there was an almost three-
fold increase in the amplitude of vertical eye position
and velocity (3.1° and 35.4°/s), which was larger than
the corresponding increase in head pitch position and ve-
locity amplitude (1.6° and 19.3°/s). There was a com-
plete reversal in the phase of both eye position and ve-

locity, which were essentially in phase with the head
pitch position and velocity, with phase lags of –3.2° and
–4.1°, respectively. Vertical head translation and linear
acceleration exhibited little change with viewing dis-
tance (Fig. 3D). Peak amplitudes for both translation
(25.3 mm, 28.6 mm and 27.9 mm) and vertical linear
acceleration (0.34 G, 0.39 G and 0.38 G) were similar at
the three target distances. Head translation and pitch
were essentially compensatory, with phase lags of
–167.3°, –174.2° and –174.8° for the near, intermediate
and far target conditions, respectively.

These trends were consistent across all five subjects
(Fig. 4). The peak vertical linear head translation was
relatively constant, narrowly ranging from 21.0±2.7 mm
at 0.75 m to 24.0±2.2 mm at 1.75 m (Fig. 4A). Peak ver-
tical linear acceleration also exhibited a restricted range
of 0.33±0.02 G at 0.25 m to 0.40±0.09 G at 1.5 m (Fig.
4B). The effect of target distance on peak head transla-
tion and linear acceleration was not significant ($P>0.05$).
Peak head pitch amplitude (Fig. 4C) ranged from
1.32±0.12° at 0.25 m to 0.94±0.10° at 2.0 m. Peak head
pitch velocity (Fig. 4D) also exhibited a limited range,
from 17.3±1.1°/s at 0.25 m to 13.1±1.7°/s at 2.0 m.
While both head pitch position and velocity tended to
decrease with target distance ($P<0.01$), these changes
were small. The phase relationship between the vertical
linear translation and pitch of the head exhibited little
variation over the range of target distances studied
($P>0.05$). Head translation and pitch were essentially
compensatory, with phase lags from –164.4±5.7° at 0.25 m
to –170.3±5.8° at 1.75 m (Fig. 4G). In general, head
movements exhibited little variation in magnitude or in
the phase relationship of head translation to pitch over
the range of target distances studied.

Fig. 4A–H Effect of target distance on eye and head movements during treadmill locomotion (mean and 95% CI of all subject trials at each target distance, plus individual subject means). There was no significant effect of target distance on **A** the peak vertical head translation and **B** peak vertical linear acceleration. **C** Peak head pitch amplitude exhibited a small increase as target distance decreased. **D** Peak head pitch velocity demonstrated a similar tendency. **E** The amplitude of both vertical eye position and **F** eye velocity increased almost threefold for near targets, and was significantly greater than head pitch. **G** The phase relationship of vertical head translation to head pitch was compensatory and was not affected by viewing distance. **H** In contrast, the phase relationship of eye velocity to head pitch velocity reversed over the range of target distance studied. For a far (2.0-m) target eye velocity was compensatory for head pitch. For a near (0.25-m) target eye velocity was in phase with head pitch velocity. The eye velocity phase varied smoothly as a function of target distance between these two states
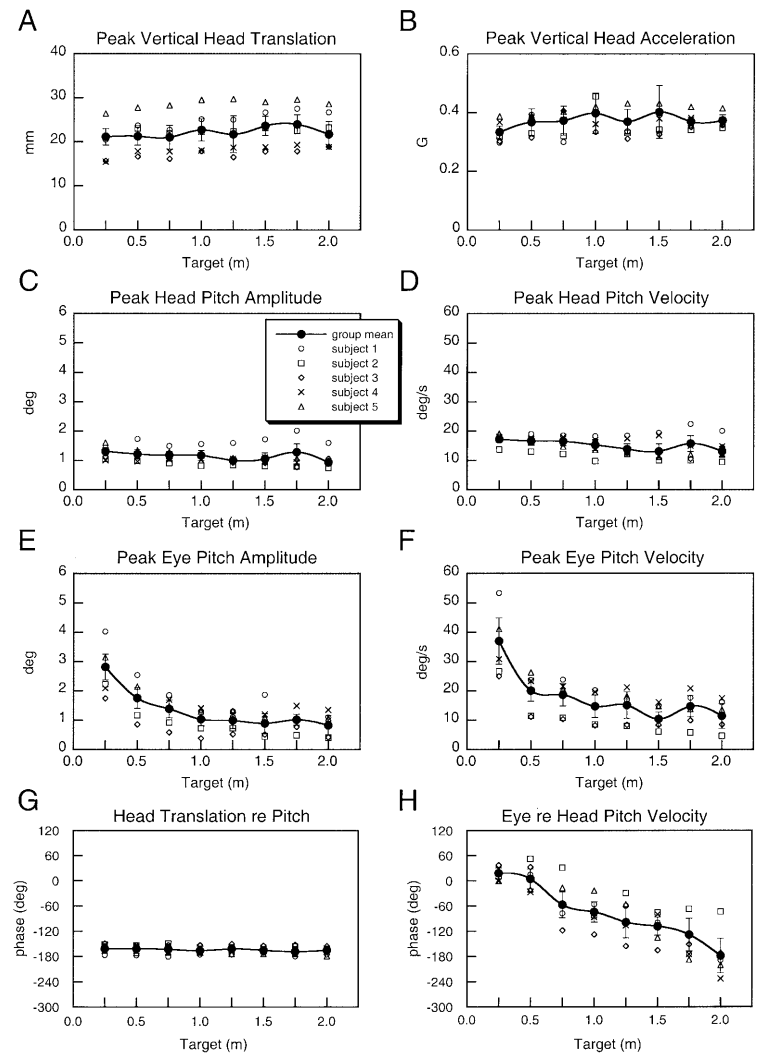
The effect of target distance on eye position and velocity was considerably more noticeable. There was a more than threefold increase in peak vertical eye position as target distance decreased ($P<0.01$), from 0.8±0.3° at 2.0 m to 2.8±0.4° at 0.25 m (Fig. 4E). The peak vertical eye velocity (Fig. 4F) increased in a similar fashion ($P<0.01$), from 11.4±4.2°/s at 2.0 m to 37.0±7.8°/s at 0.25 m. The aVOR gain, defined as the ratio of peak eye velocity to peak head pitch velocity, was 0.82±0.24 at a distance of 2.0 m. For target distances less than 1.0 m, eye position and velocity amplitudes were significantly greater than for head pitch ($P<0.01$) (Fig. 4C-F). Target distance had a significant effect ($P<0.01$) on the phase relationship of vertical eye velocity to head pitch velocity (Fig. 4H). For targets at 2.0 m the eye velocity exhibited a phase lag of –178.6±40.9° and was compensatory for head pitch velocity. This implies that eye velocity was generated largely by the aVOR. The phase lag decreased with target distance, and for near targets (0.25 m) the eye velocity was essentially in phase with the head pitch velocity, with a small phase lead of 17.9±13.3°. For targets closer than 1.0 m the compensa-

tory nature of the eye velocity with respect to vertical head translation, plus the large increase in magnitude, suggested that activation of the lVOR was contributing to the eye movement response.

Analysis of linear acceleration

When walking there is a complex stimulation of both the semicircular canals and the otoliths due to the combined translation and pitch of the head. We examined the vertical linear accelerations acting on the otoliths during locomotion using data from the subject with the largest head pitch (subject 5) for the near (0.25-m) target condition. Successive differentiation of the head pitch waveform yielded peak angular velocity and acceleration of 20°/s and 215°/s², respectively. During high-frequency active head pitch rotations of small amplitude (less than 5° peak), such as those encountered during locomotion, there is little flexion of the cervical vertebrae (Moore et al. 1997). The skull simply rocks back and forth on the atlanto-occipital joint, and the pitch rotation axes are al-
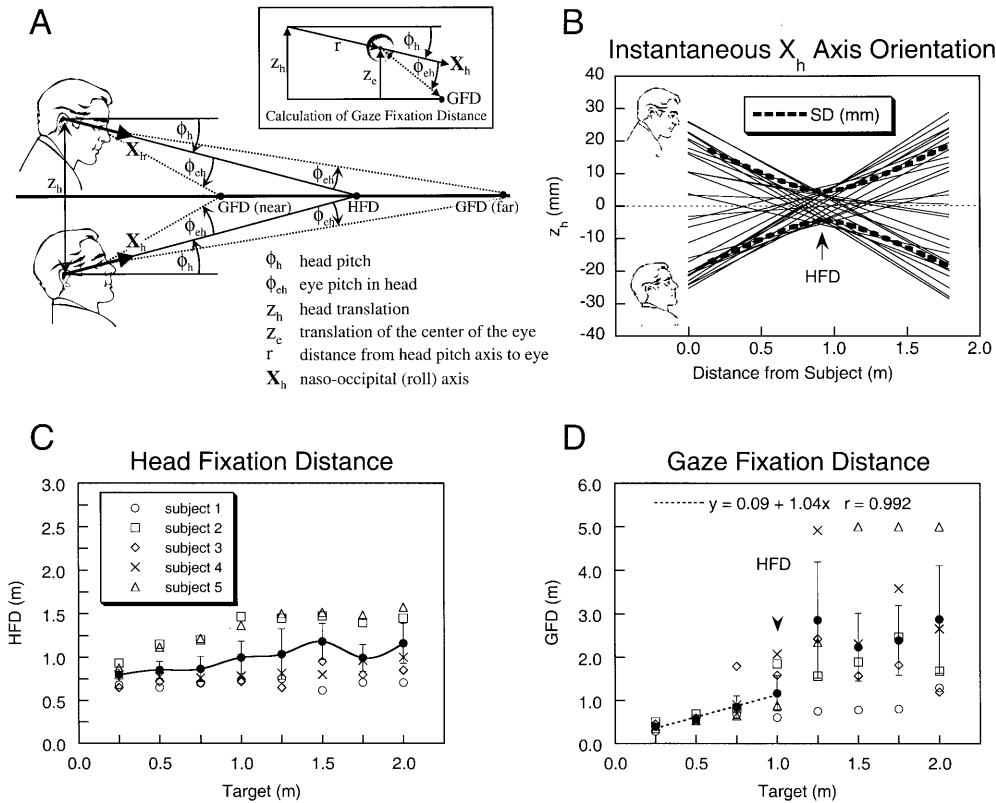
Fig. 5 A The compensatory pitch and translation of the head tend to point the naso-occipital (X_h) axis at a relatively fixed distance in front of the subject, termed the head fixation distance (HFD). In an analogous manner, the gaze fixation distance (GFD) was defined as the distance to the point in front of the subject where gaze was directed. For targets located beyond the HFD the required eye movements to maintain gaze are compensatory for head pitch, and for near targets located between the subject and the HFD eye movements that are in phase with head pitch are required. Note that for targets beyond the HFD a reduction in aVOR gain is necessary, as the required eye pitch to maintain target fixation is less than head pitch. The translation of the center of the eye (*inset*), necessary for the GFD calculation, was determined from the head pitch and translation data. **B** Instantaneous naso-occipital (X_h) axes calculated from head movement data from a single stride (subject 5) while viewing a near (0.25-m) target. In practice the HFD was defined as the distance in front of the subject where the vertical spread of the X_h-axes was minimized. **C** The HFD (mean and 95% CI of all trials plus individual subject means) was maintained at a relatively fixed distance in front of the subject. Subjects maintained their own individual HFD based on the characteristics of their head movements, which accounted for the large variance in the mean HFD. **D** GFD (mean and 95% CI of all trials plus individual subject means) as a function of target distance. For viewing distances up to the HFD (1 m), the GFD was maintained close to the target distance. Beyond the HFD gaze tended to overshoot the target

0.00016 G, respectively. These accelerations were insignificant relative to the linear acceleration generated by the vertical head translation (0.33 G).

The small pitch head movement during locomotion (maximum mean peak amplitude of $\pm 1.3°$) would also vary the orientation of the otoliths with respect to the gravitational field. This would activate the "tilt" response, which has low-frequency characteristics (Telford et al. 1997), and would not significantly contribute to the eye movement response at the frequency of head movement during locomotion (2 Hz). This is consistent with a previous study (Baloh and Demer 1991), which found no change in the gain or phase response of the vertical aVOR during active head pitch at 1.6 Hz in the upright and lying-on-side position, and concluded that movement of the otoliths relative to the gravitational field had no effect on the vertical aVOR response. Based on our analysis, we conclude that the small linear accelerations generated by the head pitch did not play a significant role in the observed eye velocity response during locomotion. The primary drive to the lVOR, therefore, was the vertical linear acceleration generated by head translation.

Head and gaze fixation distance

The compensatory pitch and translation movements of the head tend to point the X_h (naso-occipital)-axis of the head towards a confined region in front of the subject. Pozzo et al. (1990) proposed the concept of head fixation distance (HFD), which is located at a point in front of

most coincident with the interaural axis (Moore et al. 1997; Medendorp et al. 1998). Based on the stereotaxic location of the human vestibular labyrinth (Curthoys et al. 1977), we estimate the radial distance from the head pitch rotation axis to the otoliths in the sagittal plane to be 12 mm. On the basis of this estimate, the peak tangential and centripetal acceleration at the otoliths generated by head pitch during locomotion was 0.0046 G and

the subject where the X_h-axis intersects the mean elevation of the head at the maxima and minima of the head vertical translation, and is determined using triangulation (Fig. 5A). We have extended this definition using a statistical technique to define the HFD based on head movement data from an entire stride cycle. The instantaneous orientation of the naso-occipital axis was computed at 5-ms intervals (Fig. 5B). At a distance d from the subject these axes would intersect a line parallel to the spatial vertical (Z-axis), generating intersection points $\{z_1...z_n\}$. The standard deviation of these points was calculated as a function of distance d, as d varied from 0.1 to 2.5 m in front of the subject in 0.05-m increments. The HFD was defined as the distance from the subject's eye where the standard deviation of the points of intersection was at a minimum (Fig. 5B). This approach yielded robust estimates of the HFD. The standard deviation at the HFD was small and was consistent across all subjects and target distances (7.1±0.35 mm).

The HFD was maintained within a narrow band from 0.8±0.06 m for the near target (0.25 m) to 1.2±0.23 m for the far target condition (2.0 m) (Fig. 5C), although a weak but significant ($P<0.05$) tendency to increase with target distance was evident. The mean position of the HFD over all trials was 1.0 m±0.3 m. Each subject exhibited a characteristic HFD, which was dependent on each individual's head translation and pitch magnitude. Most of the variation in the mean HFD was due to this intersubject variability. For example, subjects 2 (square) and 5 (triangle) had a large HFD (1.5 m) compared to other subjects (0.75 m). This was consistent with their head movement data (see Fig. 4A,C): subject 2 had small head pitch amplitude, while subject 5 exhibited large vertical head translation. This would tend to point the head at a distance further away from the subject.

For near target distances (less than 0.75 m) the HFD was situated beyond the target (Fig. 5C), and an eye velocity response in phase with head pitch would be required to maintain fixation (Fig. 5A). For far target distances (greater than 1.5 m) the HFD lay between the subject and the target screen (Fig. 5C), and a compensatory (i.e., 180° out of phase) eye velocity response with respect to head pitch would be required (Fig. 5A). The ideal aVOR gain (i.e., the ratio of eye to head pitch velocity) is dependent on the closeness of the target to the HFD. To maintain fixation on very distant targets the ideal gain approaches unity (Demer and Viirre 1996). As the target moves closer to the HFD the required aVOR gain is reduced due to the compensatory pitch and translation of the head (Fig. 5A), approaching zero as the target approaches the HFD. Targets located in the vicinity of the HFD, within the region from 0.75 m to 1.5 m, would appear to be near stationary in a head-fixed coordinate frame, requiring an eye velocity response of close to zero to maintain fixation. The required phase of the eye velocity response could be either 0° or 180°, depending on the actual location of the HFD with respect to the target.

In an analogous manner we calculated the gaze fixation distance (GFD), using an estimate of the vertical translation of the center of the eye in space to determine the gaze direction relative to the X_h (naso-occipital)-axis (Fig. 5A, inset). A value of 100 mm was used for the distance from the center of the eye to the axis of head pitch rotation (Moore et al. 1997). The location of the GFD (Fig. 5D) increased significantly ($P<0.01$) with target distance up to a distance corresponding to the HFD (1.0 m), and was linearly related with a slope of 1.04 ($r=0.99$). This indicated that on average gaze in space was directed at the target. The GFD for the 0.25-m target was 0.38 m, however, indicating that the large vertical eye velocity generated (37°/s) was still not sufficient to maintain gaze on the target at very close viewing distances. Subjects were fixating at a point 130 mm beyond the target, which was consistent with subjective reports of appreciable target movement. For distances greater than the HFD, gaze tended to overshoot the target and there was a large variability in the location of the GFD. The GFD data suggest that for viewing distances beyond 1.0 m the observed 20% reduction in aVOR gain (see "Vertical head and eye movements" above) was not sufficient for target fixation.

Ideal eye velocity response

The ideal eye position to achieve retinal image stability $[\theta(t)]$ was calculated from the head pitch $[\phi_h(t)]$ and vertical linear translation $[z_h(t)]$ averaged stride waveforms for each trial as follows (Fig. 6A):

$$\theta(t) = \arctan\left(\frac{z_h(t) - r * \sin(\phi_h(t))}{r * (1 - \cos(\phi_h(t))) + D}\right) - \phi_h(t)$$

where D is the distance from the center of the eye to the target, and r is the distance from the axis of head pitch rotation to the center of the eye. For active head pitch rotations r is approximately 100 mm (Moore et al. 1997).

The $\theta(t)$ waveform was differentiated to yield the ideal eye velocity $\dot{\theta}(t)$. The ideal peak eye velocity (Fig. 6B, solid trace) closely approximated the measured eye velocity (Fig. 6B, dashed trace) for targets up to 1.0 m ($P>0.5$), decreasing from a maximum of 42.9±4.9°/s at 0.25 m to 7.6±2.3°/s at 2.0 m. For targets beyond 1.0 m the measured peak eye velocity was significantly greater ($P<0.01$) than the ideal response. This is consistent with the results of the GFD analysis (Fig. 5D), which indicated that for targets situated beyond the HFD eye velocity overcompensated for head pitch.

Using cross-correlation, the phase characteristic of ideal eye velocity $\dot{\theta}(t)$ relative to head pitch velocity was determined (Fig. 6C, solid trace). As predicted by the HFD analysis (Fig. 5A), the ideal phase had two distinct states ($P<0.01$). Ideal eye velocity was compensatory for head translation for near targets (leading the head pitch velocity by 25.8±5.3°), and compensatory for head pitch for far targets (phase lag of –186.2±8.0°). The ideal phase characteristic computed for each subject changed state at a distance corresponding to their individual HFD (see Fig. 5C). Subjects 1 (circle), 3 (diamond) and 4
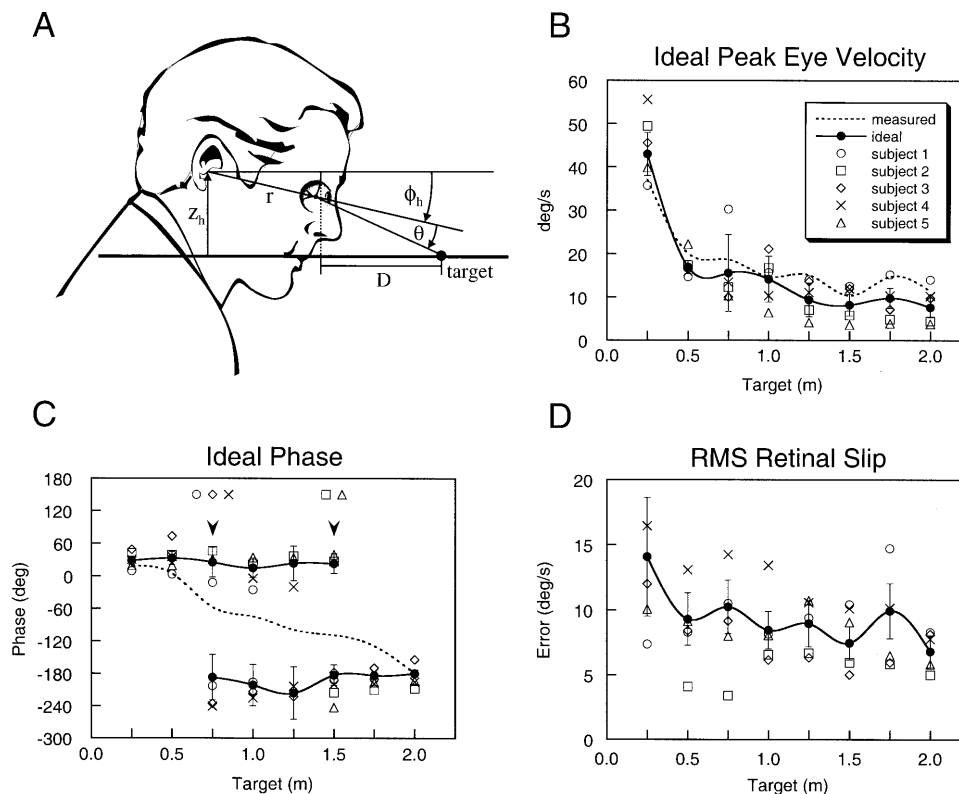
Fig. 6 A Simple model used to calculate the ideal eye position waveform [$\theta(t)$] to maintain a stable image on the retina (z_h vertical head translation, ϕ_h head pitch, r distance from the axis of head pitch rotation to the center of the eye, D distance from the center of the eye to the target, θ ideal eye position). Ideal eye velocity $\dot{\theta}(t)$ was calculated by differentiation of $\theta(t)$. **B** Ideal peak eye velocity (*solid trace*) (mean and 95% CI of all trials at each target distance plus individual subject means) was close to measured peak eye velocity (*dashed trace*) for targets up to 1 m. **C** The ideal eye velocity phase characteristic (*solid trace*) exhibited two distinct states: in phase with head pitch for near targets, and compensatory for head pitch for far targets. Subjects changed state at a viewing distance corresponding to their individual HFD (see Fig. 5C). The measured eye velocity phase (*dashed trace*) was close to ideal for the near (0.25-m) and far (2.0-m) targets, but did not exhibit a sharp transition between the two states, varying smoothly as a function of target distance. **D** The RMS retinal slip velocity was calculated from the difference between the ideal and measured eye velocity waveforms. Retinal slip tended to decrease with increasing target distance

(cross) changed state at 0.75 m, and subjects 2 (square) and 5 (triangle) at 1.5 m. Measured eye velocity phase closely approximated the ideal characteristic for targets at 0.25 and 2.0 m (*P*>0.2). The measured phase characteristic, however, did not exhibit the predicted sharp transition in the vicinity of the HFD. Rather, it varied smoothly between the two states as a function of target distance (Fig. 6C, dashed trace).

The retinal slip velocity error was determined by subtracting the measured eye velocity from the ideal eye velocity $\dot{\theta}(t)$, and calculating the RMS value of the resultant waveform over a bandwidth of 0–7 Hz. The RMS retinal velocity error exhibited a weak but significant

tendency to decrease with increasing target distance (*P*<0.05), from a maximum of 14.1±4.6°/s at a target distance of 0.25 m to 6.8±1.2°/s at 2.0 m (Fig. 6D), which was consistent with previous studies (Grossman et al. 1989; Crane and Demer 1997). Given the size of the visual target these retinal slip velocities would not have impacted on resolution of the target word. This was consistent with subject reports that the word was clearly focused during the locomotion task, although it appeared to "bounce" vertically at a rate corresponding to the step frequency.

Active head pitch

To gain further insight into the relationship between target distance and the interaction of the aVOR and lVOR in producing eye movements during locomotion, we investigated the eye velocity response to active head pitch movements at 1 and 2 Hz. Subjects were seated and viewed near (0.3-m) and far (2.0-m) space-fixed and near (0.3-m) head-fixed targets. While the amplitude of head pitch during this paradigm was slightly larger than during locomotion, the computed linear acceleration at the otoliths was negligible (see "Analysis of linear acceleration" above) and would not significantly contribute to the aVOR response (Baloh and Demer 1991).

For both near and far space-fixed targets the eye movement responses were compensatory for head pitch, with eye velocity lagging head pitch velocity by −180.1±2.2° (mean and SD of all trials). When viewing the far target the aVOR gain was close to unity at both 1
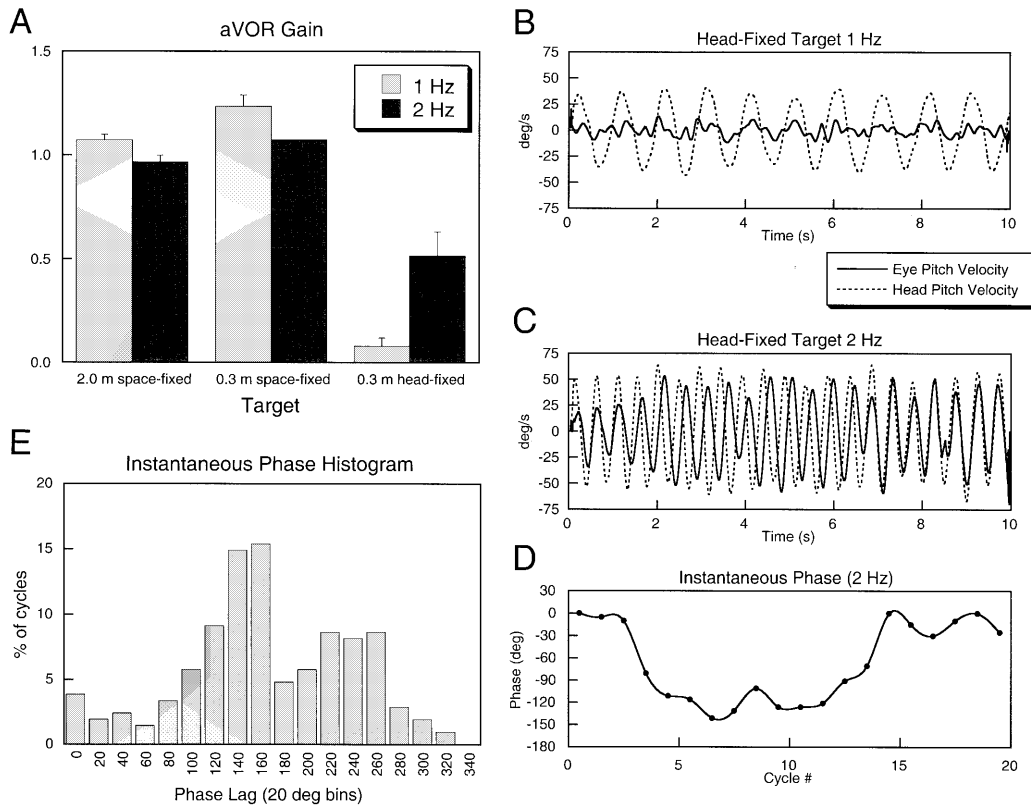
Fig. 7A–E *Clockwise from upper left:* **A** Vertical aVOR gains were calculated during active head pitch at 1 Hz (*light columns*) and 2 Hz (*dark columns*). For a far (2.0-m) space-fixed target the aVOR gain was close to unity at both 1 and 2 Hz. The gain of the aVOR increased significantly for a near (0.3-m) space-fixed target at both 1 Hz (16%) and 2 Hz (10%). For a 0.3-m head-fixed target the aVOR gain was close to zero at 1 Hz. At 2 Hz, however, there was still significant gain of approximately 0.5. **B** Eye and head pitch velocity data from a typical subject (2) during active head pitch at 1 Hz while viewing a 0.3-m head-fixed target. The eye velocity response (*solid trace*) was essentially suppressed (*dashed trace* head pitch velocity). **C** Data from the same subject while viewing a head-fixed target during 2-Hz head pitch. There was a significant eye velocity response (*solid trace*), which exhibited a variable phase characteristic with respect to the head pitch velocity (*dashed trace*). **D** The instantaneous phase of eye velocity re head pitch velocity for each cycle was calculated for the data in **C**. The eye velocity was initially in phase with head pitch, then increasingly lagged, before returning smoothly to being in phase by the end of the 10-s trial. Note that it was possible to reverse the phase of the visually modified aVOR for periods of up to 3 s using a head-fixed target. **E** The instantaneous phase for each cycle of eye velocity when viewing the head-fixed target at 2 Hz was calculated for all subject trials, and a frequency histogram calculated. In general, the eye velocity response was not compensatory for head pitch, with less than 5% of cycles exhibiting a phase lag of 180°

and 2 Hz. Gain increased significantly (*P*<0.01) when viewing the near target, from 1.07 to 1.23 at 1 Hz and from 0.97 to 1.07 at 2 Hz (Fig. 7A). The above-unity gain was required due to the eccentric location of the eyes relative to the axis of head rotation (Viirre and Demer 1996), which is situated approximately 20 mm below the interaural axis [100 mm behind the center of eye rotation (Moore et al. 1997)]. For a head-fixed target

at 0.3 m, the elicited eye velocity responses to head pitch were markedly different. At 1 Hz, the eye velocity was essentially suppressed with a gain of 0.08±0.04 (Fig. 7A,B). Due to the almost total suppression of eye movements, it was not possible to determine phase. At 2 Hz, the gain was reduced significantly (*P*<0.01) to 0.51±0.12 (Fig. 7A,C), but there was still a substantial eye movement response. The phase of the eye velocity re head pitch velocity was highly variable within each 10-s trial, tending to change smoothly from cycle to cycle over a large range (160±61°, mean and SD of all trials). A typical trial (subject 2) is shown in Fig. 7C. A large eye velocity response was generated with a mean peak amplitude of 38°/s (Fig. 7C, solid trace), which was 70% of the mean peak head pitch velocity of 54.3°/s (Fig. 7C, dashed trace). There was initially a complete reversal of the visually modified aVOR response, with eye velocity in phase with head pitch velocity. The eye velocity then increasingly lagged head pitch velocity, reaching a maximum lag of −141° by the 7th cycle before smoothly returning to 0° by the 14th cycle (Fig. 7D). It was possible to reverse the phase of the aVOR response for up to 3 s by viewing the head-fixed target.

The instantaneous phase of each cycle during the 2-Hz head-fixed paradigm for all subject trials (226 cycles) was pooled in 20° wide bins and a frequency histogram calculated (Fig. 7E). The eye velocity phase lag varied over almost the entire 360° range (from 0° to −336°). The frequency distribution was bimodal, with a local minimum at −180°. In general the eye velocity was not compensatory for head pitch, with less than 5% of cycles exhibiting a −180° phase lag. The most frequently

occurring phase shifts were either side of compensatory, within the ranges of –100° to –160° and –200° to –260°, accounting for over 76% of all cycles.

Discussion

The main finding of this study is that during moderate to fast locomotion (1.67 m/s) the phase of eye velocity relative to head pitch velocity is dependent on viewing distance. For far targets (2.0 m) eye velocity was compensatory for head pitch (180° out of phase). The phase reversed when viewing near (0.25-m) targets, such that eye velocity was in phase with head pitch velocity and compensatory for vertical head translation. There was a corresponding threefold increase in the magnitude of eye velocity for near targets. The amplitude and phase of vertical head translation and pitch remained relatively constant over the range of target distances, with only a small increase in head pitch velocity amplitude for near targets, which was not sufficient to explain the large changes observed in the eye velocity.

The eye velocity response observed in this study was consistent with the goal of maintaining gaze over a range of near to far targets in the presence of combined head translation and pitch. In accordance with previous studies, the pitch rotation of the head was compensatory for vertical head translation (Bloomberg et al. 1992; Crane and Demer 1997; Demer and Viirre 1996; Hirasaki et al. 1993, 1999; Pozzo et al. 1990). This appears to be an active rather than a passive biomechanical phenomenon, as the inertia of the head during locomotion has been shown to be negligible below 3 Hz (Keshner et al. 1992, 1995; Pozzo et al. 1990). Compensatory head pitch also occurs during locomotion with the eyes closed (Hirasaki et al. 1993; Pozzo et al. 1990); therefore vision is unlikely to be the driving force, although it may augment head pitch movements for near targets (Bloomberg et al. 1992). Compensatory head pitch movements during locomotion are degraded in patients with bilateral vestibular deficits (Grossman and Leigh 1990; Pozzo et al. 1991) and following space flight (Bloomberg et al. 1997; Reschke et al. 1994). Based on these results, and our own observations (Hirasaki et al. 1999), we have proposed that these movements may be generated through an otolith-mediated vertical linear vestibulo-collic reflex (lVCR). This is consistent with the results of Takahashi et al. (1990), which demonstrated that passive vertical linear translation of standing subjects induced compensatory head pitch movements whose amplitude increased with frequency in the range of 1–3 Hz.

As a consequence of the compensatory head pitch and translation movements, the head fixation distance (HFD) was maintained approximately 1.0 m in front of the subject regardless of the target distance. At this distance, the target would essentially appear to be "head-fixed" as far as the subject was concerned. That is, the required eye velocity response in a head-fixed coordinate frame would be close to zero (Fig. 5A). For targets located away from the HFD, significant eye movements would need to be generated to maintain gaze. For target distances greater than the HFD the head pitch would overcompensate for vertical head translation and the target would appear to move in the opposite direction as the head pitch in a head-fixed frame (Fig. 5A). This would require that eye velocity be compensatory for head pitch velocity to maintain fixation. The aVOR, with appropriate gain, could supply such additional compensation. For target distances less than the HFD, the head pitch would not be sufficient to compensate for the vertical translation of the head. The target, therefore, would appear to move with the head pitch, requiring that eye velocity be in phase with head pitch and compensatory for vertical head translation to maintain fixation (Fig. 5A). Demer and Viirre (1996), using a geometric argument based on vertical head movements during walking and running in place while viewing a 6-m target, predicted a reversal in the ideal aVOR gain from +1.0 for targets at infinity to –1.0 for a near target of 0.33 m. The computed gain characteristic passed through zero at a target distance of 0.65 m, which corresponds to the HFD. Eye velocity phase was not explicitly studied, but the predicted aVOR gain reversal implies a 180° phase shift in eye re head pitch velocity from far to near targets as observed in our study.

The gain and phase characteristics of the ideal eye velocity response indicated that during locomotion the observed eye velocity for near and far targets was close to ideal for the stabilization of gaze in space. For targets 2.0 m and beyond the effect of the linear translation of the head on image stability decreases dramatically and aVOR generated eye movements in response to head pitch are adequate to maintain gaze. At a distance of 2.0 m the eye re head pitch velocity gain (0.82) and phase (–178.6°) characteristics were typical of an aVOR response. This is in accord with a previous study, which reported a reduced vertical aVOR gain of 0.8–0.9 during treadmill walking (Crane and Demer 1997). A gain reduction is necessary due to the interaction of the head translation and pitch rotation, which partially compensates for gaze.

In the present study the measured eye velocity phase at near target distances was compensatory for vertical head translation, which indicated that activation of the lVOR was largely responsible for maintaining stable gaze relative to the target. Our analysis of vertical otolithic stimulation during locomotion indicated that the tangential and centripetal accelerations generated by head pitch, and the effect of tilting of the otoliths relative to the gravitational field, were negligible. The otoliths were primarily activated by the vertical linear acceleration of the head, and for near targets both the frequency of head movement (2 Hz) and the magnitude of head vertical linear acceleration (0.33 G) were sufficient to trigger the lVOR (Paige 1989; Paige et al. 1996). The question remains, however, of what is the nature of the interaction between the vertical lVOR and aVOR for near targets? At a frequency of 2 Hz both the sensitivity of the lVOR and the aVOR gain

increase as target distance is reduced for passive vertical head translation (Paige 1989) and pitch movements (Viirre and Demer 1996). Our study of active head pitch at 2 Hz, where the rotation axes were approximately coincident with the interaural axis and the otoliths were minimally stimulated, also demonstrated a 10% increase in the gain of the aVOR as target distance was decreased from 2.0 m to 0.3 m (Fig. 7A). For fixation on near targets during locomotion the lVOR response would produce eye movements which tend to drive the eyes opposite to the head translation (and therefore in phase with the head pitch) and in the direction of the target. An unmodified aVOR response, however, would produce paradoxical eye movements that are 180° out of phase with head pitch (i.e., in phase with head translation) and drive the eyes away from the target. The possible increase in aVOR gain for near targets, coupled with the increase in head pitch velocity, may create an even larger erroneous response.

Based on the concept that the lVOR and aVOR superpose at high frequencies (Sargent and Paige 1991; Telford et al. 1996), we considered the possibility that the lVOR sensitivity could be sufficiently enhanced by near target viewing during locomotion to generate the observed eye velocity response (Busettini et al. 1994; Paige 1989; Paige et al. 1996). The sensitivity of the human vertical lVOR has been estimated as 0.65°/cm during passive translation at a frequency of 2.7 Hz while viewing a 0.3-m target (Paige 1989). As the sensitivity of the lVOR increases with frequency (Paige et al. 1996), this value is likely to be an overestimate for the sensitivity at 2 Hz. Vertical head translation data from a typical subject when viewing a 0.25-m target (Fig. 3D, upper panel solid trace) exhibited an approximately sinusoidal waveform with an amplitude of 2.5 cm. An lVOR sensitivity of 0.65°/cm would generate an eye position response compensatory for this head translation with an amplitude of 1.6°. Differentiation of this waveform would yield an eye velocity response with peak amplitude of 20°/s in phase with head pitch velocity. The head pitch velocity waveform for the same subject and viewing condition (Fig. 3A, lower panel solid trace) had a peak amplitude of 20°/s. An unmodified aVOR (i.e., with a gain of 1.0) would generate an eye velocity waveform with a peak amplitude of 20°/s that is compensatory for this head pitch velocity, which would cancel the lVOR response. The additional lVOR sensitivity required to generate the observed eye velocity amplitude of approximately 35°/s, which was compensatory for vertical head translation and in phase with the head pitch velocity (Fig. 3A, lower panel dashed trace), would be 1.14°/cm, requiring a total of 1.8°/cm. This lVOR sensitivity would be almost 3 times greater than previously reported for passive vertical translation. One possibility is that the sensitivity of the lVOR is enhanced by proprioceptive input and motor efference copy from the active movements of the head and body during locomotion, in a similar manner to gain enhancement of the aVOR during active head pitch (Demer et al. 1993).

Vision may also contribute to the phase reversal in eye velocity when viewing near targets during locomotion. Viewing a target located at the HFD (1.0 m) is analogous to viewing a head-fixed target, and at closer distances the target would appear to move in the same direction as the head pitch (Fig. 5A). This would result in suppression of the aVOR, which has been postulated to occur via pursuit pathways (Baloh et al. 1986; Barnes and Grealy 1992; Koenig et al. 1986, 1987), although motor efference copy from planned head movements (Robinson 1982) and modulation of the aVOR gain (Huebner et al. 1992; McKinley and Peterson 1985) may also contribute. Studies of vertical smooth pursuit at a frequency of 2 Hz have reported gains of 0.4–0.6 and highly variable phase lags of up to 120° (St-Cyr and Fender 1969a, 1969b; Tokita et al. 1981). Our eye movement data during active head pitch at 2 Hz when viewing a near (30-cm) head-fixed target exhibited similarly large variations in phase (up to 180°), and a reduction in aVOR gain of around 0.5 (Fig. 7A,C–E). This phase modification was not observed when the subject viewed a near (30-cm) space-fixed target. As head movements were the same for both the space- and head-fixed target conditions, it is unlikely that proprioceptive input or motor efference copy from the neck were responsible for the phase shifts. The observed variation in phase during visual suppression may come about through interaction of smooth pursuit (and its predictive properties) with the aVOR response at 2 Hz, in conjunction with a modulation of the aVOR gain. During locomotion, such a phase modification of the aVOR could play a role in generating eye movements consistent with the goal of maintaining gaze on targets closer than the HFD. This would augment the lVOR to generate the observed eye velocity response.

The walking velocity used in this study (1.67 m/s) was close to previously reported values for the natural walking speed of adults (aged 20–60 years old), which ranged from 1.33 to 1.6 m/s (Finley and Cody 1970; Imai et al. 1998; Perry 1992). In this range step frequency is limited to a narrow band around 2 Hz and head pitch and vertical translation are highly coherent (Hirasaki et al. 1999). At slow walking velocities (below 1.2 m/s) the magnitude and frequency of head movement decreases, and head and trunk coordination is degraded (Hirasaki et al. 1999). A recent study of gaze control during treadmill locomotion at a slow (0.9 m/s) walking speed did not report a reversal in the phase relationship of vertical eye to head pitch velocity while fixating on near (0.4-m) to far (4.4-m) targets (Crane and Demer 1997). The frequency of vertical head translation was 1.4 Hz, which was less than the 2 Hz observed in our study, and may have been insufficient to fully activate the vertical lVOR to generate compensatory eye movements when viewing near targets. In addition, the compensatory head pitch and translation movements may have been sufficient to maintain gaze during slow walking, and a reversal of the eye velocity phase would not be necessary.

In the present study the magnitude and phase of the eye velocity response during locomotion was close to ideal for near and far targets (Fig. 6B,C), but there were considerable deviations from the ideal for intermediate distances. The ideal eye velocity phase approximates a step function, with close to 0° phase (with respect to head pitch velocity) for near targets, and a compensatory 180° phase for far targets, with the crossover point near the HFD. The measured phase characteristic interpolated between these two extremes in a linear fashion, passing through –74° near the mean HFD (1.0 m). Although a reversal of the eye velocity phase provides close to ideal compensation for the near and far target conditions, neither the functional significance nor the source of the variation in phase between these two extremes is clear. It is unlikely that neck proprioception or motor efference copy were responsible, as there was little change in the magnitude or timing of head movements over the range of target distance studied. One possibility is that visual interaction with the aVOR generated the smooth transition in the phase of eye velocity with viewing distance, as it was evident at target distances of up to 2.0 m, which is beyond the operational range of the lVOR.

Treadmill locomotion at moderate to fast walking velocities generates vertical head movements sufficient to stimulate the otoliths and semicircular canals. Both the compensatory pitch head rotation, and vertical eye movements when viewing near targets, are likely to be driven by activation of the segment of the otoliths sensitive to vertical linear acceleration via the lVCR and lVOR. Our findings indicate that these reflexes act in concert with the aVOR and vision to maintain gaze over a range of near to far viewing distances.

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