

# QUALITY OF RETINAL IMAGE STABILIZATION DURING SMALL NATURAL AND ARTIFICIAL BODY ROTATIONS IN MAN<sup>1</sup>

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**Abstract**—Two-dimensional head rotations recorded from 2 subjects sitting still, without artificial head support, showed appreciable movement over the frequency range d.c. to 7 Hz. Capacity of vestibulo-ocular reflex and visually guided eye movements to null motion over this dynamic range was examined by simultaneously recording 2-dimensional head and eye rotations while sinusoidally rotating subjects over the frequency range 0.1 to 15 Hz using small amplitudes. At best, oculomotor compensation removed about 90% of head motion from eye motion in space. Representative compensation was poorer. Compensation for natural motions of unsupported heads while sitting and standing was also incomplete resulting in substantially more eye motion in space than was observed with head supported.

These observations, coupled with recent demonstrations of plasticity of the vestibulo-ocular reflex, led us to suggest that the degree of compensatory oculomotor response is actively adjusted downwards so as to guarantee sufficient retinal image motion to prevent perceptual fading when the body is relatively stationary and is actively adjusted upwards, so as to guarantee sufficient retinal stability to prevent perceptual blurring when the body moves actively. Seen this way, the goal of oculomotor compensation is not retinal image stabilization, but rather controlled retinal image motion adjusted so as to be optimal for visual processing over the full range of natural motions of the body.

Most investigators of visual, oculomotor and vestibular function simplify their work by immobilizing their subjects' heads by bolting them to rigid, earth-fixed frameworks. Immobilization provides stable initial conditions for controlling visual or vestibular stimuli and for quantifying the precision of eye movements in response to these stimuli. However, widespread use of immobilization means that very little is known about stability of eye position with respect to fixed-earth references when subjects' bodies are free to move in normal ways. During normal rotary movement eye position is stabilized with respect to fixed-earth primarily by the vestibulo-ocular reflex (VOR). VOR is a reflex in which neural analogues of head angular velocity, derived from stimulation of the semicircular canals, are used to drive eye muscles to cause eye rotation at the angular velocity of the head but in the opposite direction. Retinal inputs to optokinetic and smooth pursuit eye movement subsystems are also known to assist in generating compensatory movements (Baarsma and Collewijn, 1974). Proprioceptive signals from neck muscle have also been implicated in compensatory eye movement (Meiry, 1971; Morasso *et al.*, 1973). In the vast literature documenting performance of these compensatory systems and their neural substrates we know only a few studies which have examined how this system is actually used during natural bodily movement (*viz.* see Hughes,

1971; Gresty, 1974; Collewijn, 1977). In these cases relatively insensitive recording techniques were used and, therefore, fine grain features of compensatory eye movements ( $<0.25^\circ$  arc) are not known. Experiments reported here begin to fill that gap.

We began by modifying a magnetic-field search-coil apparatus to record small natural 2-dimensional rotations of the human head and eye unconfounded with translations of the head. The heads of subjects, attempting to sit or stand as still as possible in this apparatus, were found to wiggle over the frequency range d.c. to 7 Hz. Next we examined oculomotor compensatory capacity by means of tiny artificial rotations and found that over the frequency range of natural head movement, VOR compensated for only 30–75% of head movement. Visible targets improved compensation only modestly at lower frequencies and not at all above 3 Hz. Consequently, it was not surprising that VOR, in combination with visually guided eye movements, failed to completely compensate for natural head rotations composed of combinations of frequencies from d.c. to 7 Hz. This means that images of objects viewed without artificial support of the head undergo much more retinal motion than was previously suspected.

## GENERAL METHODS

Horizontal and vertical rotations of human head and right eye were simultaneously recorded using the magnetic-field search-coil technique. Robinson (1963) described this system in detail and only the basic features and our modifications of the technique to reduce its sensitivity to translations will be summarized here. Rotations were recorded by means of potentials induced in search-coils attached to the subject's head and eye when the subject was placed

<sup>1</sup>The main features of this research were reported at the *Ninth Annual Symposium of the Center for Visual Science*, University of Rochester in May, 1975 and at the *I.E.E.E. Symposium for Cybernetics and Society*, San Francisco, 1975. Address reprint requests to A. A. Skavenski.

in two alternating magnetic fields held in temporal and spatial quadrature. Natural head and eye rotations were recorded in fields generated by passing 5.5 kHz alternating currents through pairs of square-shaped Helmholtz coils measuring about 2 m on a side. These field generating coils were roughly three times the size of those described by Robinson (1963): a design modification that improves the homogeneity of the magnetic field at its center by about 1 order of magnitude. Empirically, the 2 m fields produced translation artifacts equivalent to rotations of 1.0° arc or less for each 1.0 cm translation of the search-coil in any direction in the region of maximum field homogeneity. All of head and eye movement records obtained with the unrestrained head were made within a fixed-earth framework placed around the subject's head to prevent translations in excess of  $\pm 1.0$  cm from a rest position at the center of the region of maximum field homogeneity. During experiments subjects never allowed their heads to touch this framework. This means that natural head movements of the subjects did not contain translational components exceeding  $\pm 1$  cm. This also means that readers can be confident that our report of rotational components of head and eye motion are not contaminated by translation artifacts exceeding  $\pm 1.0^\circ$  arc.

Electric potential analogues of horizontal and vertical rotations were obtained by phase-sensitive demodulation of sinusoidal potential induced in the search-coils. Demodulation was done with two lock-in amplifiers (Princeton Applied Research, Model 129) that were adjusted to equal sensitivity and bandwidth matched to 160 Hz. All data were recorded on magnetic tape (bandwidth 2.5 kHz.) and were retrieved either on photographic paper by an ultraviolet-light mirror galvanometer recorder (bandwidth 1.0 kHz) for hand measurement or fed into the A-D converter of a PDP-8 computer for machine digitization. Both techniques permitted final resolution of eye and head position with a sensitivity of better than 1' arc and overall bandwidth of 160 Hz.

The search-coil for recording eye rotations was imbedded in a tight-fitting scleral contact lens held on the subjects' right eye by 20–40 mm Hg suction. Left eyes were closed and covered. Head rotations were recorded from a search-coil bolted to a tight-fitting dental-impression bite-board for all experiments in which the head was free of artificial support. In experiment 2, it was necessary to use a bite-board to fix the subject's head to the framework supporting the magnetic-field generating coils. Consequently, head position was recorded by holding a search-coil in the magnetic-field by means of a rigid, earth-fixed strut. Changes in potential induced in this search-coil were proportional to head position relative to fixed earth because orientation of the field was held constant relative to the subject's head. Objective calibration of head and eye search-coils was accomplished by clamping both to the same fixed-earth fixture which was rotated through known angles with respect to the fields.

Quantitative details of compensatory responses are reported for two of the authors, AS and RS. In addition, the main findings were confirmed qualitatively by examining records produced by a third author, BW. All were highly experienced in wearing scleral contact lenses and having their eye movements recorded. Detail vision was good with the lens in place. Consequently, subjects were free of distracting influences and could attend closely to the instructions to produce optimal performance.

## EXPERIMENTS

1. *There were appreciable head rotations spanning the frequency range d.c. to 7 Hz when subjects attempted to sit as still as possible*

Understanding natural image stabilization required

first describing the natural dynamic range of head movement with which the oculomotor system must contend. Two-dimensional head rotations were recorded while subjects were instructed to sit as still as possible. This instruction was adopted to study conditions under which the head should be most stable. In all, about 10 recordings of 40 sec duration each were made in each of 7 sessions that were separated from 1 day to 8 months in time. Each 40 sec head recording was made while the subject maintained fixation of a small disc of tungsten white light (10 ml) placed at optical infinity in an otherwise totally dark visual environment. Subjects were permitted to move about and relax between recordings but were required to sit as still as possible while recordings were made.

The head was not a completely stable platform as can be seen in the representative 25 sec segments of head movement records reproduced in Fig. 1 where prominent features include a persistent 3–5 Hz oscillation whose peak to peak amplitude was about 6' arc, low frequency oscillations with peak-to-peak amplitude as large as 0.25° arc, and d.c. shifts of head position larger than 0.5° arc in the 25 sec interval shown.

A quantitative description of head motion was made. Frequency components were determined from power spectra obtained by averaging 10 spectrograms for each subject on the horizontal and vertical meridians. Each spectrogram was based on a 40 sec record and was computed by an analogue spectrum analyzer (Ubiquitous Model UA-55) that is not subject to the pitfalls of digital computation techniques (Bergland, 1969). Power spectra for both subjects indicated measurable head oscillations over the frequency range d.c. to 7 Hz with the largest amplitudes occurring

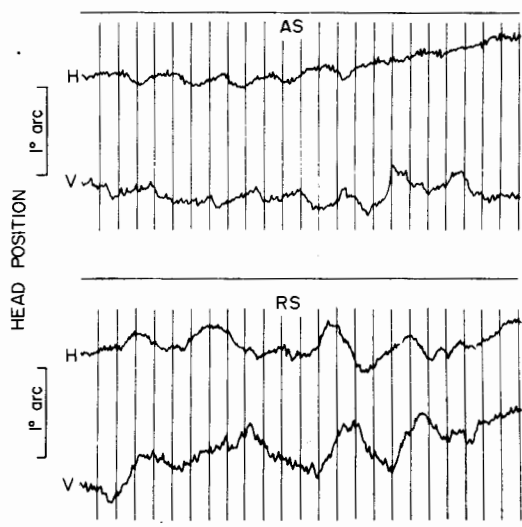


Fig. 1. Representative recordings of horizontal (H) and vertical (V) head rotations of subjects AS and RS when they maintained Head Position as still as possible while sitting without artificial support for their heads. Time began on the right and repetitive vertical stripes indicate 1 sec intervals. The length of the vertical bars on the left corresponds to a 1 arc rotation on either meridian. Upwards trace movements correspond to right in (H) and up in (V).

below 2 Hz. Above 2 Hz there were three sharp peaks indicating substantial head oscillations around 3.5, 5 and 6.5 Hz.

The extent of head motion was obtained from simultaneous measures of horizontal and vertical head position made every 50 msec for each 40 sec head record. Standard deviations of horizontal and vertical head position were computed (based on a total of 800 samples each) and used to calculate bivariate contour ellipse area of head position for each subject on each trial. Bivariate contour ellipse area is a convenient index of stability of a 2-dimensional parameter. It is analogous to the standard deviation of a 1-dimensional parameter (see Nachmias, 1959; Steinman, 1965 for descriptions and use of this measure). Mean bivariate contour ellipse area for 10 trials was 356' arc<sup>2</sup> for AS and 443' arc<sup>2</sup> for RS. This means that 68% of the head position measures would be within a circular area about 22' arc in diameter centered around mean head position, assuming that the horizontal and vertical S.D. were equal and there was no correlation between the horizontal and vertical measures. This scatter combined with frequency components known to be present in the head movements from the prior analysis suggested that head velocity was fairly high. To confirm this, instantaneous absolute head speed was approximated by computing distance moved by the head between successive 50 msec samples of horizontal and vertical head position. Mean head speed, based on 8000 samples, was 29.1' arc/sec (S.D. = 17) for AS and 33.3' arc/sec (S.D. = 20) for RS.

All of these measures indicate that both subjects followed instructions, that is, they were good at maintaining head position. However, it must not go unnoticed that the head wobbles over a range of  $\pm 1.0^\circ$  arc on both meridians at a speed of 0.5' arc/sec. The free head is not a *stable* platform. These measures of head movement are about three times larger than comparable measures of stability of the fixating eye when the head is supported by a rigid earth-fixed bite-board. Consequently, when subjects are free of artificial support for their heads, it is clear that the oculomotor system must compensate for a fair amount of head motion if retinal images are to be as stable as they are when head motion is eliminated by a bite-board. Thus, the question arises: how much does the oculomotor system compensate for movement over the dynamic range of natural head movement?

## 2. The oculomotor system incompletely compensated for imposed sinusoidal rotations of the head spanning the dynamic range of natural head movement

Studies of ocular compensation during forced sinusoidal head rotation in man have employed large angular rotations and consequently high peak acceleration over the frequency range below 5 Hz (Benson, 1970; Meiry, 1971 and Niven and Hixon, 1961). The behavior of human compensatory machinery during small oscillations of the kind seen in the head records had not been examined before which made it necessary to make such measurements. We suspected that compensation would not be complete because Baarsma and Collewyn (1974) reported that the gain (amplitude of compensatory eye movement/amplitude head movement) of VOR in rabbit varies directly with

head acceleration: i.e. the effectiveness with which VOR generated a compensatory eye movement deteriorated as the rabbit's head was moved less violently. Furthermore, Winterson, Collewyn and Steinman (1979) recently reported that gain of rabbit VOR was predictable from the large rotation result and was indeed low. Comparable non-linearities of gain in human VOR would mean that the system would have difficulty compensating small oscillations. To find out how well the compensatory machinery worked, AS, BW, and RS were sinusoidally rotated in the horizontal plane (around subject's YAW axis) using frequencies and amplitudes chosen on the basis of head movement records.

Two procedures were used. First, rotation of the subjects' whole body over the frequency range below 3 Hz was accomplished by mounting the magnetic-field generating system and the subjects' chair on a vertical pivot. Field generating coils for this apparatus were circular (dia. = 2 ft) and field density was adjusted to yield the same sensitivity to eye rotations described under general methods above. Rotational artifacts caused by head translations were minimized by fixing the subject's head to the rotating apparatus by a bite-board. Sinusoidal rotation was obtained by coupling the framework supporting the subject to a stationary fixture with stiff springs. This formed a tuned mass-compliance system which oscillated at a natural frequency that was selected by choosing the appropriate equivalent spring stiffness. Friction of bearings supporting the rotating apparatus caused oscillations to damp out, making it possible to obtain VOR responses to amplitudes varying from about 2 arc to less than 5 arc close together in time. Position of the subject's head relative to fixed-earth was determined by a search-coil attached to a stationary fixture. Eye position relative to the head was recorded by the contact-lens search coil.

Above 3 Hz, the mass of the rotating system required springs exceeding the structural strength of the system. Therefore, to study compensation above 3 Hz, the subjects' head was freed of support and was oscillated by means of a tightly fitted motorcycle helmet which was driven by a vibrating loudspeaker. Mass of the loudspeaker cone was substantially increased by gluing several large nuts and bolts to it. This speaker was driven by the amplified output of a signal generator set to the desired frequency of oscillation. Reactive forces resulting from driving the speaker cone were transmitted to the subject's skull via the mechanically coupled speaker frame and helmet. In this experiment, the field generating coils were the large 2 m squares to minimize translation artifacts and they were held rigidly in the fixed-earth framework. Head position relative to fixed-earth was recorded by a search-coil attached to the tight fitting bite-board. Eye position was recorded as before but, since the subject's head was free to move, the frame of reference was fixed-earth not the subject's head.

Performance of the compensatory machinery was examined both in total darkness to observe compensation by VOR alone and also with a small fixation target to observe compensation by VOR assisted by visually guided eye movements. A 2 log unit frequency range was studied (0.1–15 Hz).

Compensation varied from nearly perfect to very

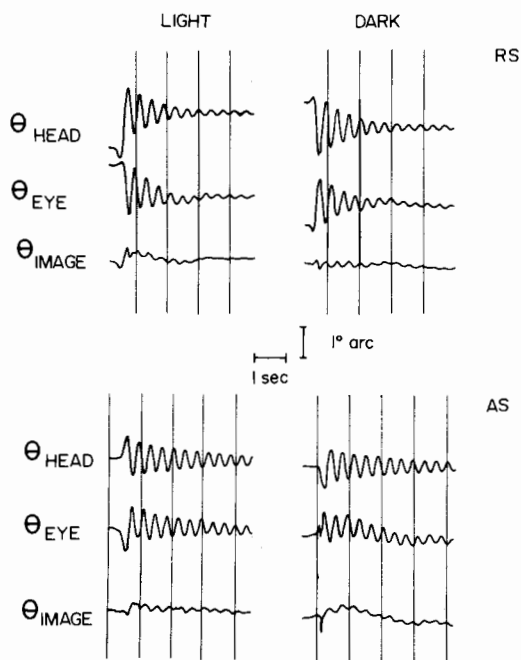


Fig. 2. Recordings representing the best oculomotor compensation for artificial head rotations of subjects AS and RS at a frequency of 2.6 Hz with room lights on (light) and total darkness (dark). In each record traces indicate horizontal rotations of the subject's head in space ( $\theta$  Head), eye in head ( $\theta$  Eye), and eye in space ( $\theta$  Image).  $\theta$  Image corresponds to the retinal image motion of stationary objects in the visual surround and was obtained by adding  $\theta$  Head and  $\theta$  Eye on an analog computer. Upward trace movement corresponds to rightwards rotation of all components. Other features are the same as Fig. 1.

poor. Recordings representing the best performance of the compensatory machinery are reproduced in Fig. 2. When a target was visible, VOR in combination with visually guided eye movements produced eye rotations whose peak to peak amplitude compensated for about 85% of corresponding head rotations, i.e. gain (amplitude of the eye rotation divided by amplitude of head rotation) was about 0.85 and eye and head rotations were nearly  $180^\circ$  out of phase. Neither gain nor phase changed much with decreasing amplitudes of head oscillations as can be seen in these records. In total darkness, gain of compensation now due exclusively to VOR dropped to about 0.65 across amplitudes and phase of eye in head and head in space remained about  $180^\circ$ . So, in the best records, in the light and in the dark, there was effective compensation at 2.6 Hz for amplitudes of rotations which spanned the range found in natural head movement. Oscillations in this range had peak head acceleration ranging from  $294$  to  $16^\circ \text{ arc/sec}^2$ .

However, the good compensation shown in Fig. 2 was more of an exception than the rule. Throughout the present series of experiments good VOR compensation in the dark proved to be erratic despite the fact that all subjects were both highly experienced and attempting to produce their best possible performance. Instructions to attempt to fixate details on

unseen but imagined earth-fixed surroundings that have been reported to enhance VOR gain (Barr *et al.*, 1976; Gauthier and Robinson, 1975) did not increase the probability of obtaining high gain on a particular trial. We decided therefore to describe the best possible performance of the compensatory machinery and all quantitative treatment of our results will be based on the best records obtained where the amplitudes of forced-head rotations fell in the range of natural head motions. This means that our estimates of the dispersion and speed of the eye in space during compensatory eye movement represent the limits of the compensatory capacity of our subjects in the range of natural head rotations. Their average performance would be a good deal poorer.

Given this caveat we now proceed to a quantitative summary of our results. Mean gain was calculated by dividing the amplitude of eye movement by the amplitude of head movement for at least 10 half cycles selected in pairs from one complete cycle. Cycles containing saccades or quick phases were not measured. Phase was determined from the difference between the times the eye and the head changed direction on the same half cycle. The measures of gain and phase were always made in pairs of one complete cycle to eliminate bias that would have been introduced by systematic drifts, particularly those known to occur in total darkness (Skavenski and Steinman, 1970). Forced head rotations had amplitudes ranging from  $0.05$ – $2.5^\circ \text{ arc}$ ; consequently, peak head acceleration spanned the range  $0.5$ – $1500^\circ \text{ arc/sec}^2$ .

Mean gain and phase plotted as a function of frequency in Fig. 3 show that the compensatory oculomotor machinery worked imperfectly when required to compensate for artificial rotations like those encountered in natural head movement. Mean gain for both AS and RS, in the dark, fell in the range  $0.25$ – $0.75$  over the entire frequency range. Below 3 Hz gain was higher in the light than in the dark, indicating that the contribution from visually guided eye movements helped compensation, but this advantage, as expected, disappeared at higher frequencies. Figure 3 also shows that mean phase shifts were within one standard deviation of a  $180^\circ$  compensatory relation between eye and head movements for all frequencies below about 8 Hz. Above this frequency the eye lagged the head by  $180^\circ$  plus an amount proportional to a mean pure delay of 5 msec for RS and 9 msec for AS.

Further analysis showed that the gain of VOR was largely independent of head angular acceleration. Least-squares fits of the equation:

$$\ln G = K \ln a_{\max} + C$$

(where  $G$  is gain of VOR and  $a_{\max}$  is peak head acceleration) produced slopes ( $K$ ) of  $-0.03$  for AS and  $0.04$  for RS. These slopes are indistinguishable from zero. A similar failure of gain to depend on frequency for small rotations was reported for rabbit by Winter-son *et al.* (1979). Note, however, our result rests on the selection of the best responses and we cannot be certain we would obtain the same result had average compensatory responses been analyzed.

We conclude that the compensatory machinery, using both visual and vestibular inputs, has the capacity to remove up to 95% of head rotation from eye

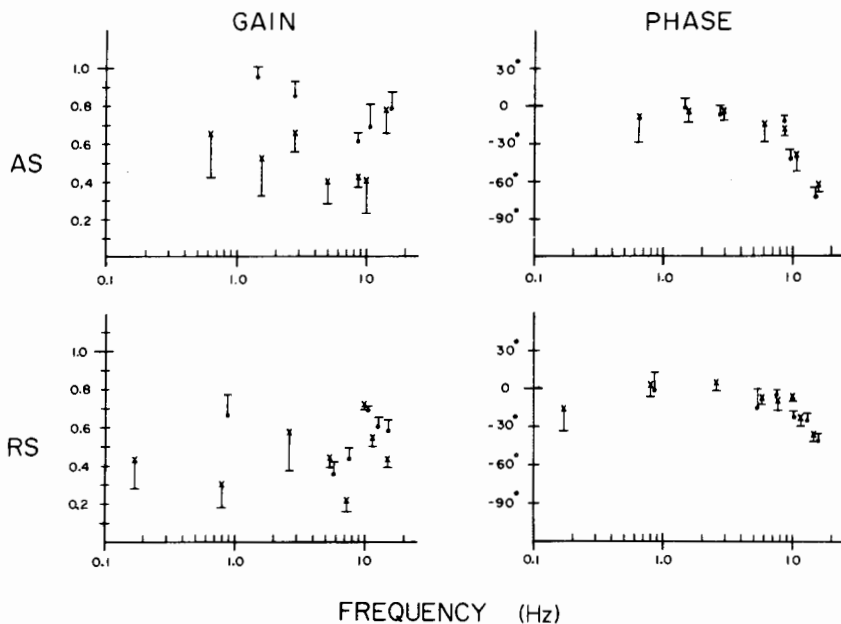


Fig. 3. Mean gain and phase of the best oculomotor compensatory responses of subjects AS and RS when their heads were rotated sinusoidally in the horizontal meridian over the frequency range 0.1–15 Hz. Compensation with room lights on was plotted with solid circles (●) and in total darkness with Xs (x). Each data point is the mean of at least 10 measurements and error bars show one standard deviation to one side of the mean. Negative values of phase indicate that change in eye position lagged behind change in head position. See text for additional details of method of computing mean gain and phase.

motion in space during forced rotation frequencies and amplitudes encountered in natural head movement. However, this capacity was not used consistently and it became of considerable interest to find out how this machinery was actually used in natural free-headed viewing.

### 3. Eye movements compensated for natural head movements as well as they did for artificial rotations

Stability of eye position in space was examined during natural head rotations that occurred during two normal postures. First, subjects attempted to fixate a target placed at optical infinity while sitting as still as possible to approximate one of the most stable postures attainable under normal viewing conditions. Then, to increase head motion while keeping head translation artifacts within  $\pm 1'$  arc (translations  $< \pm 1.0$  cm), subjects fixated a target placed at optical infinity while standing as still as possible. In both conditions, head position relative to fixed-earth was recorded by means of a coil mounted on the bite-board. Eye position was recorded relative to fixed-earth by a coil mounted on the contact-lens. All conditions were the same as those employed during measurements of 2-dimensional rotations of the free head. Recordings of horizontal and vertical eye rotations were also made on this same apparatus while subjects fixated targets when they were sitting with their heads rigidly held in the fixed earth framework by a bite-board. These recordings were made to compare the effectiveness of the compensatory machinery in dealing with natural head rotations with

the stability of oculomotor control when such compensation was not needed.

Fixation records for the sitting posture, both with the head supported by a bite-board and when the head was free of artificial support were obtained in alternating blocks of 5 trials for each condition. Trial length was 40 sec. Eye movement records of the standing subject were obtained in separate sessions to allow elevation of the recording system to accommodate the standing posture. In all conditions, subjects were instructed to keep body position as stable as possible while maintaining accurate fixation of the target.

Under these conditions, the compensatory machinery worked as well in removing natural head motion from eye motion in space as it did for forced sinusoidal oscillations. This can be seen in the representative 2-dimensional eye and head movement records reproduced in Fig. 4 and 5. Freeing the head of seated subjects produced a modest amount of head motion which resulted in only a small increase of eye motion in space relative to eye motion seen when the head was supported on a bite-board. Standing still resulted in substantially more head motion and eye motion increased because the compensatory system operated imperfectly.

How good was the compensation? We described it quantitatively by making simultaneous measures of horizontal and vertical eye and head position every 50 msec throughout each 40 sec record. Dispersion (bivariate contour ellipse area) and speed of eye and head motion were then computed for each trial and each subject as in experiment 1.

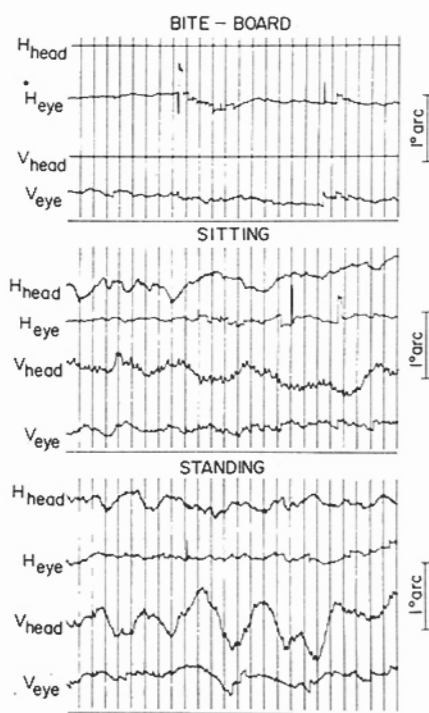
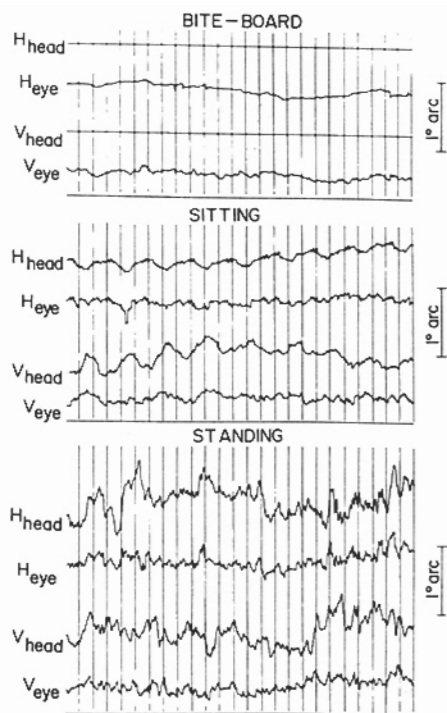


Fig. 4. Representative simultaneous recordings of horizontal (H) and vertical (V) head and eye rotations of subject AS when his head was supported by a bite-board and when sitting and standing as still as possible without artificial support. Other features of these recordings are the same as Fig. 1.

Fig. 5. Representative simultaneous recordings of horizontal (H) and vertical (V) head and eye rotations of subject RS when his head was supported by a bite-board and when sitting and standing as still as possible without artificial support. Other features of these recordings are the same as Fig. 1.

Table 1 shows that when subjects attempted to sit as still as possible without artificial supports there was only a modest increase in the dispersion of the line of sight ( $\sim 41\%$  for AS and  $3\%$  for RS) as compared with dispersion observed when their heads were supported on bite-boards. However, when subjects stood as still as possible there was a marked increase in head dispersion with a corresponding increase in dispersion of the line of sight. The story with respect to the speed of eye motion is essentially the same

except that freeing the heads of seated subjects produced a large increase in eye motion because head speed increased to about  $0.5^\circ$  arc/sec for both subjects. Standing nearly doubled the head speed of AS ( $29$  to  $58^\circ$  arc/sec) but only increased RS's head speed by  $6^\circ$  arc/sec. Note, however, in all cases eye motion was faster, by about  $30\%$  of head motion, when the head was freed of artificial support. These results show that the compensatory systems operate much the same way in natural situations (sitting or stand-

Table 1. Two measures of mean inverse fixation stability (dispersion and speed) for subjects AS and RS when their heads were supported by a bite-board or when sitting and standing as still as possible without any artificial support

	N	Dispersion Mean bivariate contour ellipse area (min arc) <sup>2</sup>		Speed (min arc/sec)	
		Head	Eye	Head	Eye
AS					
Bite-board	10	$\sim 0$	51 (16)	$\sim 0$	14.7 (10)
Sitting	10	356 (131)	72 (9)	29.1 (17)	25.7 (16)
Standing	10	1663 (684)	183 (29)	58 (39)	38.2 (23)
RS					
Bite-board	10	$\sim 0$	164 (11)	$\sim 0$	13.4 (8)
Sitting	10	443 (309)	169 (61)	33.3 (20)	20.8 (13)
Standing	5	1400 (900)	342 (183)	39.7 (24)	21.7 (12)

S.D. for each mean are given in parentheses. Each mean is based on the number  $N$  of 40 sec trials shown.

ing) as they do for experimentally induced oscillations. This means that compensation in the natural situation, even when motion is kept as modest as possible, is not perfect and the eye moves rapidly through a larger region than it does when the head is kept rigidly in place.

#### DISCUSSION

We found that there were appreciable head rotations over the frequency range d.c. to 7 Hz even when an effort was made to sit or stand as still as possible. Such head rotations could be large. For example, when standing, the head oscillated through angles as large as 0.75° arc most of the time. Such head motions might require oculomotor compensation if the world is to appear clear and stable. This finding encouraged us first to study the effectiveness of the compensatory machinery using experimentally induced rotations in this frequency/amplitude range. We found that compensatory mechanisms (visual and vestibular) operated nearly as well in this region, which included very small amplitudes, as they operate for much larger rotations—the only movement examined in prior research in primates. We then examined operation of the compensatory mechanisms in natural situations when subjects sat or stood as still as possible. We found close agreement between our experimental and naturalistic observations, that is, the quality of compensation in the natural situation was what would be expected from the compensatory responses to artificial rotations.

Our findings have both oculomotor and visual implications. Before discussing the broader implications we will compare our findings with prior reports. First, consider the relative effectiveness of the compensatory mechanisms in the artificial situation. We found that on the average only about 50% of head rotation was compensated in the dark (VOR). This value is lower than prior reports and remember, in our case, the average was based on the sample of trials which showed the best compensation. In this condition we saw only 9 instances in 65 best full cycles measured for both subjects where the gain of VOR exceeded 0.70. Much higher gains have been reported. For example, Barr *et al.* (1976) reported gains of about 0.6 when subjects performed mental arithmetic and "gains of nearly 1.0" when subjects imagined stationary points fixed on walls in the room. We tried these and a host of other instructions but were unable to obtain better performance. There are a number of plausible explanations for the differences in gain between ours and prior reports. The least interesting is perhaps that we are poorer at visual imagery than other subjects or did not try as hard. Such considerations are difficult to confirm objectively. We can only assure the reader that we did try hard. A more interesting possibility is that gain for small amplitude rotations is not as high as it is for large rotations even when the optimal instruction is used. Barr *et al.* (1976) rotated subjects sinusoidally through amplitudes as large as 40° arc while we had a maximum excursion of only 2° arc. To explore this possibility AS was rotated at 2.5 Hz through amplitudes greater than 3° arc. We found that his gain was 0.80 in the dark as compared to 0.67 when amplitude was less

than 0.25 arc. In both experiments the instruction to look at an imaginary stationary point on the wall was employed. Gain with large amplitude rotation was very close to that reported for rhesus monkey under similar conditions (Skavenski and Robinson, 1973) and is in line with gains reported by Barr *et al.* (1976) and Gauthier and Robinson, (1975). When we repeated the large rotations in the light, average best gain was 0.95 at 2.5 Hz as compared to a gain of 0.80 when amplitude of rotation was small.

These results suggest that the quality of the compensation (gain) is related to the amplitude of head rotation in man as it is in rabbit (Winterson *et al.*, 1979). So in the case of both rabbit and man, situations which result in low amplitude head rotation will produce low gain compensation which guarantees that motions of the eye in space, and therefore retinal images, will be a relatively large proportion of body movement. This effectively insures that retinal images will never be stationary.

Of course when the animal begins to move more vigorously, gain of the compensatory machinery must rise if image movement is not to become excessive. AS's gain at 2.5 Hz in the light rose from 0.80 for small oscillations to as high as 0.95 as rotation amplitude increased which means that a very large proportion of retinal image motion would be removed by his compensatory mechanisms during large rotations. For example, at this frequency root mean square retinal image speed for head movement whose amplitudes do not exceed 0.25 arc was found to be about 25° arc/sec and only rose to about 100° arc/sec (a factor of 4) when body rotation increased by a factor of 12. This degree of retinal image slip was tolerable to vision because the fixation stimulus in both conditions was seen clearly although it was perceived as moving when body motion was large as well as fast.

Considerations such as these lead us to suggest that the gain of the compensatory machinery is tuned to guarantee that the retinal image will always move at some appreciable speed which would not be the case if the gain of compensation approached 1.0 when the amplitude of body rotation was small. Note that retinal image speed when the head is supported artificially averages 14° arc/sec and also note that subjects whose heads are supported on bite-boards occasionally report periods of target fading which means that retinal image speeds seen on a bite-board are only marginal for maintaining vision. This implies that somewhat brisker image motion would be optimal. Suppose the gain of the compensatory mechanism was as high for small amplitude body movements as it was found to be for large rapid body movements. If 95% of small bodily rotations were compensated, root mean square retinal image speed would fall to about 8° arc/sec for 2.5 Hz oscillations of 0.25° arc amplitude, almost half the average speed we have already pointed out is marginal in maintaining visibility when the head is stabilized on a bite-board.

Such considerations have been overlooked by oculomotorists who describe the system as operating perfectly (Barr *et al.*, 1976; Collewijn, 1977; Melville-Jones, 1976) primarily to facilitate modelling. To a first approximation this simplifying assumption is tenable. But acceptance of this assumption obscures a

major problem. Namely, once we pay close attention to the fact that compensation is mostly less than perfect and dependent on the size and frequency of body motion, we are forced to consider how we see a perceptually clear world during such image motion. Oculomotorists have assumed that the quality of vision is a consequence of the stability of the retinal image. The retinal image is not stable and perceptual clarity must depend in part on visual as well as oculomotor activities. We have recent evidence that the visual system processes moving retinal images and keeps acuity relatively uniform as retinal image speed increases to about 100' arc/sec. Image speeds above this value are detrimental at least for relatively high (5 cpd) spatial frequencies (Murphy, 1978). Westheimer and McKee (1975) have made similar observations. These reports show that there is considerable tolerance of retinal image motion. We already knew from a large body of work on stabilized images that the visual system requires some retinal image motion to maintain visibility. Our results make sense considered in light of these facts. The failure of the oculomotor system to compensate perfectly for natural head movement is useful. It guarantees sufficient retinal image motion.

The phenomena we have observed clearly represent a successful compromise in which visual and oculomotor capacity have come to work within each other's limitations. We would like to believe that these phenomena suggest more than that. It seems as though the gain of the machinery is adjusted to maintain image motion within some range optimal for visual processing. Gain is never sufficiently high to produce functional image stabilization or sufficiently low to permit images to move too rapidly. We believe that the gain of the compensatory mechanism is tuned to visual needs. This suggestion is consistent with recent reports that gain of the compensatory machinery is quite plastic. Gains ranging from near zero to almost 2.0 have been produced by changing the demand on the compensatory machinery with reversing or magnifying optics (Gauthier and Robinson, 1975; Gonshor and Melvill-Jones, 1976a,b; Miles and Fuller, 1974). Given such demonstrated plasticity, our failure to find perfect compensation for small head rotation, coupled with improved compensation for larger rotations, suggests that the motor system adjusts its response to guarantee transient stimulation of the retina.

The generality of our findings can be illustrated by asking the reader to perform a simple experiment which has become popular in recent years to demonstrate the "perfection" of oculomotor compensation. Hold this page at arms length and move it rapidly back and forth. This causes the text to blur, illustrating two things. First, that visually guided eye movements cannot keep up with rapid motion of the page. Hence, the retinal image moves and acuity suffers. However, if you hold the page still and shake the head rapidly, the vestibuloocular reflex comes into play and acuity does not suffer. This observation has been interpreted to indicate that the compensation is perfect. Now, shake your head again, keeping in mind the measurements of oculomotor compensation reported in this paper and Murphy's (1978) and Westheimer and McKee's (1975) reports that acuity

does not suffer until retinal image motion exceeds about 2° arc/sec. Be sure to shake your head rapidly through small angles and you will notice the following. If your movements are too fast or too large, you will see the letters blur. Now reduce the angle through which you are shaking your head until the letters just appear clear. The words still appear to move. Consider what this means. When you moved rapidly through a large angle, compensation was sufficiently poor for image velocity to have detrimental effects on acuity. Slowing down a bit and making more modest demands on the compensatory machinery brought you into the range of retinal image motions where acuity is relatively unaffected by image speed and the letters were seen clearly. However, when the letters were seen clearly, the words still appeared to move because head movements were not compensated perfectly and images of the words were moving on your retina. These informal perceptual observations are consistent with our experimental demonstration that natural image stabilization is good but imperfect.

Note, however, that your active head movements were much larger and more violent than the head movements we made while sitting and standing as still as possible. We were careful to avoid head translations as large as 1 cm. With more natural active head motions, retinal image speed might be considerably higher. This must now be studied. Furthermore, you almost certainly viewed this page binocularly as you shook your head. We covered one eye when we sat still. No one knows at this time how the retinal images in each eye move relative to each other as the head moves naturally. This, like retinal image speed in the freely moving human, must now be studied if we wish to understand the functional relationship between oculomotor performance and visual perception.

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