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OSCILLATION AND THE INFLUENCE OF VOLUNTARY GAZE-CONTROL TASKS

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INTRODUCTION

High visual acuity during movements of the head requires physiological mechanisms that stabilize target images on the foveae. Two major systems perform this function, viz., the vestibular and visual tracking systems. Each has its preferred dynamic range, and each can be observed in the absence of the others (4).

Abnormal function of either of these systems can lead to compromised visual acuity, disorientation, and motion sickness, so adequate tests of each over its particular dynamic range are desirable in order to investigate the etiology of clinical conditions that present with these symptoms. Various tests have been devised and are used for this purpose, but until recently, none was based upon natural (active) head motion as the driving function. From a phylogenetic point of view, it is reasonable to assume that the dynamics of the mechanisms which produce compensatory eye movements during head motion would match the dynamic range of natural head motion, suggesting active head motion as a more suitable driving function for testing the system than, for instance, passive rotation of the whole body in a mechanized chair. Moreover, cumbersome and expensive equipment is required to produce whole-body oscillation at high frequencies, whereas suitable stimuli can be produced quite simply by active head motion.

A method of measuring eye movements during active head motion and procedures for computer analysis of the data have been previously described (6,7). This investigation was undertaken 1) to compare the gain of the vestibulo-ocular reflex (VOR) during active head motion and passive, whole-body motion in the same subjects, 2) to determine the influence of instructions relating to gaze control on VOR gain elicited in both active and passive motion in the dark, and 3) to assess the feasibility of manual passive rotation at high frequencies.

The VOR gain during active head oscillation in the horizontal plane over the range 0.1 to 4.0 Hz was studied while the subject performed four different tasks: 1) attempting to fixate upon an earth-fixed target light, 2) attempting to fixate upon an imagined earth-fixed target in darkness, 3) attempting to fixate upon a target light fixed relative to the head, 4) attempting to fixate upon an imagined target fixed relative to the head in darkness. VOR gain during passive manual oscillation of the subject over a frequency range 0.1 to 1 Hz was investigated under the same conditions.

PROCEDURE

SUBJECTS

Eight male individuals ranging in age from 20 to 39 years, with no reported vestibular or oculomotor disorders, served as subjects.

APPARATUS

Electrodes suitable for electro-oculography (EOG) were taped to the outer canthus of each eye with reference at the nasion. Direct coupled amplification of the horizontal EOG provided a signal for chart and magnetic tape recording. A light plastic head frame from a welder's helmet, fitted snugly to the head, was attached to a freely rotating potentiometer to yield a horizontal angular head position signal that was recorded along with the EOG. A light fastened to the apex of the head frame served to project a small spot onto a screen located 1.6m in front of the subject. This spot provided a head-fixed visual target during head movements. Red light-emitting diodes embedded in the screen could be illuminated selectively by the operator for calibration of horizontal eye position and to provide an earth-fixed target.

The subject was seated in a light aluminum aircraft seat, modified to provide support at feet, knees, and shoulders for body restraint and mounted upon a lockable turntable. Handles were fitted to the rear of the seat for manual oscillation. A dim blue light was mounted on the seat to project a spot of light onto a calibrated scale on the floor. By this means, the operator was able to oscillate the chair reproducibly over a 40 degree arc in time with sound cues of selected frequencies from 0.1 to 1 Hz that were pre-recorded on audio cassette tape and played back over headphones. Sound cues were not heard by subjects during passive oscillation. During active head oscillation, the chair was locked to its pedestal so that no chair movement was possible. Sound cues of selected frequencies between 0.1 and 4.0 Hz were played over a loudspeaker, and the subject was instructed to oscillate his head in time with them. The sound cue was a rising and falling tone (a frequency-modulated sine wave) with a mid-frequency of 700 Hz and varying sinusoidally from 400 to 1000 Hz.

Analog signals representing EOG and head positions were recorded in f.m. mode on 2 channels of a Phillips Mini Log 4 tape recorder. Voice commentary occupied a third channel. Replayed data were digitized and analyzed using a Hewlett-Packard Model 3482A Spectrum Analyzer and 9830A computer system as previously described (6).

METHOD

After a period of dark adaptation, tests were done in the following sequence, with abbreviations for each condition in brackets:

1. Active head oscillation while viewing a head-fixed real target (AHR) at 1.0, 0.5, 0.2, 0.1, 1.0, 2.0, 3.0, and 4.0 Hz.
2. Active head oscillation while imagining a head-fixed target (AHI) at 1.0, 0.5, 0.2, 0.1, 1.0, 2.0, 3.0, and 4.0 Hz.
3. Passive whole-body oscillation while viewing a head-fixed real target (PHR) at 1.0, 0.5, 0.2, 0.1, and 1.0 Hz.

4. Passive whole-body oscillation while imagining a head-fixed target (PHI) at 1.0, 0.5, 0.2, 0.1, and 1.0 Hz.

5. Active head oscillation while viewing an earth-fixed real target (AER) at 1.0, 0.5, 0.2, 0.1, 1.0, 2.0, 3.0, and 4.0 Hz.

6. Active head oscillation while imaging an earth-fixed target (AEI) at 1.0, 0.5, 0.2, 0.1, 1.0, 2.0, 3.0, and 4.0 Hz.

7. Passive whole-body oscillation while viewing a real earth-fixed target (PER) at 1.0, 0.5, 0.2, 0.1, and 1.0 Hz.

8. Passive whole-body oscillation while imagining an earth-fixed target (PEI) at 1.0, 0.5, 0.2, 0.1, and 1.0 Hz.

Eye position calibrations preceded each of these 8 test conditions and variations in calibration were used to adjust the gain of the eye movement signal where necessary. Duration of the sound cues and Analog to Digital (A/D) conversion parameters for the various oscillation frequencies are described in Table I.

TABLE I

Sound cues and Analog to Digital conversion parameters

Sound Cue		A/D Conversion	
Frequency	Duration	Rate	Time
0.1 Hz	70 sec	10/sec	51.2 sec
0.2	30	20	25.6
0.5	15	40	12.3
1.0	15	40	12.8
2.0	15	40	12.8
3.0	15	40	12.8
4.0	8	100	5.12

For each test, the data analysis program (6) yielded a VOR velocity gain, defined as the best-fitting estimate (by the method of least squares) of a straight line describing the relationship between eye and head velocity, with saccadic eye movements removed. After computation of VOR velocity gains, examination of the effect of each testing condition on VOR gain was performed using a fixed effects analysis of variance (9). Since the experimental design was unbalanced in terms of frequencies of oscillation with active compared to passive oscillation, the data were analyzed in two separate treatments: Treatment 1, in which only frequencies between 0.1, and 1.0 Hz were used, with four factors - active-head rotation/passive whole-body rotation, earth-fixed target/head-fixed target, imagined target/real target and oscillation frequency; and Treatment 2, in which only active head oscillation was considered, with three factors - earth-fixed target/head-fixed target, imagined target/real target, and oscillation frequency.

RESULTS

No difficulties were encountered in recording eye movements during active head oscillation over the entire range of frequencies, and results were similar in appearance to those previously reported (7). Whole-body manual oscillation of the subject proved feasible over the range of frequencies chosen, and the procedure yielded data which qualitatively fitted our expectations.

Mean VOR velocity gains computed for all frequencies used in each of the eight tests are shown in Table II, and plotted in Figure 1. A fixed effects analysis of variance of data obtained at head oscillation frequencies of 1.0 Hz and below showed that most of the interactions were significant, so it was decided to make post hoc comparisons between individual means at each frequency by computing the 95% confidence interval for the means, using the method of Boniferroni (10). For test frequencies of 1.0 Hz and below, the 95% confidence interval for the mean was ± 0.0235 , indicating that if two means at a given oscillation frequency differed by more than twice this interval, or 0.047, the probability was at least 95% that the difference was real. We were specifically interested in the comparison between active and passive oscillation and in the effects of instructions to the subject during oscillation in the dark.

For the comparison between active and passive oscillation when subjects tracked the real earth-fixed target, mean VOR velocity gain was slightly but consistently higher (for corresponding frequencies) under the active condition. Similar results were obtained with imagined earth-fixed targets. These slight differences were of marginal statistical significance and they may be attributable to an order effect. Order effects between test conditions were not controlled in the present study except that the 1 Hz frequency was run twice, at the beginning and midway in the course of each test condition sequence; within-sequence declines of between 2 and 4% occurred. Thus the slight difference in gain between active and passive oscillation with head-fixed targets (apparent in Fig. 1 and Table 2) may not be a significant effect. With imagined head-fixed targets, substantial differences in gain between active and passive conditions were significant and probably not attributable to order effects.

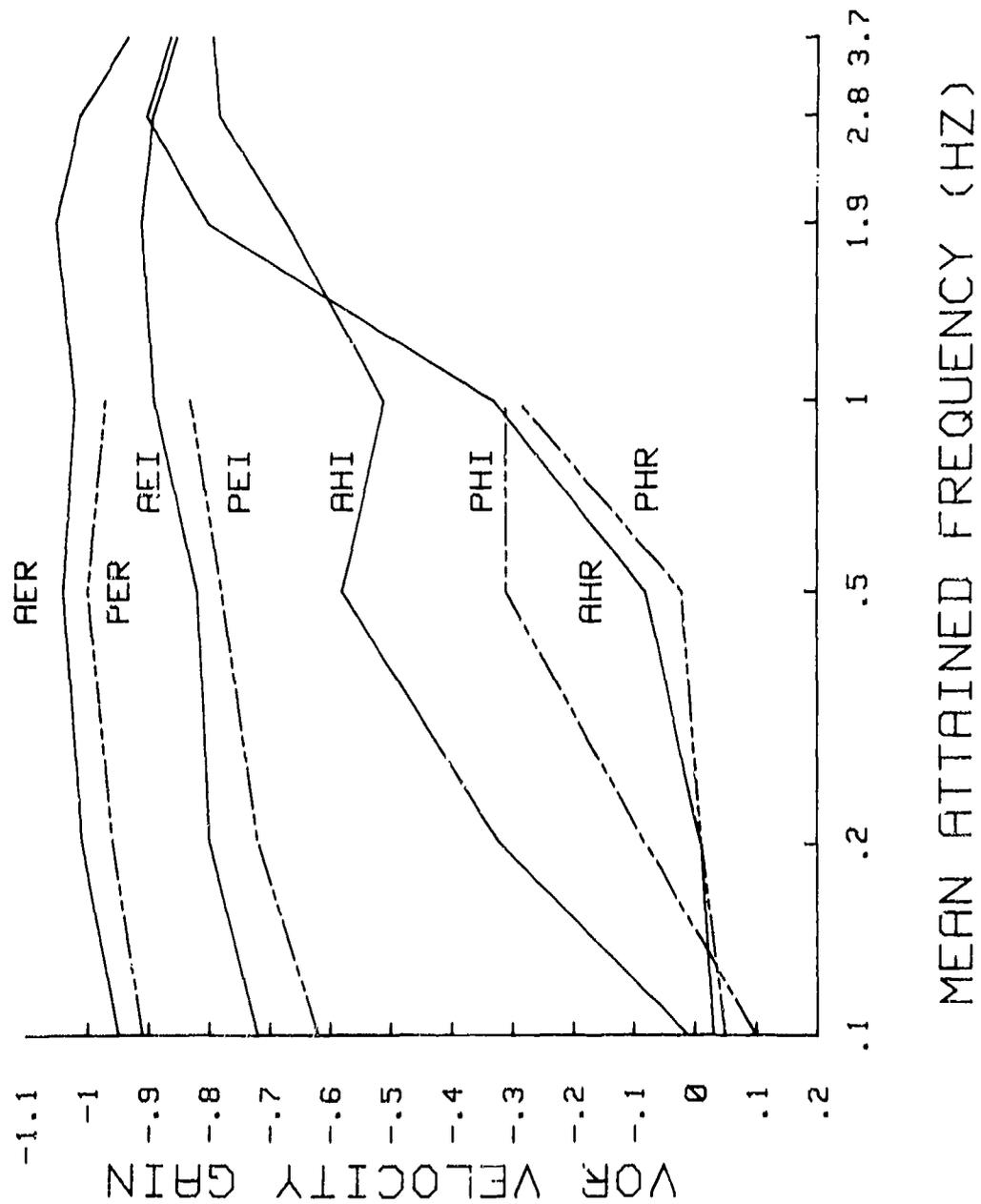


Figure 1

Mean vestibulo-ocular (VOR) gains (slopes of eye vs head velocity throughout cycle by least square fit) for each mean attained frequency in each condition of the experiment. A signifies active head oscillation; P signifies passive whole-body oscillation; E signifies Farth-fixed target; H signifies head-fixed target; R signifies real target; I signifies imagined target.

TABLE II

Mean Vestibulo-ocular Reflex Velocity Gains

Requested Frequency (Hz)		0.1	0.2	0.5	1.0	2.0	3.0	4.0
Mean Attained Frequency (Hz)		0.1	0.2	0.5	1.0	1.9	2.8	3.7
AHI	Mean Gain (S.D.)	-0.01 (.21)	-0.32 (.24)	-0.58 (.30)	-0.51 (.27)	-0.67 (.31)	-0.78 (.24)	-0.79 (.20)
AEI	Mean Gain (S.D.)	-0.72 (.11)	-0.80 (.06)	-0.82 (.10)	-0.89 (.14)	-0.91 (.14)	-0.89 (.11)	-0.85 (.11)
PHI	Mean Gain (S.D.)	0.10 (.11)	-0.08 (.12)	-0.31 (.13)	-0.31 (.28)			
PEI	Mean Gain (S.D.)	0.62 (.26)	-0.72 (.14)	-0.78 (.06)	-0.83 (.05)			
AHR	Mean Gain (S.D.)	0.03 (.05)	0.01 (.05)	-0.08 (.08)	-0.33 (.18)	-0.80 (.13)	-0.90 (.18)	-0.86 (.12)
AER	Mean Gain (S.D.)	-0.95 (.07)	-1.01 (.07)	-1.04 (.06)	-1.02 (.07)	-1.05 (.16)	-1.01 (.16)	-0.93 (.16)
PHR	Mean Gain (S.D.)	0.05 (.03)	0.01 (.5)	-0.02 (0.5)	-0.29 (.16)			
PER	Mean Gain (S.D.)	-0.91 (.05)	-0.96 (.05)	-1.00 (.04)	-0.97 (.07)			

Instructions to the subject during oscillation in the dark had a pronounced effect on VOR velocity gain. When the subject was instructed to track an imagined earth-fixed target, gain was relatively high and was little affected by oscillation frequency, rising slightly from between -0.6 and -0.7 at 0.1 Hz to between -0.8 and -0.9 at 1 Hz. When he was instructed to track an imagined head-fixed target, gain was much lower and more strongly affected by oscillation frequency. It rose from between 0.1 and 0.0 at 1 Hz to between -0.3 and -0.5 at 1.0 Hz.

Active head oscillation at 2.0 Hz and above produced a frequency-dependent discrepancy between requested frequency and mean attained frequency, as shown in Table II. The discrepancy was worse in some subjects than it was in others, and this variability casts doubt on the validity of a fixed effects analysis of variance of data at these frequencies. However, examination of the mean VOR velocity gains in Table II and Figure 1 shows that the effects of the various testing conditions were greatly attenuated at oscillation frequencies of 2.0 Hz and above. VOR velocity gains converged at approximately -0.9 regardless of whether the visual target was head-fixed or earth-fixed, real or imagined.

DISCUSSION

In agreement with previous findings (7) VOR gain during active head oscillation while tracking a real, earth-fixed target is within one standard deviation of -1.0 in the frequency range from 0.1 Hz to 4.0 Hz. The tendency for the gain to drop slightly at the highest frequencies does not agree with our previous data (7), which showed a tendency for VOR gain to increase in this range. However, intersubject variability was considerable at the highest frequencies both in this study and in our previous study, so the reliability of these gains is probably poorer than it is for those at lower frequencies. Although some investigators (3,8) have described a similar tendency for an increase in gain at around 4 Hz during passive oscillation of man and monkey, Tomlinson *et al.*, (11) have obtained results in humans during active head shaking which correspond more closely with those presented here.

VOR gain was consistently less than -1.0 during active head oscillation while the subject attempted to track an imagined earth-fixed target in the dark at all frequencies, the effect being strongest at the lowest frequencies. Our previous findings showed similar incomplete compensation, although there was a tendency for VOR gain to increase slightly below 1.0 Hz. Tomlinson *et al.* (11) also reported that VOR gain gradually increases with frequency, becoming -1.0 at and above 1 Hz. The data of Tomlinson *et al.* are in agreement with results obtained by Hixson (5) and Barnes and Forbat (1) in man in the dark.

When the subject oscillated his head while attempting to fixate upon a head-fixed target, visual suppression of the VOR was complete below 1.0 Hz, as indicated by gain values close to zero. Above 1.0 Hz the VOR increasingly overcame the visual pursuit drive, peaking at about 3 Hz with a gain of -0.9. Similar results were described in our previous study (7), with the exception that VOR gain below 1 Hz did not fall below -0.25.

In comparing present results with those obtained in our previous study, it is important to take note of a difference in analytical procedure. In our previous study, maximum eye velocity for a given cycle of oscillation was determined. Gain for that cycle was then calculated as the ratio of maximum eye velocity and temporally corresponding head velocity. The mean of the gains for individual cycles was taken as the gain for the trial. This procedure is sensitive to artifacts that would tend to yield an overestimate of gain. In the present study, gain was computed as the ratio of eye and head velocity throughout the oscillation cycle from linear regression analysis. This procedure is less sensitive to artifacts that would tend to cause an overestimate of the gain, but it is sensitive to the presence of any saccades missed by the saccade-detection algorithm. Since saccades are generally opposite the direction of prevailing eye velocity, any missed saccades would tend to cause an underestimate of the gain. The effect of this procedural difference on the results was not considered to be great, but it probably accounts for some of the differences that were observed.

The present results clearly demonstrate that actively generated head movements provide a satisfactory way to test VOR function and that passive oscillation at 1 Hz and below is a reasonable alternative when the subject has a real visual target, either earth-fixed or head-fixed. VOR gain was consistently lowered by the change from a real to an imagined earth-fixed target, and the magnitude of the reduction appeared not to depend upon whether oscillation was active or passive. VOR gain was further decreased when the subject was instructed to track a head-fixed target. These results suggest that passively produced VOR gain can be adjusted by higher centers in the absence of a visual pursuit stimulus, in agreement with the findings of Barr *et al.* (2), and further, that at frequencies below 2.0 Hz, this gain adjustment also is present during compensatory eye movements caused by active head oscillation. The results also suggest that the motor program producing head movement and the feedback from neck proprioceptors exert little and possibly no influence on VOR gain to improve foveation in normal subjects, either because of an absence of efference copy and proprioception connections with the pathways which determine gain, or because these neural signals can be overridden by higher centers.

The only instance in which there was a substantial significant difference between active and passive VOR gain was the one in which the subject was instructed to track an imagined head-fixed target in darkness. This result may indicate that proprioceptive and/or efference copy information is able to influence VOR gain under these particular conditions. However, a more likely explanation is that the task of tracking an imagined head-fixed target while performing active head oscillations in the dark was simply too difficult. Subjects did report difficulty in concentrating on this task and these reports were supported by the greater intersubject variability of VOR gains for this condition than for any of the other conditions (Table II). This large variability was probably due to occasional lapses in concentration. The relatively greater effectiveness of VOR suppression during passive oscillation may be attributable to the fact that subjects were better able

to focus attention on the imagined head-fixed target, whereas, during active head oscillation, they were distracted by also having to move their head in consonance with the auditory cue.

A prominent feature of the results is the differential alteration of VOR in the dark by mental effort to view imagined head-fixed targets vis-a-vis imagined earth-fixed targets in both passive and active head motion conditions, particularly at stimulus frequencies below 2 Hz. This source of response variation left uncontrolled could reduce test sensitivity and it can be avoided by instruction to view an imagined earth-fixed target. Alternatively both mental tasks may be further explored in the hope that diagnostic significance will be found for the different functions obtained with the different mental tasks. However, it would appear at this point that the imagined head-fixed target during active head oscillation is a condition that should be dropped.

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