

EFFECTS OF VISUAL AND NON-VISUAL MECHANISMS ON THE VESTIBULO-OCULAR REFLEX DURING PSEUDO-RANDOM HEAD MOVEMENTS IN MAN

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SUMMARY

1. The behaviour of the vestibulo-ocular reflex (VOR) in man was examined using pseudo-random and sinusoidal whole-body angular-motion stimuli applied about the yaw axis by a servo-controlled turn-table.

2. The VOR response was assessed in four conditions; during fixation on a head-fixed target (HFT); during attempted fixation in the dark of an imagined head-fixed (IHFT) or earth-fixed target (IEFT) and in darkness (DRK) whilst performing an auditory discrimination task.

3. When the pseudo-random stimulus was composed of four sinusoids, the three lowest frequencies (0.11, 0.24 and 0.37 Hz) were maintained constant whilst the highest frequency (F_4) was varied from 0.39 to 2.08 Hz. In darkness (DRK condition) and when imagining a head-fixed target (IHFT condition) the gain of slow-phase eye velocity was not significantly affected by the frequency of the highest-frequency component, although there were significant changes in the phase for the IHFT condition.

4. During fixation of a real head-fixed target (HFT condition), both the gain and phase of eye velocity were significantly modified by the frequency (F_4) of the highest-frequency component. When F_4 was 0.39 Hz, all frequency components had a low gain (mean 0.05), but as F_4 was increased there was a significant ($P < 0.001$) increase in gain for all three low-frequency components which reached a maximum (mean 0.17) when F_4 was 2.08 Hz. However, the gain for the highest frequency component always remained comparable to that obtained in response to a single discrete sinusoid of the same frequency.

5. When the stimulus was composed of only two sinusoids a similar increase in gain of the lower-frequency (0.22 Hz) component was observed in the head-fixed target condition as the frequency of the higher-frequency component was increased from 0.39 to 2.78 Hz. However, VOR gain was not significantly modified by the frequency of the higher-frequency component when subjects imagined a head-fixed or earth-fixed target in darkness.

6. The findings indicate that high levels of VOR suppression can be achieved in the head-fixed target condition with pseudo-random stimuli when all frequency components are below 0.4 Hz. But if the highest-frequency component rises above

0.8 Hz, optimum suppression is confined to the highest-frequency component, whilst suppression of the low-frequency components is significantly reduced.

7. The frequency-dependent effects observed during visual suppression of the VOR are shown to be directly comparable to those observed previously during ocular pursuit (Barnes, Donnelly, & Eason, 1987) and provide further evidence for the similarity of pursuit and visual-vestibular interaction.

INTRODUCTION

In several previous experiments (Barnes, Benson & Prior, 1978; Lau, Honrubia, Jenkins, Baloh & Yee, 1978) it has been shown that the ability to suppress eye movements of vestibular origin is impaired when the frequency of head movement exceeds 1–2 Hz or when the angular velocity exceeds 50–60 deg/s. These limitations in vestibulo-ocular reflex (VOR) suppression are similar to those observed in the behaviour of the pursuit reflex, and this has led to the suggestion that the same basic neural mechanisms are involved in these two oculomotor control activities. The majority of the experiments in which such comparisons have been made have involved the use of sinusoidal stimuli. It is well established that such stimuli induce a predictive response during pursuit of a moving target (Stark, Vossius & Young, 1962; Dallos & Jones, 1963; Michael & Jones, 1966; Yasui & Young, 1984) and that when a pseudo-random stimulus is used performance is significantly impaired. In accord with such findings Hyden, Istl & Schwarz (1982) were able to show that VOR suppression during random stimulation was also inferior to that obtained during sinusoidal stimulation.

In a recent experiment (Barnes, Donnelly & Eason, 1987) it has been shown that the predictability of a pseudo-random stimulus during pursuit is governed, not by the complexity of the stimulus, but simply by the frequency of its highest-frequency component. When a mixed-frequency, pseudo-random stimulus contained only low-frequency (< 0.4 Hz) components the ratio of eye velocity to target velocity (i.e. eye velocity gain) was high (> 0.90) and was comparable to the response to a discrete frequency sinusoid. In contrast, when the highest frequency was above 0.8 Hz, eye velocity gain was reduced to 0.5–0.6 for all lower-frequency components, whereas the gain of the highest frequency remained as high as for the response to a discrete sinusoid of identical frequency. It thus appeared that the resources of active pursuit were being channelled preferentially into the highest-frequency component of the stimulus whereas the lower frequencies no longer had this enhancement of gain. Further experiments in which responses to target step displacement stimuli were examined revealed that the enhancement of gain was probably being carried out by a centrally controlled velocity estimation mechanism which was not dependent on continuous retinal velocity error feed-back.

In the following experiments the type of mixed-frequency pseudo-random stimulus used previously to investigate the pursuit reflex has now been used to examine the effects of prediction on VOR suppression. Responses were obtained using combinations of either two or four sinusoidal angular-motion stimuli applied to the whole body in the yaw axis. In addition to investigating the effects of visual fixation on VOR suppression, we have also examined the effects of prediction on the

modification of VOR responses by the instruction to imagine the presence of earth-fixed or head-fixed visual targets, in the manner first described by Barr, Schultheis & Robinson (1976).

METHODS

The subject was seated on a large (200 N m torque), direct-drive turn-table, to which he was firmly harnessed. Lateral clamps were applied to the head to prevent rotation with respect to the turn-table. The subject was able to view a visual target (luminance 4 cd/m²) consisting of a small fixation dot within two concentric circles, the diameters of which subtended angles of 10 and 50 min of arc at the eye. The target was projected on to a semicircular screen 1 m from the subject and could be made to rotate with the turn-table, so as to form a head-fixed target, or to remain stationary in space for purposes of calibration. The experiment was carried out in a completely darkened room so that the target appeared against a featureless black background. The subjects, none of whom had any known disorder of the vestibular apparatus, were all easily able to view the visual stimuli without corrective lenses. Three experiments were performed as follows.

Experiment I. In the first experiment the oscillating stimulus to the turn-table was composed of two sinusoids, each having a peak velocity of ± 25 deg/s. The lower-frequency component was maintained at 0.22 Hz whilst the higher frequency was varied in eight increments between 0.39 and 2.78 Hz. Three visual stimulus conditions were presented in succession at each frequency combination. First, the response in darkness (DRK) was evoked, with the instruction to the subject to stare blankly ahead. Second, the subject was required to maintain fixation on the head-fixed target (HFT) and finally the subject was requested to imagine the presence of a head-fixed target (IHFT) in darkness. The turn-table was brought to a halt for a period of 3–4 s between each visual stimulus condition. Eye movements were recorded by an infra-red limbus tracking technique as described elsewhere (Barnes, 1983) and a calibration was carried out prior to each change of the motion stimulus. Eight subjects took part in this experiment.

Experiment II. In this experiment the motion stimulus was identical to that of Experiment I, but the three stimulus conditions tested were somewhat different. In the first condition, subjects were instructed to imagine the presence of an earth-fixed target whilst being oscillated in darkness (IEFT). In the second, eye movements were evoked in the dark (DRK) but the subject was distracted and kept alert by carrying out a simple but demanding auditory pitch discrimination task. Two pure tone signals were presented in succession through an earpiece and the subject was required to indicate which of the two was of higher pitch by operating one of two push-button switches. In the third condition subjects were again required to imagine the presence of a head-fixed target (IHFT) in darkness. Eye movements were recorded by electro-oculography because the eye movements evoked in the imagined earth-fixed target (IEFT) condition were of too large an amplitude to use the limbus tracking method. Eight subjects, three of whom had performed Experiment I, took part in this experiment.

Experiment III. In the third experiment the motion stimulus was composed of four sinusoids, each of peak velocity ± 17.5 deg/s. The three lower frequencies (F_1 , F_2 , F_3) remained constant at 0.112, 0.240 and 0.368 Hz whilst the highest frequency (F_4) took values of 0.391, 0.781, 1.563 and 2.083 Hz in four separate stimulus conditions. Three visual conditions similar to those of Experiment I were examined, except that the dark response (DRK) was evoked whilst the subject carried out the auditory pitch discrimination task described above. The head-fixed target (HFT) and dark (DRK) conditions were also examined using discrete-frequency sinusoidal stimuli (peak velocity ± 35 deg/s) at identical frequencies to those which made up the mixed-frequency combinations. Eye movements were recorded by the limbus tracking method. Eight subjects took part in this experiment. In a subsidiary experiment four of the eight subjects were exposed to the same experimental conditions except that in the imagined head-fixed target condition a degraded visual stimulus was presented in order to enhance the percept of a head-fixed target. For this purpose two small light-emitting diodes were rigidly located on the turn-table so that they appeared at 10 deg to the left and right of centre. Subjects were requested to stare at the point midway between the light-emitting diodes, which were tachistoscopically illuminated once every second for a duration of 100 μ s.

The motion stimuli were generated by computer (Hewlett-Packard 9816S) and the eye movement responses were recorded on-line and analysed in a manner similar to that described

previously for pursuit reflex responses (Barnes *et al.* 1987). Only the slow-phase components of eye movement have been considered in the analysis and these are characterized by the ratio of eye velocity to head velocity (i.e. eye velocity gain) for each frequency component of the stimulus, together with the associated phase relationship.

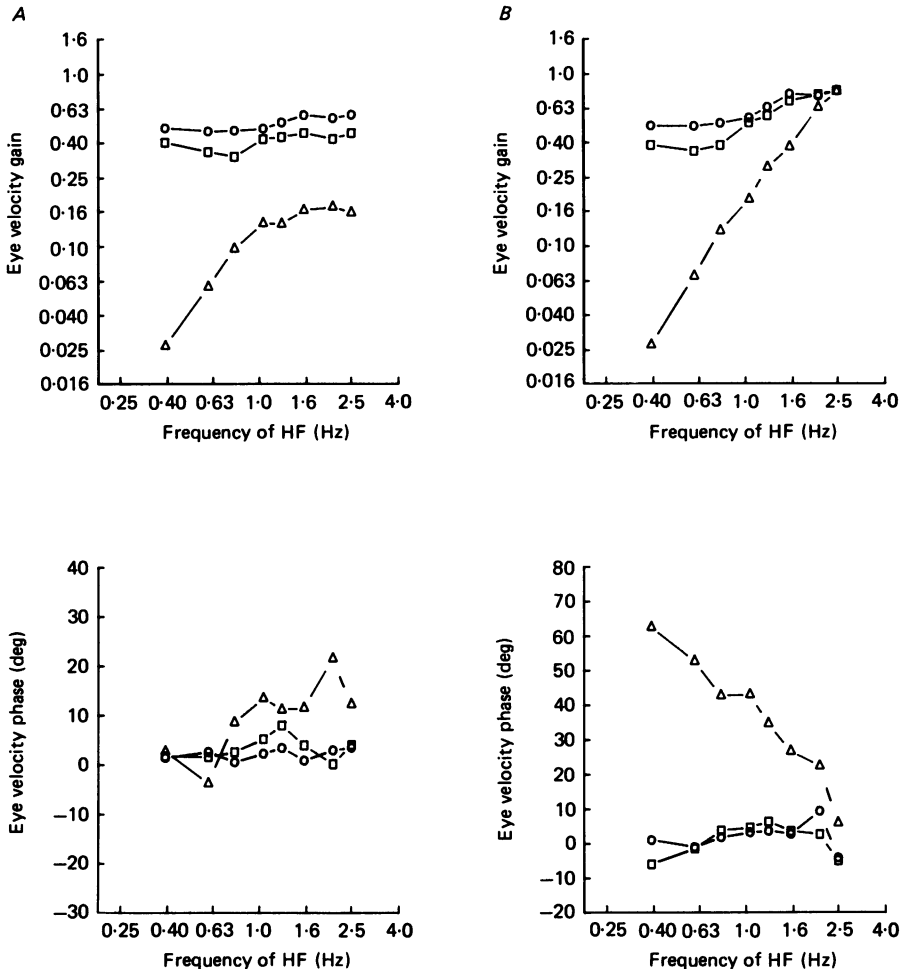


Fig. 1. The gain and phase of the slow-phase component of the VOR in three stimulus conditions: DRK (○), rotation in darkness; HFT (△), fixation of head-fixed target; IHFT (□), attempted fixation of an imaginary head-fixed target. Stimulus motion composed of two sinusoids. Responses for the lower-frequency component are plotted in A, those for the higher-frequency component in B. Both are plotted as a function of the frequency (F_2) of the higher-frequency (HF) component, which varied from 0.39 to 2.78 Hz. The frequency of the lower-frequency component was 0.22 Hz. Mean of eight subjects.

RESULTS

Experiment I: the comparison of visual and non-visual VOR suppression

VOR responses in the dark. For each combination of sinusoidal stimulus frequencies the mean eye velocity gain of the low-frequency component increased slightly with

the frequency (F_2) of the high-frequency component (Fig. 1A) although the effect was not statistically significant because four of the subjects showed no increase whereas the remaining four exhibited a considerable increase. The gain of the high-frequency component showed a steady and significant ($P < 0.001$ by analysis of variance) increase with frequency (Fig. 1B) as recorded in previous experiments (Barnes, 1980). Mean gain for the high-frequency component increased from 0.46 at 0.39 Hz to 0.80 at 2.5 Hz. The phase associated with the eye velocity (Fig. 1B) of both frequency components did not change significantly with the frequency of the higher-frequency component, remaining close to zero (i.e. compensatory to head movement).

Head-fixed target. When subjects maintained fixation on the head-fixed target eye movements were markedly suppressed (Fig. 1A). The degree of suppression was greatest when both frequencies were at their lowest level ($F_1 = 0.22$ Hz; $F_2 = 0.39$ Hz); mean eye velocity gain being 0.03. However, as the higher frequency (F_2) was increased there was a progressive increase in the gain of the lower-frequency component, which reached an asymptotic mean level of 0.16 when F_2 was between 1.04 and 2.78 Hz. Eye velocity phase for the low-frequency component was close to zero when the frequency (F_2) of the higher-frequency component was less than 0.60 Hz but exhibited a phase advance at higher levels of F_2 (Fig. 1B). The gain of the high-frequency component itself showed a progressive increase with frequency in the manner described previously (Barnes, 1983). When F_2 was greater than 2.08 Hz there was no significant suppression of the response recorded in darkness. Eye velocity for the higher-frequency component exhibited considerable phase advance when its frequency (F_2) was 0.39 Hz (Fig. 1B), declining steadily as F_2 was increased, so that there was no significant difference from the dark response when F_2 was 2.78 Hz.

Imagined head-fixed target. Some subjects found it considerably easier than others to imagine the presence of a head-fixed target in darkness, and thereby to reduce eye velocity gain. On average, the gain for the low-frequency component was less than that observed in darkness (Fig. 1A) but the effect was only significant ($P < 0.05$ by t test) at four of the eight frequencies tested (0.78, 1.56, 2.08 and 2.78 Hz). The gain of the low-frequency component did show a significant ($P < 0.001$) change with the frequency (F_2) of the higher-frequency component but this was not similar to the changes observed in the head-fixed target (HFT) condition, taking the form of an optimum suppression at intermediate frequencies (0.60 and 0.78 Hz). The gain of the high-frequency component similarly showed an optimum suppression when its own frequency (F_2) was 0.60 and 0.78 Hz. At these frequencies the gain of the high-frequency component was significantly less ($P < 0.05$ by t test) than that recorded in darkness, whereas at all frequencies above 1.04 Hz gains were not significantly different for the two conditions. Eye velocity phase for both frequency components remained close to zero (Fig. 1B) and was not significantly different from the phases recorded in darkness (DRK condition).

Experiment II: responses to fixation of imagined earth-fixed and imagined head-fixed targets

VOR responses in darkness. Mean eye velocity gain for the low-frequency component in this second experiment was somewhat higher than in Experiment I, although not significantly so, and remained at a much more constant level as the

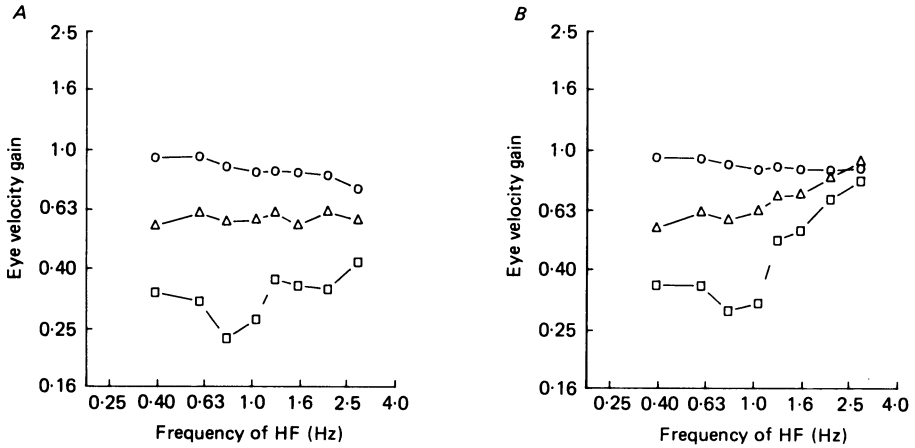


Fig. 2. Eye velocity gain for motion conditions identical to those defined in Fig. 1. *A*, low-frequency (LF) component; *B*, high-frequency (HF) component. DRK (Δ), rotation in darkness carrying out pitch discrimination task. IHFT (\square), attempted fixation of an imaginary head-fixed target. IEF (\circ), attempted fixation of an imaginary earth-fixed target in darkness. Mean of eight subjects.

frequency of the high-frequency component was increased (Fig. 2). It is likely that this improved consistency was associated with the performance of the secondary pitch-discrimination task which served to keep the subject alert. The mean gain for the three subjects who performed Experiments I and II was increased in the second experiment, although the difference was not significant. Two of these subjects exhibited an increase in gain of the low-frequency component as F_2 was increased in Experiment I, but not in Experiment II. On subsequent questioning it was evident that these subjects had interpreted the instruction to stare blankly ahead as an indication that they should imagine a head-fixed target, whereas the auditory task distracted them from making any particular visualization of this type. The gain of the high-frequency component showed a trend of increase with its own frequency (F_2) similar to that found in Experiment I. Eye velocity phase was close to zero for both frequency components.

Imagined head-fixed target. In this condition the eye velocity gain for both frequency components exhibited a trend with increase of the higher frequency (F_2) similar to that observed in Experiment I, although average gains were approximately 15% lower (Fig. 2). It is notable that, as in Experiment I, optimum suppression for both frequency components was obtained when F_2 was 0.78 and 1.04 Hz (Fig. 2). For the low-frequency component, eye velocity gain in the imagined head-fixed target

condition was significantly less ($P < 0.01$: t test) than that in the dark at all values of F_2 except the highest frequency (2.78 Hz). This finding was somewhat different to that made in Experiment I and is largely attributable to the higher levels of suppression achieved by the group of subjects in Experiment II. The gain of the high-frequency component exhibited the same pattern of increase above 1.04 Hz as found

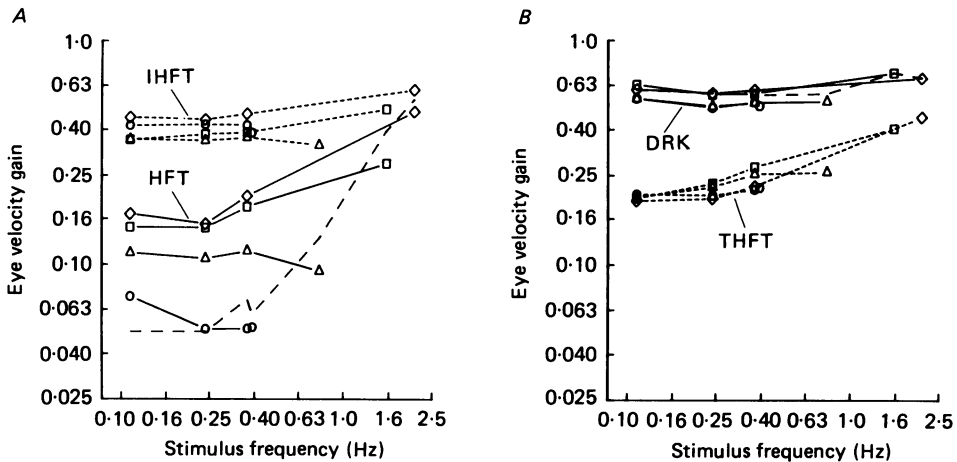


Fig. 3. Eye velocity gain during pseudo-random whole-body rotation plotted as a function of the frequency of its individual frequency components. The stimulus motion was composed of four sinusoids, each with peak velocity of ± 17.5 deg/s. The three lowest frequencies remained constant (0.112, 0.240 and 0.368 Hz), whilst the highest frequency was varied, having values of 0.391 (\circ), 0.781 (\triangle), 1.563 (\square) and 2.083 (\diamond) Hz. Responses were examined in four conditions: DRK, darkness; HFT, fixation of a head-fixed target; IHFT, attempted fixation of imaginary target; THFT, attempted fixation midway between tachistoscopically illuminated peripheral targets. Dashed lines without symbols indicate responses to discrete frequency sinusoidal stimuli. Mean of eight subjects.

in Experiment I with no significant suppression at the highest frequency (2.78 Hz). The high-frequency component exhibited a phase lag (mean -7.2 deg) at the three lowest frequencies of F_2 (0.39, 0.60, 0.78 Hz) which was significantly ($P < 0.05$) less than that for the dark (DRK) condition. At higher frequencies the phase was close to zero.

Imagined earth-fixed target. When subjects attempted to fixate an imaginary earth-fixed target there was a considerable increase in eye velocity gain for both frequency components (Fig. 2) when compared with the response in darkness (DRK condition). For both components there was a similar, significant ($P < 0.01$ by analysis of variance) trend of decreasing gain with increasing frequency. The difference in gain obtained in the dark (DRK) and imagined earth-fixed target (IEFT) conditions for the low-frequency component was significant ($P < 0.05$ by t test) for all values of the higher frequency (F_2) whereas that for the high-frequency component was significant ($P < 0.05$) at all but the two highest values of F_2 (2.08 and 2.78 Hz). Eye velocity phase for the imagined earth-fixed target condition was not significantly different from that in the dark (DRK) condition, being close to zero at all frequencies.

Experiment III: VOR responses to a combination of four sinusoids

VOR responses in darkness. The gain of the three lower-frequency components of the VOR response in darkness was not significantly modified by the frequency (F_4) of the highest-frequency component. The mean gain across all conditions for the three lowest frequencies was 0.56 (Fig. 3B). The gain of the high frequency itself rose

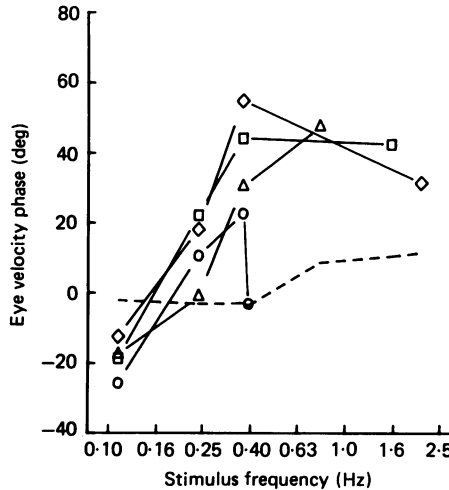


Fig. 4. Eye velocity phase for the motion conditions defined in Fig. 3 for the head-fixed target (HFT) condition. Dashed line indicates response to sinusoidal oscillation at discrete frequencies. Mean of eight subjects. F_4 = ○, 0.39 Hz; △, 0.78 Hz; □, 1.56 Hz; ◇, 2.08 Hz.

from 0.52 at 0.39 Hz to a peak of 0.72 at 1.56 Hz. There was no significant difference between the gains for each frequency component of the mixed-frequency stimulus and the gains obtained in response to discrete sinusoidal stimuli of identical frequency (Fig. 3B). Eye velocity phase was also not significantly modified by the effect of the highest-frequency component and there was no significant difference from the responses to discrete sinusoids, the overall mean being +1.1 deg.

Head-fixed target. When the subjects fixated the head-fixed target and attempted to suppress the VOR responses there were significant changes in gain and phase as the frequency (F_4) of the highest-frequency component was increased (Fig. 3A). When all frequencies of the stimulus were below 0.39 Hz suppression was optimal, mean gain for the three lowest frequencies being 0.06. As F_4 was increased there was a progressive increase in eye velocity gain for the low-frequency components which reached a maximum level (averaged over the three lowest frequencies) of 0.17. For each value of F_4 there was no significant difference in gain between the three lowest-frequency components, which thus exhibited a very similar change in gain as F_4 was increased. In the frequency combination in which the highest frequency was 0.39 Hz, the gain of the three lowest-frequency components was not significantly different from that obtained when the motion stimulus was a discrete sinusoid of identical frequency (Fig. 3A). As F_4 was increased the gain of the highest-frequency

component was, on average, lower than that for the discrete sinusoid of corresponding frequency, although the difference was not significant (Fig. 3A). Eye velocity phase (Fig. 4) also exhibited a change with the frequency (F_4) of the highest frequency component. When F_4 was 0.39 Hz there was a progressive change from a mean phase

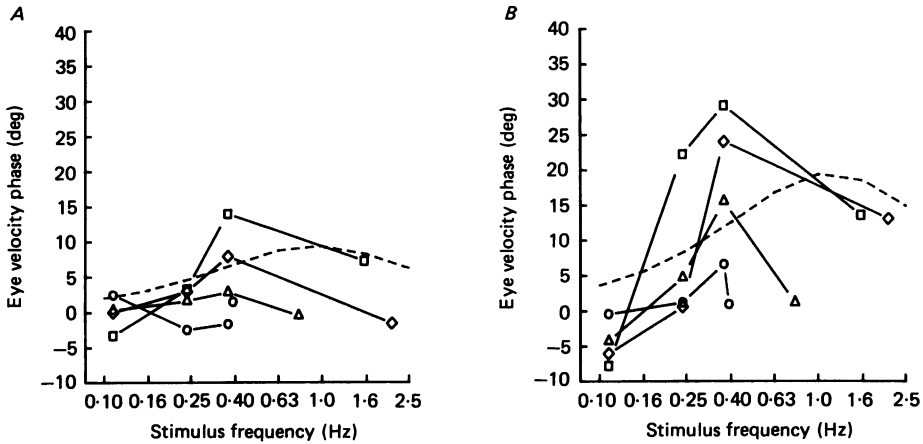


Fig. 5. Eye velocity phase for the motion conditions defined in Fig. 3 during A, fixation of an imagined head-fixed target (IHFT condition) and B, presentation of peripheral strobed targets (THFT condition). Mean of eight subjects. Dashed line indicates phase predicted by internal efference copy, negative feed-back suppression model. (See Fig. 6.) $F_4 =$: \circ , 0.39 Hz; \triangle , 0.78 Hz; \square , 1.56 Hz; \diamond , 2.08 Hz.

lag of 18.0 deg for the lowest-frequency component ($F_1 = 0.11$ Hz) to a phase lead of 21.7 deg for the third frequency component ($F_3 = 0.39$ Hz). The same trend with frequency was observed for other values of F_4 , but as F_4 increased there was less phase lag for the lowest-frequency component and more phase lead for the intermediate frequency components. Comparison of the phases obtained from discrete sinusoidal stimuli with the phases corresponding to optimum levels of suppression (Fig. 4) indicated a highly significant difference, the sinusoidal responses exhibiting less phase lag at the lowest frequency (0.11 Hz) and less phase lead at all other frequencies.

Imagined head-fixed target. When the subjects attempted to suppress the VOR response by imagining a head-fixed target in darkness eye velocity gain for each of the three lower frequencies was significantly ($P < 0.01$ by analysis of variance) less than that recorded when the subject carried out the auditory pitch discrimination task in darkness, with a mean gain of 0.44 (Fig. 3A). There were some changes in gain of the low-frequency components as the frequency (F_4) of the highest-frequency component was increased, although they were not found to be significant. Minimum levels were attained for the intermediate values of F_4 (0.78 and 1.56 Hz), an effect which was somewhat similar to that observed in the response to the combination of two sinusoids. The gain of the highest frequency itself was significantly less ($P < 0.05$) than for the response obtained in the dark (DRK condition) at all values of F_4 except 2.08 Hz. The phase angles in the imagined head-fixed target condition (Fig. 5A) exhibited significant ($P < 0.05$ by analysis of variance) changes with the

frequency of F_4 which were not dissimilar to those in the head-fixed target condition. As F_4 was increased from 0.39 to 1.56 Hz more phase lag appeared for the lowest-frequency component (0.11 Hz) and more phase lead for the third frequency component (0.37 Hz), whereas when F_4 was 2.08 Hz this trend was reversed. Taken together with the changes in gain at the intermediate values of F_4 (0.78 and 1.56 Hz) this indicates that the value of F_4 did have some influence on the process of non-visual suppression, although the inter-subject variability tended to obscure the small differences in gain in this condition.

Responses to tachistoscopic target presentation. When the subjects viewed the tachistoscopically illuminated head-fixed targets (THFT condition) and attempted to fixate an imaginary point between them, the eye velocity gains evoked fell midway between those for the IHFT and HFT conditions (Fig. 3B). There was no significant change in the gain of the three low-frequency components when the frequency (F_4) of the highest-frequency component was increased as there had been in the head-fixed target (HFT) condition. When the averaged gain for the three low-frequency components was compared with the corresponding gain in the imagined head-fixed target (IHFT) condition, those obtained during presentation of the peripheral strobed targets (THFT condition) were found to be significantly lower ($P < 0.01$, $t = 4.35$, d.f. = 11). In contrast, no significant difference was found when a similar comparison was made between the average gain for the three lowest-frequency components in the THFT condition and the highest average gain in the head-fixed target (HFT) condition, obtained when F_4 was 2.08 Hz. The phase angles in the THFT condition, like the gains, were much more consistent than those in the imagined head-fixed target condition, but showed a similar significant ($P < 0.01$) trend as F_4 was increased (Fig. 5B). The mean values of phase lag for the lowest-frequency component and phase lead for the third frequency component were, however, approximately twice those in the imagined head-fixed target (IHFT) condition, though not as large as those in the head-fixed target (HFT) condition (Fig. 4).

DISCUSSION

VOR suppression by fixation of a head-fixed target

The results of the experiments described here demonstrate that the ability to achieve the maximum level of VOR suppression by fixation of a head-fixed target is dependent on the nature of the stimulus movement. If all frequency components of a mixed-frequency stimulus are less than 0.4 Hz the level of suppression achieved is comparable to that achieved when the stimulus is a discrete frequency sinusoid. In contrast, when the highest-frequency component has a frequency in excess of 0.8 Hz there is significantly less suppression for the lower-frequency components, although gains obtained for the highest frequency itself remain comparable to those obtained with discrete sinusoids of the same frequency. The observation that such effects occur when only two sinusoids are mixed to form the stimulus indicates that it is not the complexity of the stimulus waveform which leads to the break-down in suppression, but simply the frequency of the highest-frequency component of the stimulus.

Comparison of VOR suppression and pursuit

These findings are comparable to those obtained previously during pursuit of visual targets moving with similar pseudo-random waveforms (Barnes *et al.* 1987). In previous publications (Barnes *et al.* 1978; Barnes, 1983; Barnes, Crombie & Edge,

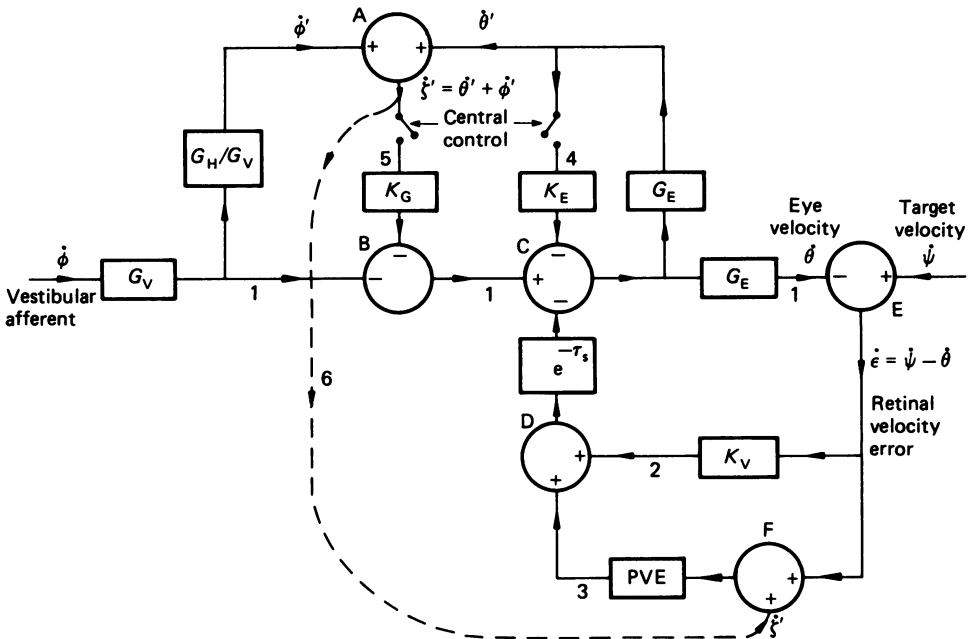


Fig. 6. A proposed model of visual-vestibular interaction. Major pathways are as follows: 1, basic disynaptic vestibulo-ocular reflex arc emanating from semicircular canals; 2, continuous retinal velocity error feed-back; 3, predictive velocity estimation (PVE); 4, oculomotor efference copy feed-back; 5, gaze velocity estimation derived from vestibular afference and oculomotor efference; 6, positive feed-back of central gaze velocity estimate to provide estimate of target velocity in space. $\dot{\phi}$, head velocity; $\dot{\psi}$, target velocity with respect to the head; $\dot{\theta}$, eye velocity; $\dot{\epsilon}$, retinal velocity error; $\dot{\zeta}$, estimate of gaze velocity. $\dot{\phi}'$, $\dot{\theta}'$, central estimates of $\dot{\phi}$ and $\dot{\theta}$. $K_V = 1-2$; $G_V = 0.6$; $\tau = 0.08$ s; $G_E = (1 + sT_E)^{-1}$, where $T_E = 0.2$ s.

1985) this similarity has been investigated with reference to a model of the mechanisms of visual-vestibular interaction, a revised version of which is shown in Fig. 6.

In this model it is assumed that identical visual feed-back mechanisms (pathways 2 and 3 in Fig. 6) are responsible for the reduction of retinal velocity error during both pursuit and VOR suppression. The details of this visual feed-back system will be discussed later but, irrespective of its precise nature, it is possible to show, as indicated in previous publications (Barnes *et al.* 1978; Barnes, 1983), that the relationship between eye velocity during pursuit ($\dot{\theta}_p$) and that obtained during VOR suppression ($\dot{\theta}_{HFT}$) is given by the equation:

$$\frac{\dot{\theta}_P}{\dot{\psi}} = 1 - \frac{\dot{\theta}_{HFT}}{\dot{\theta}_{DRK}}, \tag{1}$$

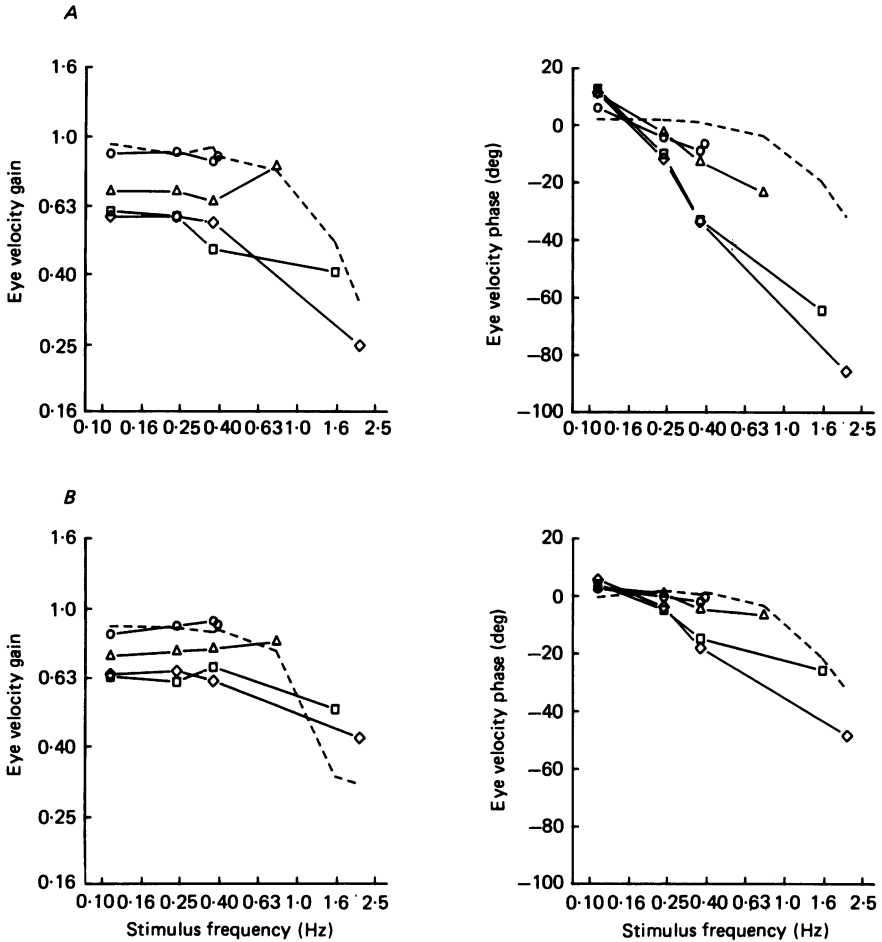


Fig. 7. *A*, eye velocity gain and phase evoked in response to a pseudo-random stimulus composed of four sinusoids, each with peak velocity of ± 3.37 deg/s (Barnes *et al.* 1987). *B*, gain and phase for the efficiency of VOR suppression derived from the results of Fig. 3 in the manner explained in the text. Dashed line, sine; F_4 : \circ , 0.39 Hz; \triangle , 0.78 Hz; \square , 1.56 Hz; \diamond , 2.08 Hz.

where $\dot{\psi}$ = target velocity with respect to the head during pursuit, and $\dot{\theta}_{\text{HFT}}/\dot{\theta}_{\text{DRK}}$ = ratio of eye velocity recorded during visual suppression to eye velocity (θ_{DRK}) recorded in darkness.

The right-hand side of eqn (1) may be thought of as representing the efficiency of VOR suppression. In Fig. 7 the gain and phase characteristics of pursuit (obtained from Barnes *et al.* 1987) and the efficiency of VOR suppression (obtained from the results of Fig. 3) are compared for responses to stimuli composed of four sinusoids. Although there are small differences in the magnitude of the gains and phases of these two measures of oculomotor function, which may be partially attributable to the fact that they are taken from two different subject groups, they nevertheless exhibit a remarkable ordinal similarity. The gain of all three of the low-frequency components

declines steadily as the frequency (F_4) of the highest frequency is increased for both the pursuit responses and those based on VOR suppression. On the other hand, the gain for the highest-frequency component itself, in both responses, remains similar to, or actually exceeds, the gain obtained in response to a discrete, predictable sinusoidal stimulus of equivalent frequency. The phase associated with the efficiency of VOR suppression also exhibits similar changes to that of pursuit (Fig. 7). In particular, the phase lag for the two intermediate frequencies (F_2 and F_3) increases as F_4 increases, although the values are somewhat less than for real pursuit, whereas the lowest-frequency component exhibits a consistent phase advance which increases as F_4 increases. An important aspect of the similarity in phase is that the phase advance at the lowest frequency (0.11 Hz) for the efficiency of VOR suppression arises as a direct consequence of the phase lag observed in the head-fixed target (HFT) condition at that frequency (Fig. 4). The same phase lag is also observed to a lesser extent in the sinusoidal responses, and has been observed previously for both sinusoidal and random stimuli (Hyden *et al.* 1982; Barnes, 1983; Larsby, Hyden & Odqvist, 1984), although McKinley & Peterson (1985) did not find such an effect.

Derivation of the efficiency of VOR suppression for the responses to a combination of two sinusoids shown in Fig. 1 (HFT condition) also revealed frequency-dependent characteristics similar to those observed during pursuit (Barnes *et al.* 1987). That is, as the frequency of the high-frequency component was increased from 0.39 Hz there was a steady reduction in the gain of the low-frequency component which reached an asymptotic level when the higher frequency was 1.25 Hz (cf. Fig. 4 of Barnes *et al.* 1987).

The characteristics of the gain and phase relationships for the efficiency of VOR suppression indicate that the non-linear frequency-dependent mechanisms associated previously with pursuit (Barnes *et al.* 1987) also function in a similar manner during VOR suppression by visual fixation. These non-linear frequency characteristics are closely associated with the mechanisms of prediction in pursuit. The model depicted in Fig. 6 indicates one way in which these non-linear characteristics may be represented. It is postulated that two feed-back mechanisms combine in an attempt to minimize retinal velocity error; (a) a direct low-gain retinal velocity error feed-back (pathway 2, Fig. 6) and (b) a predictive velocity estimation mechanism (pathway 3), that serves to enhance the gain provided by the direct velocity feed-back. In response to any motion stimulus in which all frequencies are less than 0.4 Hz, the predictive velocity estimation mechanism is able to enhance the gain of all frequency components so as to induce gains comparable to those evoked by discrete frequency sinusoids. In contrast, when the highest frequency rises above 0.4 Hz, the frequency characteristics of the velocity estimation mechanism change in such a way that the highest-frequency component of the stimulus is enhanced in relation to the lower frequencies. As a consequence, the response at low frequencies becomes more dependent on continuous retinal velocity error feed-back (pathway 2) and the gains of the low-frequency components fall to a common base level (Fig. 5).

The mechanism by which the change in frequency characteristics might be derived is unclear. Such behaviour may imply the existence of a set of frequency-tuned channels within the predictive velocity estimation pathway which individually sense

the various frequency components of the stimulus and modify the dynamic characteristics of the secondary pathway so as to limit low-frequency gain and accentuate the gain of the highest-frequency component. In order to achieve stability within the feed-back pathways it is possible that the input to the predictive velocity estimation mechanism is derived from the summation of signals representing head velocity (derived from the semicircular canals), eye velocity (derived from oculomotor efference) and the actual retinal velocity error (junction F, Fig 6) giving an internal signal representing target velocity in space. This concept is essentially identical to that of the efference copy model put forward previously by Yasui & Young (1975) and subsequently elaborated by others (Robinson, 1981; Miles & Lisberger, 1981). The details of the dynamic characteristics of the model shown in Fig. 6 will be presented in a future publication.

Changes in the VOR associated with imagined targets

In contrast to the effects observed with a head-fixed target, the changes in the VOR brought about by the instruction to imagine a head-fixed or earth-fixed target were virtually unaffected by the frequency composition of the stimulus. All subjects were able to increase or decrease the gain of the VOR in darkness with pseudo-random stimuli, although there was considerable intersubject variability in the degree of modification obtained. However, in all of the subjects the changes in gain with the frequency of the highest-frequency component of the stimulus were insignificant compared with those obtained when a real visual stimulus was used. This confirms the findings of McKinley & Peterson (1985), who used a broader frequency band of mixed-sinusoidal stimuli. The levels of suppression achieved in the imagined head-fixed target (IHFT) condition are, in general, rather less than those reported previously (Barr *et al.* 1976; Larsby *et al.* 1984; McKinley & Peterson, 1985), but this is almost certainly attributable to subject variability. The degree of suppression varied from 50% in one subject to as little as 10% in another. However, when the subjects were presented with the peripheral strobed targets (THFT condition) a much more consistent performance was evoked even in subjects who did not perform well in the IHFT condition, the gain being reduced to a level comparable to the best performance reported by other authors. It is difficult to know to what extent the response evoked by the minimal visual stimulus used in the THFT condition can be equated with the response to a truly imagined target in darkness. Nevertheless the phases in the THFT condition clearly lie on a continuum between those recorded in the IHFT and HFT conditions. An understanding of the way in which this non-linear but consistent pattern of phase changes is brought about will almost certainly provide vital information about the mechanisms of pursuit and VOR suppression.

Although the frequency composition of the stimulus had little effect on the gains in the IHFT and IEFT conditions, the gains for both conditions were frequency dependent, tending towards the gain for the DRK condition at any frequency above 1 Hz. In other words, the modifying element during voluntary, non-visual changes exhibited the characteristics of a low-pass filter, as previously demonstrated by Barr *et al.* (1976), whereas that found during visual suppression was more akin to a rather specialized high-pass filter. Thus it would appear that visual and non-visual

suppression of the vestibulo-ocular reflex are accomplished by completely different neural mechanisms.

The mechanism of voluntary, non-visual, VOR suppression

Some confusion has arisen about whether the pursuit reflex is responsible for VOR suppression since the original observation by Barr *et al.* (1976) that the VOR could be modified by non-visual means. It was argued by Barr *et al.* that this modification could not represent the activity of a subset of the pursuit mechanism because there was no parallel ability within the pursuit system to generate smooth eye movements in the absence of a visual stimulus. But there is an important difference in the experimental conditions of voluntary VOR suppression and attempted non-visual pursuit. In the former, the subject has at least some stimulus, namely the vestibular outflow, on which to operate continuously, whereas during attempted pursuit in darkness there is no input stimulus whatsoever. What, then, is the mechanism involved when the subject imagines the presence of a head-fixed target and achieves a limited suppression of the VOR? In this condition the subject is well aware of head-centre and aims to maintain his eye position in this direction. One way in which this might be achieved is by the negative feed-back of the efference copy of eye velocity to inhibit the vestibular drive, as shown in the model (pathway 4 in Fig. 6). This would serve to minimize the unwanted eye velocity. The ratio between eye velocity ($\dot{\theta}_{\text{IHFT}}$) and head velocity ($\dot{\phi}$) would be given by the equation:

$$\frac{\dot{\theta}_{\text{IHFT}}}{\dot{\phi}} = \frac{-G_v G_E(s)}{1 + K_E G_E(s)}, \tag{2}$$

where K_E represents the gain of efferent feed-back, and $G_E(s)$ represents the oculomotor drive dynamics. G_E may be approximately represented by a function of the form: $G_E(s) = (1 + T_E s)^{-1}$, where s = Laplace operator and $T_E = 0.2$ s. The relationship between eye velocity in the IHFT condition and that in the dark ($\dot{\theta}_{\text{DRK}} = -G_v G_E$) may thus be represented by the equation:

$$\frac{\dot{\theta}_{\text{IHFT}}}{\dot{\theta}_{\text{DRK}}} = \frac{1}{(1 + K_E)} \frac{1 + T_E s}{1 + T'_E s}, \tag{3}$$

where $T'_E = T_E / (1 + K_E)$.

On the basis of eqn (3), it would be expected that the ratio of $\dot{\theta}_{\text{IHFT}}$ to $\dot{\theta}_{\text{DRK}}$ at low frequencies would be dependent on K_E but at frequencies beyond 1 Hz the ratio would be close to unity. In other words there would be little suppression by voluntary effort beyond 1 Hz, which is in accord with the results shown in Figs 1, 2 and 3. The suppression mechanism thus exhibits the characteristic of a low-pass filter, as noted by previous authors. However, McKinley & Peterson (1985) discounted the concept of filtering on the basis that the observed changes in gain were not compatible with the lack of change in phase in their results. But our results do show phase changes which are reasonably compatible with the changes in gain. The relationship expressed by eqn (3) would lead to an increasing phase advance over a limited frequency range up to 1 Hz as found experimentally (Fig. 5). Moreover, the phase advance would be greater for higher values of K_E which would also increase the degree of suppression. Thus, the greater suppression ratio ($\dot{\theta}_{\text{IHFT}}/\dot{\theta}_{\text{DRK}} = 0.5$)

encountered in the THFT condition would give rise to a greater peak phase advance than that found in the IHFT condition, for which the suppression ratio was only 0.75 (Fig. 5).

The mechanism of gain enhancement in the IEFT condition

When the subject is instructed to imagine an earth-fixed target during rotation in the dark, the perceptual concept used is similar to that when imagining a head-fixed target, except that the objective is to maintain eye position in a specific direction in space. To achieve this the subject effectively attempts to use his best estimate of head position to drive the eyes in a manner which compensates for the imposed motion. In the absence of other sensory cues, information concerning orientation must be derived from the semicircular canals. Experiments by Guedry, Stockwell, Norman & Owens (1971) have established that such sensory information is available to the subject, since reasonably accurate estimates of rotational displacement can be made in darkness, at least for small (< 50 deg) displacements. This implies that the gain of the vestibular sensory system subserving the perception of whole-body rotation is close to unity even though the vestibulo-ocular gain is rarely greater than 0.6 at low frequencies. In order to provide a good estimate of head velocity ($\dot{\phi}'$ in the model of Fig. 6) the output of the vestibular sensory pathway must be calibrated, (i.e. G_H in Fig. 6 must tend towards unity). Such a function is presumably carried out on the basis of sensory information derived from the co-ordination of voluntary head and eye movements in every-day life.

There are a number of ways in which this central percept of head velocity might be used to generate the appropriate eye movements. It is possible that the system simply switches over to being driven by the higher-gain perceptual signal. Another possibility, suggested previously by a number of authors (Yasui & Young, 1975; Barr *et al.* 1976; Miles & Lisberger, 1981), is that the head velocity estimate is combined with an efference copy of eye velocity (as indicated at junction B in Fig. 6), to give a central estimate of gaze velocity. The objective in the imagined earth-fixed target (IEFT) condition would then be to minimize gaze velocity error and this could be achieved either by a direct high-gain inhibitory influence at junction B in the model or by a short-term parametric increase in the gain G_V of the vestibulo-ocular pathway as proposed for long-term adaptation by Miles & Lisberger (1981). If an inhibitory mechanism of the type shown in Fig. 6 were postulated, the relationship between eye velocity ($\dot{\theta}_{IEFT}$) and head velocity ($\dot{\phi}$) would be given by the equation:

$$\frac{\dot{\theta}_{IEFT}}{\dot{\phi}} = - \frac{G_V + K_G G_H}{1 + K_G} \frac{1}{(1 + T_E'' s)}, \quad (4)$$

where $T_E'' = T_E (1 + K_G)^{-1}$ and K_G represents the gain of the inhibitory feed-back.

If K_G is large ($\gg 1$) and $G_H = 1$ then this ratio could easily be brought close to unity up to quite high frequencies

$$\text{(e.g. } \frac{\dot{\theta}_{IEFT}}{\dot{\phi}} = 0.93 \text{ if } G_V = 0.6 \text{ and } K_G = 5).$$

The ability to achieve near-unity gain in the IEFT condition would thus be dependent on the efficacy of the inhibitory feed-back gain (K_G) and the accuracy of the perceptual calibration (i.e. the value of G_H).

Conclusions

The results of the experiments described here demonstrate that during visual suppression of the vestibulo-ocular reflex a non-linear pattern of changes in gain and phase may be observed which is very similar to that obtained during ocular pursuit. This further strengthens the argument that these two oculomotor control functions are subserved by the same neurological mechanisms, as indicated in a number of previous publications (Barnes *et al.* 1978; Lau *et al.* 1978; Barnes *et al.* 1985; Paige, 1983; Waespe, Büttner & Henn, 1981). Suppression of the VOR by non-visual means shows little evidence of the influence of the non-linear predictive mechanisms and probably represents the activity of a completely separate mechanism similar to that represented by pathway 4 in the model of Fig. 6. Such a mechanism would not participate during normal active pursuit. Whether this non-visual suppression mechanism operates in addition to visual feed-back during visual suppression of the VOR is uncertain. If the frequency characteristics for the efficiency of VOR suppression shown in Fig. 7 had been derived with respect to the gains and phases obtained in the imagined head-fixed target (IHFT) condition rather than those obtained in darkness (DRK condition), the same ordinal changes in gain and phase would have been observed. However, mean gain for the three low-frequency components would have been reduced from 0.91 to 0.88 when the frequency (F_4) of the highest-frequency component was 0.39 Hz and from 0.64 to 0.50 when F_4 was 2.08 Hz. This larger spread in gains is more compatible with that observed for pursuit (Fig. 7A) and indicates that the hypothesis that visual and non-visual mechanisms act synergistically cannot be ruled out. Ideally, a direct comparison between pursuit and VOR suppression in the same group of subjects is required in order to confirm this hypothesis.

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