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Modulation of High-Frequency Vestibuloocular Reflex During Visual Tracking in Humans

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SUMMARY AND CONCLUSIONS

1. Humans may visually track a moving object either when they are stationary or in motion. To investigate visual-vestibular interaction during both conditions, we compared horizontal smooth pursuit (SP) and active combined eye-head tracking (CEHT) of a target moving sinusoidally at 0.4 Hz in four normal subjects while the subjects were either stationary or vibrated in yaw at 2.8 Hz. We also measured the visually enhanced vestibuloocular reflex (VVOR) during vibration in yaw at 2.8 Hz over a peak head velocity range of 5–40°/s.

2. We found that the gain of the VVOR at 2.8 Hz increased in all four subjects as peak head velocity increased ($P < 0.001$), with minimal phase changes, such that mean retinal image slip was held below 5°/s. However, no corresponding modulation in vestibuloocular reflex gain occurred with increasing peak head velocity during a control condition when subjects were rotated in darkness.

3. During both horizontal SP and CEHT, tracking gains were similar, and the mean slip speed of the target's image on the retina was held below 5.5°/s whether subjects were stationary or being vibrated at 2.8 Hz. During both horizontal SP and CEHT of target motion at 0.4 Hz, while subjects were vibrated in yaw, VVOR gain for the 2.8-Hz head rotations was similar to or higher than that achieved during fixation of a stationary target. This is in contrast to the decrease of VVOR gain that is reported while stationary subjects perform CEHT.

4. In a control experiment in which subjects carried out vertical SP and CEHT while they were vibrated in yaw at 2.8 Hz, we found that three of four subjects showed an increase in horizontal VVOR gain at 2.8 Hz compared with that achieved during fixation of a stationary target; such an increased horizontal gain would not be required to reduce retinal image slip in the vertical plane.

5. On the basis of these findings, we draw the following conclusions. *1*) During sinusoidal oscillations at 2.8 Hz, the gain of the VVOR is adjusted in accordance with peak head velocity in order to hold retinal slip of the image of the visual target below ~5°/s. *2*) During visual tracking of a moving target while the subject is in motion, there are two potential sources of retinal image slip: imperfect visual tracking and an inadequate VVOR. When tracking deteriorates, it becomes necessary to increase the gain of the VVOR to levels that prevent additional retinal image slip, so that vision is not compromised. *3*) The increase of horizontal VVOR gain that occurs during both horizontal and vertical visual tracking while subjects are in motion may not be wholly due to retinal slip per se, but may also involve a nonvisual mechanism that effectively constrains retinal image slip to levels that permit clear vision.

INTRODUCTION

The vestibuloocular reflex (VOR) acts to hold images of stationary objects fairly steady on the retina during head perturbations. Under natural conditions, the VOR is supplemented by visually mediated eye movements—the visually enhanced VOR (VVOR). During combined eye-head tracking (CEHT), vestibular eye movements that are induced by tracking head movements must be negated in order for gaze to follow the target. Evidence has been presented that at least two mechanisms act to negate vestibular eye movements during CEHT. First, an internal command for smooth pursuit (SP) eye movements may cancel the VOR signal due to tracking head movements (Barnes et al. 1978; Huebner et al. 1992a; Lanman et al. 1978). Second, a downmodulation of VOR gain may occur (Barr et al. 1976; Cullen et al. 1991; Huebner et al. 1992a; Lisberger 1990); because this occurs at short latency, it is unlikely to be visually mediated. Electrophysiological studies have provided evidence regarding possible neurobiological substrates for both mechanisms (Cullen and McCrea 1993a,b). The relative importance of these two mechanisms during tracking in humans is reviewed in detail elsewhere (Barnes 1993).

To date, most studies of the VVOR and visual tracking have used stimuli that can be reliably presented in the laboratory; however, these may not reflect naturally occurring conditions that, during locomotion, are rotational head perturbations with predominant frequencies ranging from 0.5 to 5.0 Hz and peak velocities of >100°/s (Das et al. 1993; Grossman et al. 1988). The VOR seems indispensable for coping with these head movements, because patients who have lost vestibular function complain, for example, that "During a walk I found too much motion in my visual picture of the surroundings to permit recognition of fine detail" (J. C. 1952; Leigh and Brandt 1993). Visual tracking of a moving object may also be carried out while we are in motion, and this is normally accomplished with combined movements of eyes and head. Such a strategy would be important, for example, during hunting. Under these conditions, the VVOR must compensate for the high-frequency perturbations that occur during locomotion, but the vestibular response induced by the tracking head movements must be negated. This raises the issue: how are vestibular eye movements due to tracking head movements negated while the subject is in motion? A more specific question, which this study addresses, concerns whether the gain of the VVOR is modulated down during CEHT if the subject is in motion. We found that during CEHT while the subjects are being vibrated, the gain of the VVOR for the high-frequency vibrations was modulated up. This is contrary to previous reports of downward modulation

of the VVOR gain when stationary subjects' heads rotate with the target. These changes in VVOR gain were appropriate to hold retinal image motion at levels that permit clear vision during CEHT, when the subject is in motion. Some preliminary results have been previously reported (Das et al. 1994). The work reported in this paper constitutes a portion of the research performed by Vallabh E. Das as part of the requirements for his Master's Dissertation.

METHODS

Subjects and experimental equipment

We studied four normal subjects (3 male, 1 female) whose ages ranged from 23 to 47 yr and whose weights ranged from 140 to 210 lbs. Three of the four subjects were emmetropes. All four were authors, but two were not made aware of the purpose of the experiments until after they were performed. *Subject VED* was myopic (usually wearing −3.0-diopter spectacle correction); however, the subject could see and follow the visual target (a small spot of light) without difficulty, allowing all testing to be conducted with uncorrected vision. No subjects were taking medication; all gave informed consent. Head and gaze rotations were measured using the magnetic search coil technique, with 6-ft field coils (CNC engineering, Seattle, WA) that used a rotating magnetic field in the horizontal plane and an alternating magnetic field in the vertical plane. Each subject wore a scleral search coil (Skalar Delft, Netherlands) on the dominant eye. Each also wore a search coil firmly attached to the forehead to measure angular head position. The search coils were calibrated before the experiment using a special protractor device. Subjects sat in a 30-ft.-lb vestibular chair (Templin Engineering, Laytonville, CA) during all the experimental paradigms. The subjects' heads were firmly braced against the headrest of the chair for all the experimental paradigms except during CEHT.

Experimental stimuli

The target was a spot of white light back-projected onto a white semitranslucent display screen located at a distance of 1.3 m from the subject; the room was otherwise dimly illuminated (mesopic range). The target subtended 0.3° and had a luminance of 0.77 ft.-L. The position of the target was controlled using a mirror galvanometer (model CCX-660, General Scanning, Watertown, MA) and was driven by a signal generator. The visual stimulus was stationary during VVOR experiments and moved sinusoidally through either ±20° at 0.4 Hz or ±1° at 2.8 Hz during visual tracking trials. In one control experiment (see below), the latter target motion was superimposed on a ramp of 10°/s. Vestibular stimuli were generated by an 80486/33 computer and consisted of horizontal chair rotations at 2.8 or 0.2 Hz. During all experimental paradigms, subjects were instructed to look at the visual target and follow it if it moved. During CEHT they were instructed to "move your eyes and head together." We mainly tested the horizontal VVOR, SP, and CEHT, but in control experiments we also measured the horizontal VOR in the dark and vertical SP and CEHT. In the control experiments, the visual stimulus for vertical tracking was a laser spot that moved ±10° at 0.4 Hz.

Experimental paradigms

VVOR. *Trial 1.* Subjects were asked to fixate the stationary target while they were passively rotated in the chair at 2.8 Hz with peak velocities ranging from 5 to 40°/s during several trials (VVOR).

Trial 2. Subjects were asked to imagine the stationary target in complete darkness while they were passively rotated in the chair at 2.8 Hz with different peak head velocities (VOR—control).

Trial 3. Subjects were rotated at 0.2 Hz with a peak velocity of 20°/s while they viewed the stationary target (control trial to confirm that measurements of VVOR gain were appropriate as subjects continuously foveated the fixation target).

SP. *Trial 4.* Subjects were asked to track the target moving horizontally through ±20° at 0.4 Hz while the head was stationary.

Trial 5. Subjects were asked to track the target moving horizontally through ±20° at 0.4 Hz with the head braced against the chair that was rotating at 2.8 Hz. The amplitude of chair rotations varied slightly with subjects' weights, ranging from ±1.07 to ±1.44°.

Trial 6. Subjects were asked to attempt to track the target moving horizontally through ±1° at 2.8 Hz while the head was stationary (control to quantify the contribution of SP to visual tracking at 2.8 Hz).

Trial 7. Subjects were asked to attempt to track the target moving horizontally through ±1° at 2.8 Hz and superimposed on a ramp of 10°/s while the head was stationary, a technique that facilitates tracking at high frequencies in monkeys (Goldreich et al. 1992).

Trial 8. Subjects were asked to track the target moving vertically through ±10° at 0.4 Hz while the head was stationary.

Trial 9. Subjects were asked to track the target moving vertically through ±10° at 0.4 Hz, with the head braced against the chair that was rotating horizontally at 2.8 Hz (control to determine whether the VVOR during CEHT was influenced by retinal slip orthogonal to head vibrations). The amplitude of chair rotations ranged from ±0.79 to ±1.56°.

CEHT. *Trial 10.* Subjects were asked to track the target moving horizontally through ±20° at 0.4 Hz with combined movements of the eyes and head, while the chair was stationary.

Trial 11. Subjects were asked to track the target moving horizontally through ±20° at 0.4 Hz with the head free as the chair was rotated at 2.8 Hz.

Trial 12. Subjects were asked to track the target moving horizontally through ±1° at 2.8 Hz with combined movements of the eyes and head, while the chair was stationary (control to quantify the contribution of CEHT to visual tracking at 2.8 Hz).

Trial 13. Subjects were asked to track the target moving vertically through ±10° at 0.4 Hz with combined movements of the eyes and head, while the chair was stationary.

Trial 14. Subjects were asked to track the target moving vertically through ±10° at 0.4 Hz with head-free CEHT as the chair was rotated horizontally at 2.8 Hz (control to determine whether the VVOR during CEHT was influenced by retinal slip orthogonal to head vibrations).

Data acquisition and analysis

Target, head, and gaze position signals were filtered with analog Butterworth filters (Krohn-Hite, Avon, MA), set at a bandwidth of 0–90 Hz, before digitization at 220 Hz with 16-bit resolution. The data were stored in an 80486/33 computer for later analysis. Gaze, target, and head positions were recorded in trials that lasted for 29 s each. The analysis was performed using programs written in ASYST (Keithley, Rochester, NY) and MATLAB (The Math Works, Natick, MA) software.

The first step in the analysis was to correct the eye and gaze signals for the eccentricity of eye position and the target distance (Huebner et al. 1992b). The parameters of head geometry were measured for each subject, and a correction to the eye movement records was made that corresponded to moving the eye to the axis of rotation of the head. In this way, data from different subjects, including measurements of retinal error speed, could be compared.

Data were then digitally differentiated using a two-point differentiation technique to obtain velocity signals. Before filtering, sac-

cades were removed from the eye and gaze movement records via an interactive routine. Saccades were first identified using a velocity criterion that was set after examining each record individually. Points characterizing saccades were removed and replaced with points generated by spline interpolation. The new points were such that they appeared as a low-amplitude, high-frequency signal peak in the power spectrum of the data array. This peak could then be filtered out before analysis. Thus the desaccading procedure did not add any new data to the array. Corresponding records before and after removal of saccades were compared to ensure the reliability of this process. We then calculated, for each trial, mean ± SD and root-mean-square retinal slip speed from the difference between gaze and target velocities.

Data were then filtered using Chebyshev Type II filters. The filters were designed to isolate the eye and head movement signals at the two frequencies of interest (0.4 and 2.8 Hz). We used a Chebyshev Type II low-pass filter to isolate the 0.4-Hz signal and a Chebyshev Type II band-pass filter to isolate the 2.8-Hz signal using a technique previously described (Huebner et al. 1988; Thomas et al. 1988). The frequency responses of the Chebyshev Type II filters were examined to ensure that the filters had unity gain at the appropriate frequencies and that the 0.4- and 2.8-Hz signals could be clearly isolated. The attenuation at 0.4 Hz was found to be 0.0015 dB for the low-pass filter and 51.2342 dB for the band-pass filter. The attenuation at 2.8 Hz was 61.6743 dB for the low-pass filter and 0.0673 dB for the band-pass filter. This enabled us to determine the stimulus to the ocular motor system and also the response of the system at each frequency of interest (0.4 and 2.8 Hz) independently. Once the data were filtered, the smooth tracking (SP or CEHT) gain was calculated as the ratio of gaze velocity to target velocity; the VVOR and VOR gains were calculated as the ratio of eye-in-orbit velocity to head velocity. The respective ratios were determined by performing a linear regression between the arrays of interest (gaze and target velocity for SP, eye and head velocity for VVOR). The arrays were typically ≥1,000 points each. The mean peak speed of the head was also calculated for each trial by first identifying the turning points of ≥10 cycles by a change in sign of the slope and then calculating the mean of their absolute values. We determined the phases of the tracking and VVOR response for each trial by calculating the phase differences between the signals in the frequency domain and recording the phase shift at the frequency of interest. We checked that the nonlinear phase characteristic of the Chebyshev filters did not affect our calculations of phase. This is expected because we were inspecting the phase difference at a particular frequency between two arrays that had similar frequency content before filtering.

RESULTS

VVOR

After geometric correction, the mean gain of the VVOR at 0.2 Hz for the four subjects ranged from 0.94 to 0.97, and phase ranged from 180.06 to 181.14° (i.e., eye movements almost completely compensated for head rotations); these results are consistent with previous studies (Collewijn et al. 1981). Figure 1 shows representative data from one subject during two trials of VVOR testing at 2.8 Hz, in which peak head velocities differed by a factor of 2. Note that the perturbations of gaze velocity (and thus retinal error velocity) remained relatively constant despite the large difference in peak head velocity; this indicates that the gain of the VVOR had increased for the trial with higher peak head velocity. Measured values of horizontal VVOR gain and phase during 2.8-Hz rotation for a range of peak head velocities for each subject are shown in Fig. 2, *A* and *B*. We found that VVOR gains ranged from 0.64 to 0.91 and, using the *t*-test, that gain increased with increasing peak head velocity (i.e., the slope of the regression line was different from 0 with $P < 0.001$). There was no significant change in VVOR phase within the range of head velocities tested for three of four subjects ($P > 0.15$); *subject VED* (a myope) showed a statistically significant increase in phase lag with head velocity. A consequence of higher VVOR gain values with higher peak head velocities was that mean retinal image speed was always held below 5.0°/s in each subject. We found the mean retinal slip speed to range from 0.5 to 4°/s.

Figure 3*A* summarizes the VOR gain values of the four subjects for different peak head velocities while the subjects attempted, in darkness, to fixate an imagined stationary target. The peak velocities of the chair were selected to correspond to the boundaries of the head velocity stimuli that had been applied in the light (VVOR). There was no change in the gain of the VOR with different peak head velocities (ranging from 15 to 38°/s) for three of the four subjects when they attempted to view an imaginary target in darkness ($P > 0.15$); *subject RJL* showed a significant decrease in VOR gain with increasing peak head velocity ($P < 0.05$). There was no change in the phase of the VOR with increasing peak head velocity (Fig. 3*B*).

SP

SP gain during tracking of a target moving horizontally at 0.4 Hz ranged from 0.9 to 1.01, and mean retinal speed (target velocity minus gaze velocity) was always <5.0°/s. Results for each subject are summarized in Table 1. During SP of a target moving horizontally at 0.4 Hz, while the subjects were rotated at 2.8 Hz, tracking gain (for the 0.4-Hz tracking) ranged from 0.89 to 1.01 and mean retinal image speed ranged from 3.55 to 5.23°/s (Table 1). Thus the tracking gain of the target moving at 0.4 Hz was similar whether subjects' heads were stationary or oscillating at 2.8 Hz; representative examples of raw data are shown in Fig. 5. In all four subjects, VVOR gains for the 2.8-Hz perturbations during SP were higher than that achieved during fixation of a stationary target at similar head velocities (Fig. 2*A*), and the VVOR phase values during SP did not show any consistent trends (Fig. 2*B*). During attempted SP of a target moving at 2.8 Hz, tracking gain ranged from 0.09 to 0.31, phase lag ranged from 36.89 to 63.40°, and mean retinal image speed ranged from 7.98 to 9.57°/s. This indicated that SP contributed little to visual following of targets moving at this frequency. The SP performance at 2.8 Hz did not improve when the oscillating target was superimposed on a 10°/s ramp ($\dot{P} > 0.4$); tracking gain ranged from 0.13 to 0.26, phase lag ranged from 44.08 to 64.17°, and mean retinal image speed ranged from 8.78 to 10.29°/s. Representative data from one subject comparing SP during the two tracking conditions are shown in Fig. 4.

SP gain during tracking of a target moving vertically at 0.4 Hz ranged from 0.66 to 1.03, with mean retinal image speed in the vertical plane ranging from 1.85 to 6.80°/s. During SP of a target moving vertically at 0.4 Hz, while the subjects were rotated horizontally at 2.8 Hz, tracking gain ranged from 0.71 to 0.99 and mean retinal image speed in the vertical plane ranged from 1.93 to 6.10°/s. In two sub-

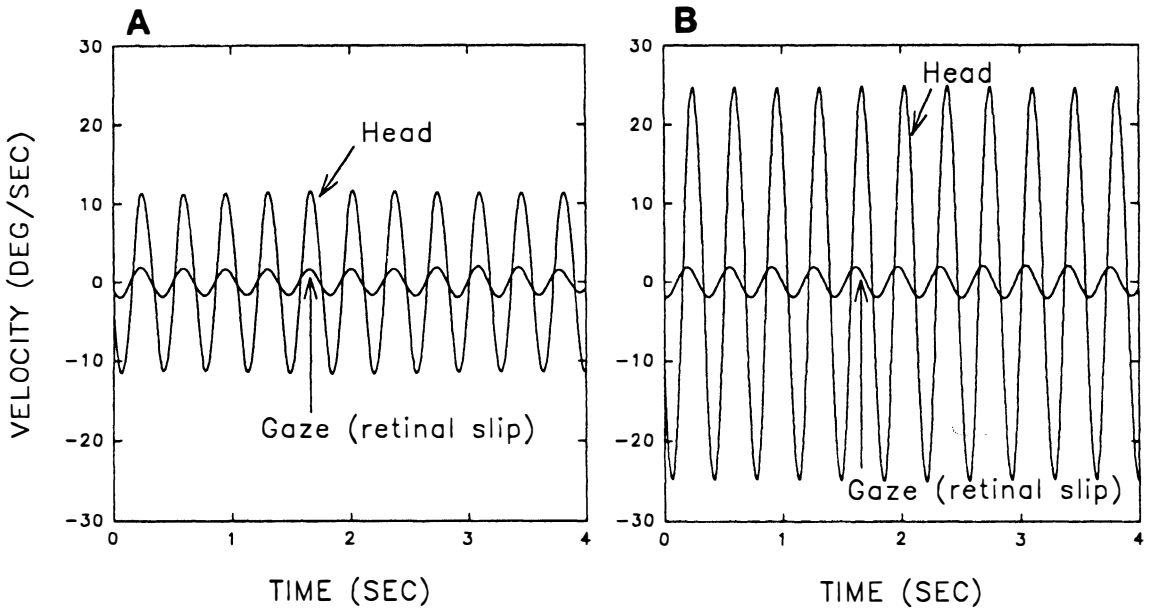

FIG. 1. Representative data from 2 visually enhanced vestibuloocular reflex (VVOR) trials during which the head was passively rotated at 2.8 Hz at 2 different amplitudes. Note that despite a 2-fold change in peak head velocity (between *A* and *B*), gaze speed (i.e., retinal slip speed) remains relatively constant, indicating that the gain of the VVOR has been modulated up in *B* in order to keep retinal slip within the threshold of clear vision. In this and the following records, upward deflections indicate rightward movements.

jects, VVOR gain for the 2.8-Hz horizontal perturbations during vertical SP was greater than that achieved during fixation of a stationary target at similar head velocities; in none was it lower (Fig. 2*A*). However, in all four subjects the VVOR gain for the 2.8-Hz perturbations during vertical SP was less than the VVOR gain for 2.8-Hz perturbations during horizontal SP. Phase shifts in the VVOR response for the 2.8-Hz perturbations during vertical SP (Fig. 2B) were greater than during fixation of a stationary target in three of four subjects ($P < 0.05$).

CEHT

During *horizontal* CEHT with the chair stationary, tracking gains ranged from 0.90 to 0.99, and mean retinal image speed was <5°/s (similar to SP). The data are summarized in Table 1. The mean amplitudes of tracking head movements for each subject ranged from ±12 to ±19°. During CEHT of a target moving horizontally at 0.4 Hz, while subjects' bodies were exposed to chair rotation at 2.8 Hz, tracking gains (for the 0.4-Hz signal) ranged from 0.92 to 1.00, and mean retinal image speed was <5°/s. The mean amplitudes of tracking head movements for each subject ranged from ±15 to ±24°. Thus tracking gains of the target moving at 0.4 Hz were similar, regardless of whether the chair in which subjects sat was stationary or oscillating at 2.8 Hz; representative examples of raw data are shown in Fig. 6. In two subjects, VVOR gain for the 2.8-Hz perturbations during horizontal CEHT was higher than that achieved during fixation of a stationary target at similar head velocities; in none was it lower (Fig. 2*A*). The VVOR phase lag was greater than during fixation of a stationary target in three of four subjects (Fig. 2B). During attempted CEHT of a target moving at 2.8 Hz (subjects stationary), tracking gain ranged from 0.17 to 0.33, phase lag ranged from 30.94 to 76.32°, and mean retinal image speed ranged from 7.89 to 10.84°/s, indicating that, with subjects' heads free, visual following contributed little at this frequency.

While sitting in a stationary chair, tracking gains during CEHT of a target moving vertically at 0.4 Hz ranged from 0.68 to 0.98, with mean retinal image speeds in the vertical plane ranging from 1.60 to 5.87°/s. This is similar to the vertical SP with the chair stationary condition (trial 8). During CEHT of a target moving vertically at 0.4 Hz, while the chair in which subjects sat was rotated horizontally at 2.8 Hz, tracking gains (for the 0.4-Hz tracking) ranged from 0.57 to 0.90 and mean retinal image speeds in the vertical plane ranged from 2.32 to 7.55°/s. Thus the tracking gain of the vertically moving target was somewhat better when the chair in which subjects sat was stationary rather than oscillating horizontally at 2.8 Hz. In three of four subjects, VVOR gain for the horizontal 2.8-Hz perturbations during vertical CEHT was higher than that achieved during fixation of a stationary target at similar head velocities; in none was it lower (Fig. 2*A*). All subjects showed increased phase lag of VVOR response during vertical CEHT compared with phase lag during viewing of a stationary target (Fig. 2*B*). There was no consistent difference between the gains of the VVOR for the 2.8-Hz perturbations during vertical CEHT or horizontal CEHT.

DISCUSSION

We investigated the behavior of the VVOR during visual tracking as subjects were in motion. We applied rotational head perturbations of a frequency (2.8 Hz) that falls within the range observed during locomotion so that our findings might have some relevance to naturally occurring behavior. Our first finding was that VVOR gain for 2.8-Hz head rotations depends on peak head velocity. As peak head velocity increased, so did VVOR gain. Our second finding was that during CEHT while

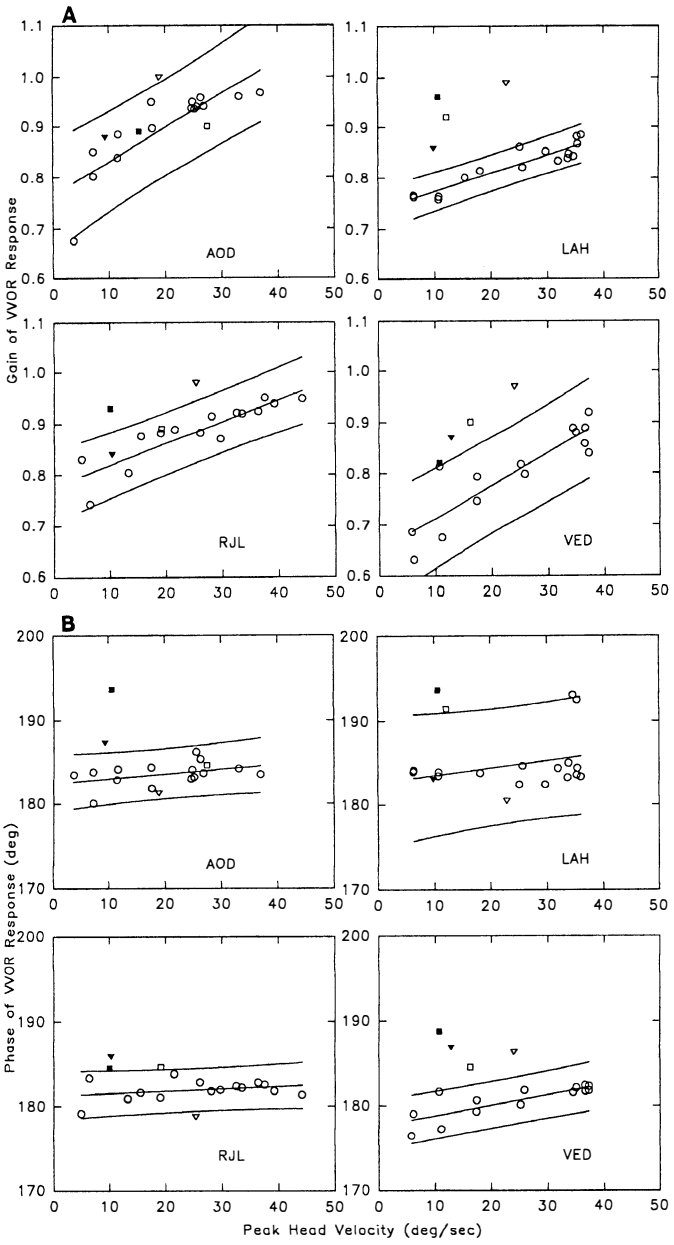

FIG. 2. Summary of (*A*) VVOR gain and (*B*) phase values for head vibrations at 2.8 Hz during fixation of a stationary target (○), during smooth pursuit (SP) (▽: horizontal; □: vertical) or during combined eye-head tracking (CEHT) (▼: horizontal; ■: vertical). Note how VVOR gain increases in each subject as peak head velocity increases ($P < 0.001$). Also note that VVOR gain sometimes rises further during SP and CEHT. Lines: mean and 95% confidence limits for the population of values during viewing the stationary target. There are no significant changes in phase of the VVOR response with an increase in peak head velocity.

subjects are in motion VVOR gain tends to be increased closer to a value of 1.0 rather than being decreased, as may occur during CEHT while subjects are stationary.

Dependence of VVOR gain on head velocity

The velocity dependence of VVOR gain in our four subjects as they were rotated at 2.8 Hz (Fig. 2*A*) was an unexpected finding that emerged as we attempted to apply similar head velocities during fixation of a stationary or moving target. The striking finding was that mean gaze speed (and thus retinal image speed) was always held below ~5°/s irrespective of peak head velocity, so that clear vision was still possible (Fig. 1). Psychophysical studies indicate that the upper limit of retinal image speed that can be tolerated for clear vision depends on the spatial frequency of the stimulus (Burr and Ross 1982). For higher spatial frequencies, such as are tested during conventional measurements of vision, image motion exceeding ~5–6°/s is associated with declining visual acuity (Burr and Ross 1982; Carpenter 1991). Given this visual constraint, then, for example, a VVOR gain of 0.8 will suffice for a head velocity of 25°/s but not for 50°/s. As head velocity increases, so must VVOR

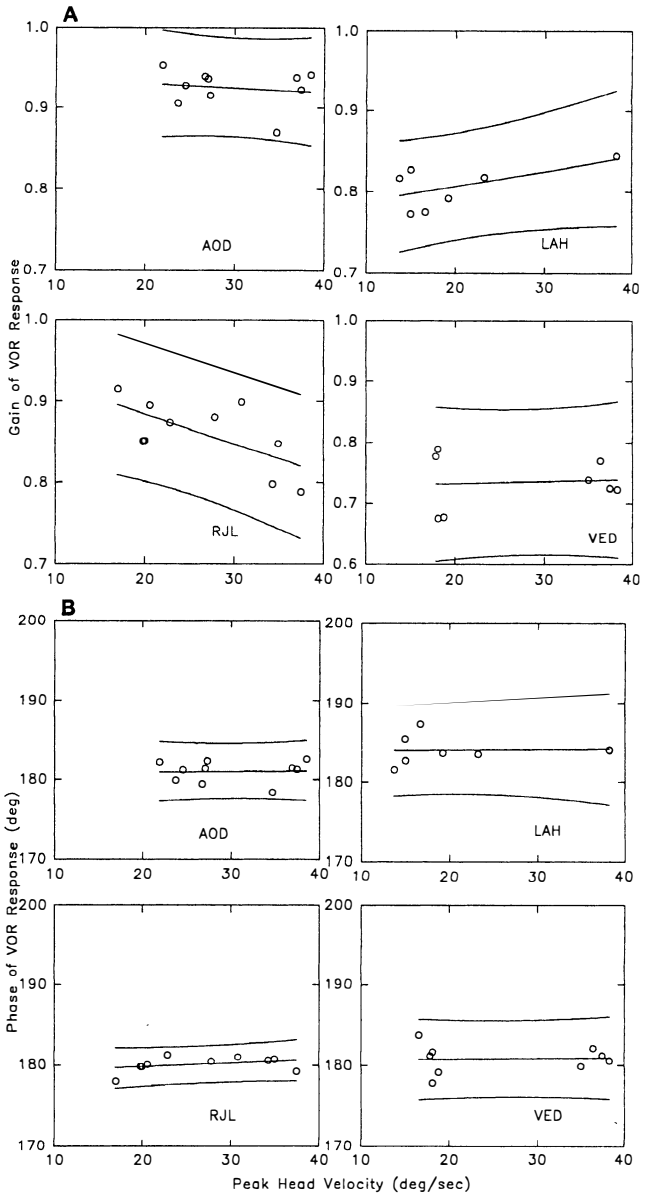

FIG. 3. Summary of (*A*) vestibuloocular reflex (VOR) gain values and (*B*) VOR phase values for head vibrations at 2.8 Hz during fixation of an imagined stationary target in darkness. VOR gain does not change as peak head velocity increases for 3 of 4 subjects ($P > 0.15$); *subject RJL* shows a decrease in VOR gain with increasing peak head velocity ($P < 0.05$). There are no significant changes in phase of the VOR response with an increase in peak head velocity.

TABLE 1. *Tracking performance and retinal slip speed during SP and CEHT trials*

S.No	Description of Run	Tracking		VVOR		Retinal Slip	
		Gain	Phase	Gain	Phase	Mean	RMS
1	SP, 0.4 Hz, chair stationary	*RJL* 0.93	−2.60			2.93 (2.29)	3.72
		AOD 1.01	0.45			2.59 (2.16)	3.37
		LAH 0.92	−1.18			3.79 (2.93)	4.79
		VED 0.90	−0.40			4.50 (3.44)	5.66
2	CEHT, 0.4 Hz, chair stationary	*RJL* 0.97	−0.12			1.70 (1.43)	2.22
		AOD 0.99	0.98			2.38 (1.87)	3.03
		LAH 0.96	−1.56			3.25 (2.58)	4.15
		VED 0.90	0.83			4.09 (2.97)	5.06
3	Horizontal SP, 0.4 Hz, chair moving at 2.8 Hz	*RJL* 0.89	−1.59	0.98 (0.05)	178.84	3.96 (3.21)	5.10
		AOD 1.01	0.84	1.00 (0.05)	181.36	3.55 (2.88)	4.57
		LAH 0.94	−0.28	0.99 (0.03)	180.52	5.23 (4.03)	6.60
		VED 0.92	−0.46	0.97 (0.04)	186.36	4.81 (3.84)	6.15
4	Horizontal CEHT, 0.4 Hz, chair moving at 2.8 Hz	*RJL* 0.96	−0.36	0.84 (0.07)	185.81	2.46 (1.98)	3.16
		AOD 1.00	1.81	0.88 (0.08)	187.45	3.29 (2.57)	4.17
		LAH 0.99	−0.24	0.86 (0.07)	183.19	3.87 (2.96)	4.88
		VED 0.92	−0.09	0.87 (0.07)	186.92	4.02 (2.92)	4.97
5	Vertical SP, 0.4 Hz, chair moving at 2.8 Hz	*RJL* 0.99*	−0.85	0.89 (0.02)	184.51	1.48 (1.23)	1.92
		AOD 0.96	−0.51	0.90 (0.02)	184.70	1.84 (1.33)	2.27
		LAH 0.79	−4.05	0.92 (0.03)	191.40	2.50 (2.08)	3.26
		VED 0.71	−3.87	0.90 (0.06)	184.43	2.14 (1.67)	2.72
6	Vertical CEHT, 0.4 Hz, chair moving at 2.8 Hz	*RJL* 0.89*	−0.46	0.93 (0.06)	184.39	1.22 (1.04)	1.60
		AOD 0.90	0.78	0.89 (0.02)	189.41	1.72 (1.29)	2.15
		LAH 0.75	−4.22	0.96 (0.09)	193.78	3.32 (2.84)	4.37
		VED 0.57	−5.59	0.82 (0.04)	188.80	1.86 (1.50)	2.39

In columns 5 and 7, values in parentheses are SD. SP, smooth pursuit; CEHT, combined eye-head tracking; VVOR, visually enhanced vestibuloocular reflex; RMS, root mean square. * Contents of this cell indicate the tracking gains in the vertical plane. The corresponding phase entries are also in the vertical plane. The measurements of retinal slip speed are all in the horizontal plane.

gain if retinal slip is to be held within limits necessary for clear vision.

Although the gain and phase of the VOR response in the light and the dark have been well characterized for a range of head perturbation frequencies (Collewijn et al. 1981, 1983; Correia et al. 1985; Gauthier et al. 1984; Paige 1994; Skavenski et al. 1979), including those occurring during locomotion (Grossman et al. 1989), the question of whether the VVOR gain varies with peak head velocity has only received occasional study. Paige (1989) showed no influence of peak velocity on gain of the VOR in darkness, but that study concerned low frequencies (0.2 Hz and 0.025 Hz) that do not correspond to the range of natural head movements. Hydén and Larsby (1991), using electrooculography, showed some velocity dependence of the VOR in darkness, but this was only statistically significant at 0.5 Hz. Correia and colleagues (1985) found no consistent velocity dependence of the VVOR in cynomolgus monkeys. None of these investigators measured the gain of the VVOR at one frequency over a range of peak head velocities. We found a consistent increase of VVOR gain in each of our four subjects. Furthermore, this increase in gain was absent when the VOR was tested at different peak head velocities in darkness. This indicates that visual inputs play a role in the VOR modulation. Kasteel-van Linge and Maas (1990) also showed that visual inputs may modulate the VOR during rotational head frequencies >2.5 Hz.

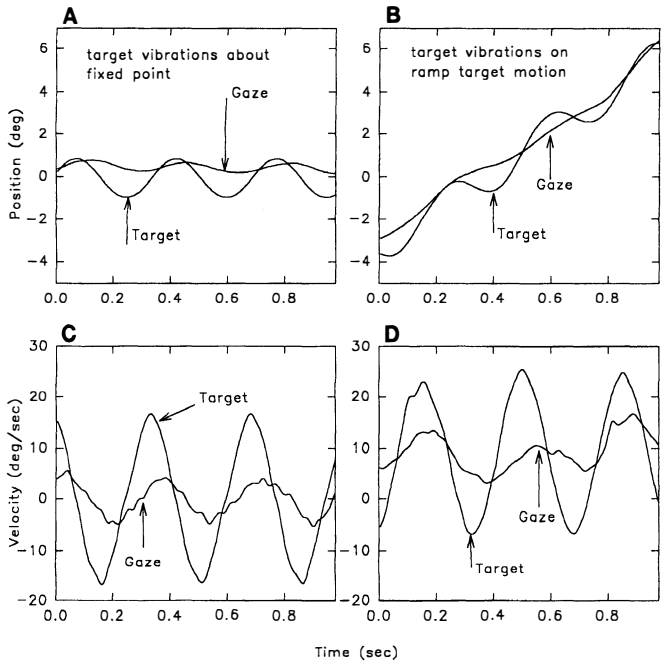

FIG. 4. Representative data from 1 subject during attempted SP of target moving at 2.8 Hz about a fixed point (*A* and *C*) or superimposed on a ramp of 10°/s (*B* and *D*). *Top panels*: target and gaze position. *Bottom panels*: corresponding velocities. SP perfomance did not improve when the target vibrations were superimposed on the ramp.

What mechanism could account for such modulation of the VOR by visual inputs at these frequencies? Our subjects showed low gains of visual tracking (SP or CEHT) responses to target motion at 2.8 Hz, similar to the results reported by Paige (1994). Furthermore, we found that SP remained poor, even if the target oscillations were superimposed on ramp motion, a strategy that improves high-frequency pursuit in monkeys (Goldreich et al. 1992). Even though our subjects' pursuit at 2.8 Hz had low gain and

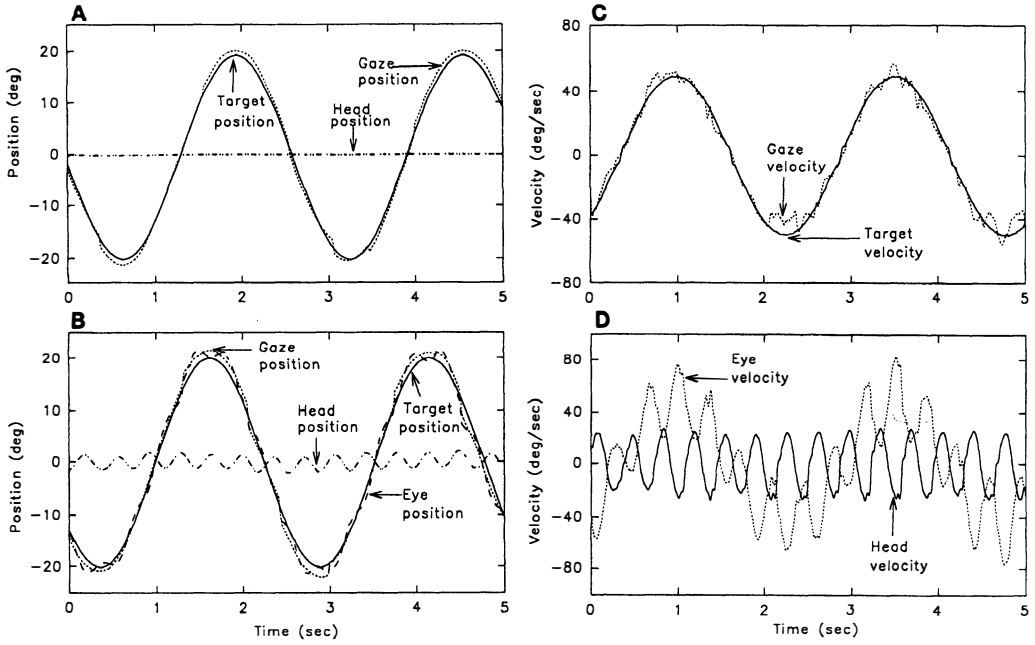

FIG. 5. Representative position records comparing SP with the subject stationary (*A*) or during chair vibration at 2.8 Hz (*B–D*). *A*: gaze closely follows target motion and the head is stationary, so eye in head is not shown. *B*: gaze also closely follows target motion, even though the head is being vibrated. The compensatory eye movements are evident. *C* and *D*: velocity tracings from the response of *B*. The eye and gaze velocity arrays have been desaccaded. *C*: target and gaze velocities. Gaze velocity closely follows the target velocity. The compensatory eye movements for the 2.8-Hz head vibrations are evident in *D*.

large phase lag, could it still account for the increase in VVOR gain at higher head velocities? Linear addition of vestibular and SP signals could account for VVOR gain being greater than VOR gain, but not for increasing gain with higher head velocities. For this, SP would be required to change its performance at higher speeds in a way that guaranteed the low retinal image velocities required for clear vision, which seems unlikely. For example, appropriate mod-

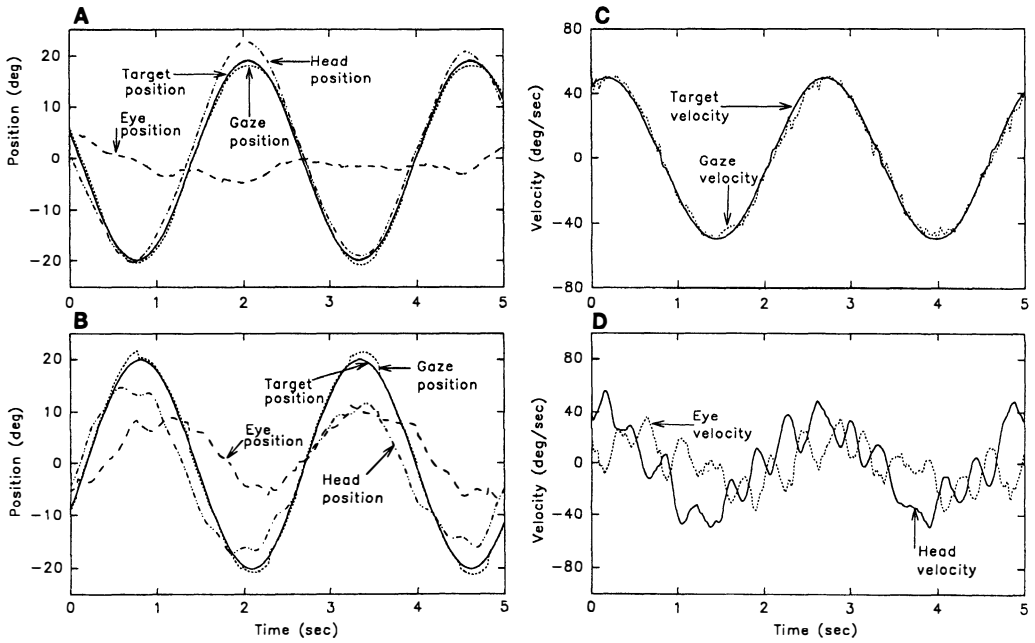

FIG. 6. Representative position records comparing CEHT with the subject stationary (*A*) or during chair vibration at 2.8 Hz (*B–D*). *A*: gaze closely follows the motion of the target, whereas head tracking is less precise. Eye-in-orbit movements reflect the difference between gaze and head tracking. *B*: gaze also follows the target quite closely, but head tracking again is less precise and the 2.8-Hz perturbations are evident on both head and eye records. *C* and *D*: velocity tracings from the response of *B*. The eye and gaze velocity arrays have been desaccaded. *C*: target and gaze velocities. Gaze velocity closely follows the target velocity. Both tracking head movements (0.4 Hz) and high-frequency head perturbations (2.8 Hz) with compensatory eye movements are evident in *D*.

ulation could be achieved if the SP phase lag subtracted from the VOR at low speeds while enhancing it at higher speeds. An alternative hypotheses is that, at high frequencies, the VOR is enhanced by a separate visual fixation system (Leigh et al. 1994; Luebke and Robinson 1988). Further studies are required to systematically examine the extent to which the gain of the VVOR may be modulated by peak head velocity over a range of frequencies.

Modulation of VVOR gain during visual tracking

Our second finding was that VVOR gain for the 2.8-Hz perturbations generally increased during visual tracking as compared with that achieved during fixation of a stationary target. This was the case irrespective of whether visual tracking was performed with the eyes alone (SP) or with combined movements of the eyes and head (CEHT). Because peak head velocities at 2.8 Hz were generally lower during CEHT (when subjects' heads were moving freely) than during SP (when subjects' heads were braced back against the headrest of the chair), it was possible to compare VVOR gains during visual tracking over a range of head velocities (Fig. 2*A*). No subject showed a decrease of VVOR gain during either tracking task compared with viewing a stationary target, and all subjects showed an increase on at least one tracking test. This result is in contrast to the reported decreases in VVOR gain that may occur during CEHT while human subjects (Huebner et al. 1992a) or monkey species (Cullen et al. 1991; Lisberger 1990) are rotated passively en bloc with the visual stimulus. This difference can be explained if one considers the potential factors that may lead to excessive slip of retinal images. One source of retinal image slip is deficient smooth tracking, which, for example, is more common in elderly individuals and occurs with a variety of neurological disorders. A second source of retinal image slip is from any inadequacy in the VVOR. So, during fixation of distant targets, if the VVOR gain is above or below 1.0, some retinal slip will occur with head movements. In our experiments, either or both of these sources of retinal slip could sum to produce retinal image slip that impaired vision. With the target motion that we selected, tracking gain was sometimes less than ideal (for example, in *Subject VED,* who was myopic). In this situation, net retinal image slip could be minimized by increasing VVOR gain toward 1.0. We found that mean retinal slip speed of the moving target increased only slightly in each subject during 2.8-Hz chair vibration compared with sitting stationary, and was generally held below 5°/s (Table 1). The situation is different if subjects are passively rotated in synchrony with the visual stimulus; in this case, a reduction of VOR gain will enhance visual tracking (Huebner et al. 1993) and will not lead to additional retinal slip because CEHT is the only source of head rotation.

What mechanisms could account for the increase of VVOR gain at 2.8 Hz during visual tracking compared with during fixation of a stationary target (Fig. 2*A*)? Our initial hypothesis, developed above, was that the brain monitors retinal image slip and responds to the combined sources from deficient visual tracking and an inadequate VVOR. Although this remains a possibility, our control experiment, in which we measured horizontal VVOR gain during tracking of vertical target motion, argues against this as being the only mechanism. We found an increase of horizontal VVOR gain during vertical tracking as compared with horizontal VVOR gain during fixation of a stationary target in three of four subjects; no subject showed a decrease. Because retinal slip due to inadequacies of vertical tracking was not additive with retinal slip due to inadequacies of the horizontal VVOR, it seemed unlikely that visual tracking signals per se were wholly responsible for modulating the VVOR gain. The question then remains: what nonvisual signal could modulate VVOR gain during the experimental paradigms that we used? During VVOR testing, head velocity might be a signal that the vestibular system uses to adjust VVOR gain (Huebner and Leigh 1992), and studies in monkeys indicate a nonvisual, short-latency modulation of VOR gain during CEHT (Cullen et al. 1991; Lisberger 1990). Another possible factor is predictive mechanisms, which are known to be important in visual tracking of sinusoidal target motion (Barnes 1993). Some recent studies have shown that when monkeys track a target moving predictably, in a circle, interaction between the horizontal and vertical pursuit responses occurs (Kettner et al. 1994; Leung et al. 1994). Whatever the mechanism, its goal seems to be constraining retinal image slip to levels that permit clear vision.

An assumption implicit in the conceptualization and analysis of our experiments was that the gain of the VVOR remained the same for all the stimulus frequencies. Thus we assumed that the gain of the VVOR at 2.8 Hz that we measured was the same gain that had to be negated at the tracking frequency (0.4 Hz). Studies of adaptation of the VVOR (Lisberger et al. 1983) have suggested the existence of a series of parallel temporal channels, each of which has an independently adjustable gain element. More recent electrophysiological studies have provided some support for this concept (Brontë-Stewart and Lisberger 1994). However, whether such channels could selectively modulate the VVOR responses differently for high-frequency head perturbations and low-frequency head tracking movements remains to be proven. If this were possible, we have to allow for the possibility that the gain of the VVOR is modulated up for the high-frequency head perturbations and modulated down for the low tracking frequency.

The original impetus for this study was to better understand how the VVOR operates during natural activities, especially visual tracking during locomotion. Because the head perturbations during locomotion are small, nonpredictable, and of high frequency, precise methods of measurement are required. It was for this reason that we chose to use the magnetic search coil technique. However, as other methods for recording eye and head movements improve, it seems that measurement of truly natural behaviors, such as the head perturbations that occur during locomotion (Grossman et al. 1988), may become possible. Such approaches are relevant to understanding the symptoms that patients with certain vestibular and neurological disorders experience when they walk through the environment.

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