

BINOCULAR RETINAL IMAGE MOTION DURING ACTIVE HEAD ROTATION*

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Abstract—Horizontal binocular eye and head movements of 4 human subjects were recorded by means of the sensor coil-rotating magnetic field technique while they actively rotated their heads about a vertical axis and maintained fixation on a distant target. The frequency and peak-to-peak amplitude of these rotations ranged from about 0.25 Hz to 5 Hz and 30° to 15'. Eye movement compensation of such head rotations was far from perfect and compensation was different in each eye. Average retinal image speed was on the order of 4 deg/sec within each eye and the speed of the changes in retinal image position between the eyes was on the order of 3 deg/sec. Vision, subjectively, remained fused, stable and clear. Attention is called to implications of these results for visual and oculomotor physiology.

INTRODUCTION

Recently, Skavenski *et al.* (1979) described monocular retinal image motion of human subjects sitting and standing as still as possible while they maintained the line of sight on a target at optical infinity. These authors reported that the retinal image of the fixation target moved 2–4 times faster when retinal image stability depended on oculomotor compensation (vestibular and visual) than when the head was supported artificially on a dental bite-board. Retinal image motion was, however, relatively modest under these conditions, averaging only about 20 min/sec to 40 min/sec. Such retinal image speeds would be expected to be beneficial for processing of visual information because they are sufficiently fast to prevent perceptual fading (King-Smith and Riggs, 1978) and yet slow enough to fall below the speed (about 2 deg/sec) at which retinal image motion begins to have marked adverse effects on contrast sensitivity (Murphy, 1978) and on visual acuity (Westheimer and MacKee, 1975). So, the Skavenski *et al.* (1979) oculomotor results make sense visually because the degree of oculomotor compensation observed produces retinal conditions that have been shown to be optimal for visual processing. However, as Skavenski *et al.* (1979) pointed out, the amount of retinal image motion observed in a single eye when the subject sits or stands, *as still as possible*, is a special limiting case. Human beings usually process visual information binocularly and they allow themselves to move their bodies even though they wish to see. Skavenski *et al.* (1979) sug-

gested that retinal image motion might be appreciably greater under such natural conditions than when bodily motion is restricted as much as is humanly possible.

We found that this is true when we measured binocular retinal image motion of seated subjects instructed to maintain their lines of sight on a distant target while they made active head rotations. The characteristics of the rotations of the head were varied by means of verbal instructions given to the subject by the experimenter. The frequency of active head rotations studied ranged from about 0.25 Hz to 5 Hz and their peak-to-peak amplitudes ranged from about 30° to 15'. These experimentally solicited head rotations were studied because they mimic natural head movements. For example, they are similar to what a human being does automatically when he rotates his head about a vertical axis to emphasize a negative comment or when he nods his head about a horizontal axis to signal agreement. The frequency and amplitude of such natural head movements vary with the emotional content of the agreement or disagreement being communicated by these almost universal gestures.

We found appreciable retinal image motion (several deg/sec) in each eye over the range of frequencies and amplitudes of head rotations studied. Moreover, retinal image motions were different in each eye leading to considerable relative binocular motion of the fixated target. Vision was not affected, subjectively, by such motions of the retinal image. The visual scene appeared fused, clear and stable when the average retinal image speed was more than 3 deg/sec.

METHODS

Recording

Eye, head and visual field rotations with respect to a fixed-earth framework were recorded, free from

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translations, by means of a rotating magnetic field technique suggested by Hartmann and Klinke (1976) and developed and used by one of us to describe eye movements of the unrestrained rabbit (Collewijn, 1977). The recording method is described in detail in that paper and only its performance as used in the present experiments will be described here. Briefly, two horizontal a.c. magnetic fields of equal magnitude, in spatial and phase quadrature, generate a magnetic vector of constant magnitude rotating with uniform angular velocity through 360° during every period of the field frequency. The phase of the voltage induced in a sensor coil, placed in the field, will vary linearly with the angular orientation of the coil, and thus by phase detection the angular orientation of any object in the field can be measured. By suitable orientation of the magnetic field coils either horizontal or vertical angular orientations of the sensor coil can be measured by means of this technique. To use this principle to its full advantage it is crucial that the two magnetic fields be homogeneous in direction and magnitude and truly orthogonal in space and phase. A simple arrangement for creating a suitable uniform magnetic field has been described by Rubens (1945).

The sensor coils, which consisted of 9 turns of fine copper wire, were embedded in an annulus of silicone rubber moulded so as to adhere to the eye near the limbus. This manner of mounting sensor coils on the eyes is described in Collewijn *et al.* (1975). One such annulus was attached to each of the eyes and one was taped to the forehead, permitting measurement of head rotation. On some occasions this third coil was taped to a large plane mirror (about 75×30 cm) mounted on pivots that rotated around a vertical axis, permitting the visual field to be oscillated horizontally through known angles.

Signals from these 3 sensor coils were amplified, phase detected, and an analog voltage directly proportional to the orientation of each sensor coil was recorded on FM instrumentation tape. An analog signal directly proportional to the difference in the angular position of the two eye coils was also obtained by subtraction and recorded on FM instrumentation tape. The data recorded on FM tape were subsequently filtered at 50 Hz and sampled at 100 Hz by a 12-bit analog-to-digital converter (A/D) controlled by a minicomputer (DGC Nova 2/10). The FM tape records were digitized in 10 sec swatches and stored on LINC tape for subsequent analysis. The digitized samples for each of 4 variables (right eye position, left eye position, difference in eye position, head or mirror position) were obtained within the same millisecond and each digital value was the average of 4 A/D conversions. The noise levels of each of the variables after digitization was estimated by calculating standard deviations during 5 sec periods when the 3 sensor coils were attached to a mechanical calibration jig. Noise, expressed as a standard deviation, was less than $2'$ on the eye position and difference in eye position channels and less than $6'$ on the head or mirror channel.

Subjects

Four subjects served in the experiments. Two (RS and HC) were the authors. They were familiar with the purpose of the experiment and had considerable prior experience as eye movement subjects. A third subject (LK) was familiar with the eye movement literature and also experienced in wearing the sensor coil annulus but he did not know the specific purpose of the experiments. The fourth subject (HS) was neither familiar with the eye movement literature nor had served as a subject in prior eye movement research. Three of the four (RS, HS, LK) were emmetropes and had 20:20 uncorrected distance vision in both and in each of the eyes when the sensor coils were in place. The other subject (HC) was myopic and wore his correcting spectacles while he participated in the experiments. His distance vision with the spectacles in place was corrected to 20:20 and his reports of visual phenomena during the course of the experiment were the same as those made by the emmetropes. However, when the experiments were completed HC noticed that when he wore his glasses and rotated his head while maintaining the line of sight on a distant stationary object, the object appeared to be quite stable in space. This was no longer the case, however, when he took off his spectacles; then the object moved left when the head moved right. In other words, the retinal image slipped in the direction of his eye movement because the eye movements were too small for compensation of head motion when the spectacles were not in place. We would expect this situation to occur because the corrected myope always sees the world in reduced size and it has already been shown by Miles and Fuller (1974) that compensatory eye movements will adapt to magnifying and minifying lenses. For this reason a psychophysical experiment to determine the reduction factor of HCs spectacles was undertaken and correction factors of ranging between 13% and 18% were calculated. Subsequently, all of HCs data were corrected accordingly and the records and velocities reported for this subject represent his performance after correction for the mismatch between head movement and eye rotation introduced by wearing spectacles during the experiment.

Protocol

A subject, with sensor coils attached to both eyes and his forehead, sat near the center of the revolving magnetic field and looked out through a convenient window on the 15th floor of the Medical Faculty at a scene of Rotterdam and its environs. Initially, he looked with both eyes at a distant object, typically the control tower at the Rotterdam airport which was 5000 m from where he was seated. On particularly clear days a building at the outskirts of Den Haag was fixated, providing a target at about 35,000 m. The subject's task was to maintain his line of sight on the distant target and rotate his head back and forth

through an angle which could be recorded successfully. As he rotated his head, the experimenter instructed him to increase the frequency of its oscillations. This continued until the highest possible frequency was obtained—about 5 Hz for each of the subjects. Such high frequencies are obtained by clenching the teeth and straining the neck and facial muscles.

The subject was instructed to report any disturbances in vision as they occurred and such disturbances were noted on the voice track of the tape recorder. After having done a series of such oscillations, the subject was instructed next to cover one eye and view the distant target monocularly. The experiment was then repeated. This was followed by another binocular experiment. The subject was next required to cover the other eye and repeat the experiment once again. Following this procedure, the room lights were turned off and blackout shades were drawn. The subject was then required to make similar head movements in total darkness, imagining that he was looking at the distant target. Following this measurement of the vestibulo-ocular response, the lights were turned on again and the subject changed his position so as to view the distant landscape after reflection from a plain mirror that could be rotated about a vertical axis, causing the entire visual field to oscillate horizontally. At this time the coil, which had been taped to the forehead, was removed and was taped to the surface of the mirror, allowing us to record the rotations of the visual scene. In this part of the experiment the subject was asked to sit still and maintain the line of sight on a target which oscillated back and forth through various amplitudes at various frequencies. In other words, we examined binocular smooth pursuit while the subject sat with his head as still as possible. Following completion of these experiments, the field coils were rearranged and a portion of the experiment was repeated while one of the subjects (HS) made vertical oscillations of his head. Vertical smooth pursuit of the visual field was not attempted.

RESULTS

It is important to remember five things while considering the results we will now present. First, eye rotations were recorded with respect to a fixed-earth framework. This means that the eye position traces represent retinal image motion of the fixation target and will, therefore, be referred to as retinal image motion. If rotations of the eye exactly compensated for rotations of the head, the eye position traces would be horizontal straight lines. In other words the fixation target image would not move on the retina. Second, the difference in the retinal image positions between the eyes, which was obtained by subtracting the position of the right eye from the position of the left eye, represents vergence. If there were no vergence changes while viewing the distant target, the difference trace would also be a horizontal straight line.

Vergence changes would not normally be expected in the present experiment because the subjects fixated a target at great distance. Third, the revolving magnetic field technique, as implemented in the instrument used, is insensitive to translations of the subject over a distance of at least 40 cm in any direction. It is also capable of absolute calibration since the angular orientation of the sensor coil is signaled by the phase and not the magnitude of the induced signal. By absolute calibration we mean that the angular orientation of each sensor coil was measured with reference to the fixed-earth framework provided by the magnetic field coils. Calibration is not influenced either by the oculomotor behavior of the subject or by differences in the physical properties of the sensor coils. Great care was exercised in calibrating each of the channels by mounting the 3 sensor coils used on the eyes and head on a rotating mechanical jig. Calibrations were checked throughout the experiment. Fourth, the head position traces have been scaled to 1/10 of their actual value in the analog records to permit reproduction of all the phenomena in the same plate. This means that if the retinal image trace moves about the same amount as the head position trace, the eye did not compensate for about 10% of the head movement. If the motion of the retinal image is in the same direction as the motion of the head, it means that compensation was insufficient to keep the fixation target in position on the retina, i.e. the compensatory eye movement was in the correct direction (opposite to the rotation of the head) but it was too small to keep the retinal image in place. If the retinal image trace is seen to move opposite in direction to the movement of the head, it also means that the compensatory oculomotor response was in the correct direction (opposite to the motion of the head) but it was too large, causing the retinal image to move away from the assigned position. Said differently, the eye moved farther than it needed to move to keep the retinal image in the same locus. Fifth, it is important to remember that the vision of all four subjects remained fused, clear and stable until the head attained the highest natural head frequencies that could be produced by each subject. At that time vision continued to be single but the target object and surrounding details began to be perceived as moving slightly. When the high frequency oscillations continued for a second or two, some blurring of visual detail was usually reported. Now consider the representative records of each of the subjects reproduced in Figure 1.

Binocular viewing during head rotation

These records reproduce the results of the most natural conditions studied, namely, retinal image motion during binocular viewing of a distant object while the head moved about a vertical axis at various frequencies. Three general characteristics can be seen. First, saccades were infrequent when the line of sight was maintained on a stationary distant object in the presence of head motion. Second, there was consider-

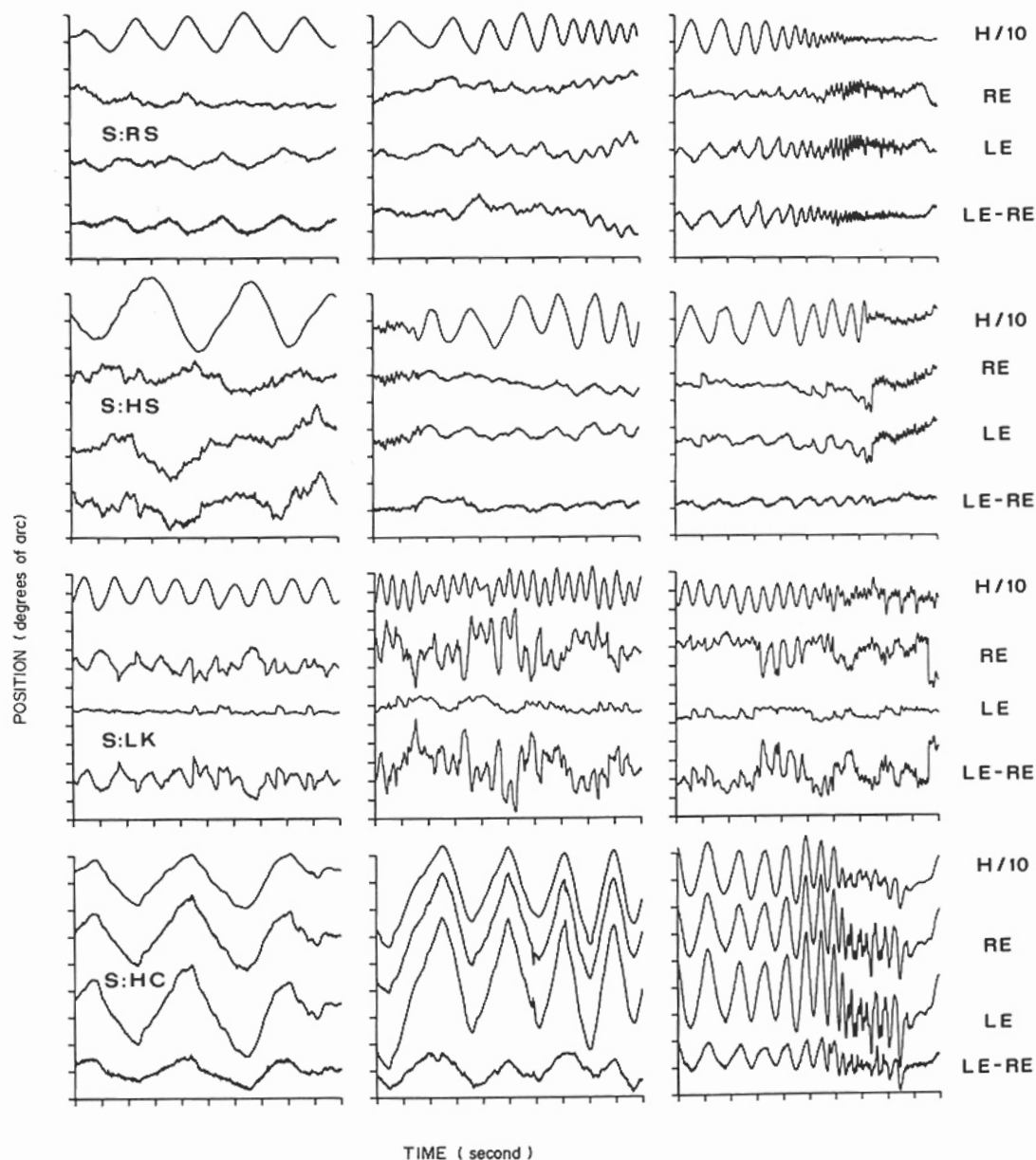


Fig. 1. Representative horizontal eye and head movement records of 4 subjects (RS, HS, LK and HC) while they fixated a distant object as they moved their heads. Each of the 12 records begins on the left. The time scale-marks signify 1 sec intervals. The ordinate in each record shows position of the head and eyes in space. The position scale-marks signify 1° distances. The head position trace (H/10) shows the position of the head scaled to 1/10th of its actual value. The position of the retinal image in the right eye (RE) is shown just below the head, the position of the retinal image in the left eye (LE) just below the right eye, and the vergence of the eyes (LE-RE) is shown at the bottom of each record. Position changes upwards in the head and eye records signify rightward movements. Upwards changes in the vergence trace signify convergence.

able retinal image motion in each of the eyes and considerable change in vergence (relative motion between the eyes). Third, details of these motions were subject to large individual differences. Consider first the three top records which show the performance of the subject (RS) whose compensatory oculomotor activities were most effective over the entire range studied, i.e. his retinal image speeds, position errors and

vergence changes were the most modest. Look at subject RS's left hand record in which his head was moving relatively slowly, about 0.5 Hz, through a peak-to-peak amplitude of about 5° to about 12° . Oculomotor compensation was very good in his right eye during the last 5 sec—retinal image motion seldom exceeded $15'$ —a displacement only about twice as big as would be made by this subject if his head were supported

artificially on a bite board. Motion was greater during the first 5 sec, averaging about 0.5° peak to peak. These retinal image motions were generally in the direction of the head motions. In other words RS's right eye did not move far enough in the compensatory direction to completely stabilize the retinal image. Now consider what RS's left eye was doing at the same time. During the first three seconds of the trial the retinal image in the left eye was behaving in a manner similar to the retinal image in the right eye, i.e. compensation was not complete. However, in the last 5 sec of the record the left eye image, unlike the right eye image, was not stabilized very well. Rather, it was moving through about a degree in a direction opposite to the direction of the head. In other words compensatory motions in the left eye in the second half of the record were too large to keep the retinal image stable. These different activities in each of the eyes led to relatively large variations in vergence that persisted throughout the record. The peak-to-peak amplitude of these vergence changes was approximately 1° . The story remains essentially the same throughout the remaining head frequencies shown until head frequency became high (the last 5 sec of the right hand record). In this portion of this record head frequency was greater than 3 Hz and the motions in each of the eyes become more similar to each other. Both tended to move in the same direction as the head. In other words, at the higher frequencies compensatory movements in both eyes were too small to stabilize the retinal image. At such frequencies compensation is accomplished almost exclusively by vestibular signals as visual input becomes ineffective when the retinal image slips very fast. It was only in the most extreme condition, in the last 2 sec of the right hand record, that motion of the visual field and blurring began to be perceived. On the whole subject RS's compensation for head rotation was slightly better in his right eye than in his left eye as will be seen later when his results are summarized quantitatively.

The second best subject (HS) is shown in the three records just below. His performance was in most respects similar to the performance of RS. The third subject (LK) is an entirely different story. Note that the position scale for this subject is 30% smaller than the scale used for the other subjects. Compensatory movement in LK's left eye was excellent, but his right eye showed poor and erratic compensation. At all frequencies LK's right eye tended to overcompensate for rotations of his head. This very different performance in each of his eyes, of course, caused large vergence changes with peak-to-peak amplitudes as large as 5° . The fourth subject (HC) is shown in the bottom three records. His performance, unlike the other 3 subjects, is simple to describe because both of his eyes did the same thing consistently. Namely, they always undercompensated head movement by a considerable amount. On the average HC compensated for only about 80% of the rotations of his head. His retinal

images moved through as much as 5° in each of his eyes when he fixated a distant object while he rotated his head. Note, also, that the amount of compensation was not identical in each eye which led to vergence changes ranging from about $1-2^\circ$ peak-to-peak. It should not be forgotten while considering the records reproduced in Fig. 1 that these four subjects tested as having 20:20 vision and also that their phenomenological reports of the appearance of the fixation stimulus were the same.

The results of this basic experiment are summarized quantitatively in Fig. 2 which shows velocity histograms for each of the subjects. The velocities are calculated for 100 msec periods. This period was chosen because it is representative of the integration time of the human visual system. The head histogram plots velocities in 4 deg/sec bins which makes it possible to cover the full range of head movements observed. The retinal image velocity histograms for each eye and the vergence velocity histograms are plotted in 1deg/sec bins which are suitable for summarizing the range of velocities observed. The few saccades that were made during this experiment have been removed so the velocities plotted result exclusively from deficiencies in smooth compensatory eye movements. Each histogram for subjects RS, HS and HC contain about 1000 velocities. Histograms for subject LK, who participated in fewer sessions, are based on about 600 observations. It should be noted while considering these velocity histograms that similar histograms obtained for these subjects with their heads supported artificially would have all of the velocities falling in the 1 deg/sec bins immediately to the right and left of 0. This is not an assumption. All of these subjects have participated in such experiments and are known to have excellent slow control which effectively stabilizes retinal images when their heads are not free to move. Their 100 msec retinal image velocities with their heads stabilized artificially are less than $10 \text{ min/sec} - \frac{1}{6}$ th the size of the bins adjacent to zero. We also know that one of the subjects (RS) has retinal image speeds well under 1 deg/sec when he sits or stands as still as possible (Skavenski, *et al.*, 1979). These facts are important because they mean that retinal image velocities in Fig. 2 are representative of performance of normal subjects. These 4 subjects are in the range of subjects normally observed in experiments in which the head is artificially stabilized. So, the retinal image velocities in Fig. 2 reflect the degree to which the compensatory systems fail to compensate or choose incomplete compensation in normal subjects when they move their heads.

The general features revealed by these histograms are rather obvious. All four subjects show considerable retinal image motion in each eye and considerable changes in vergence as well. The top two subjects (RS and HS) performed rather similarly as could be seen in the analog records in Fig. 1. Subject HC, on bottom, shows considerably more high velocity image motion in each of his eyes than subjects RS and HS

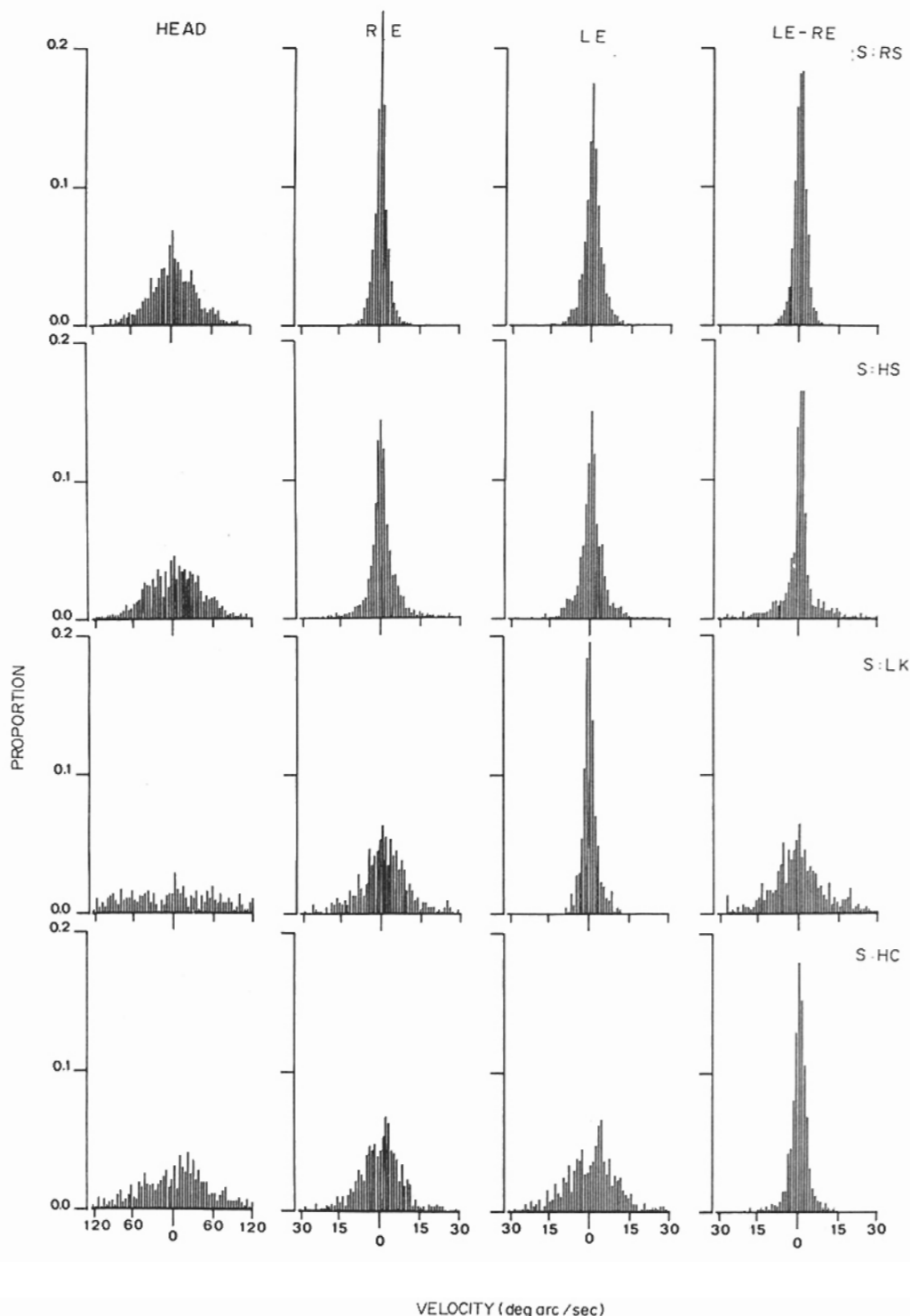


Fig. 2. Horizontal velocity histograms of 4 subjects (RS, HS, LK and HC) while they fixated a distant object as they moved their heads. The histograms plot proportions of velocities. Leftward velocities are plotted to the left of zero and rightward velocities to the right of zero. Head velocities (HEAD) are grouped in 4 deg/sec bins. Right eye (RE), left eye (LE) and vergence (LE-RE) velocities are grouped in 1 deg/sec bins. Vergence velocities to the right of zero signify convergence. Vergence velocities to the left of zero signify divergence.

but his changes in vergence were essentially the same as the changes in vergence of subjects RS and HS. Subject LK has one eye (the left) like subjects RS and

HS while his other eye (the right) was similar to both eyes of subject HC. LK's vergence velocities were the largest observed.

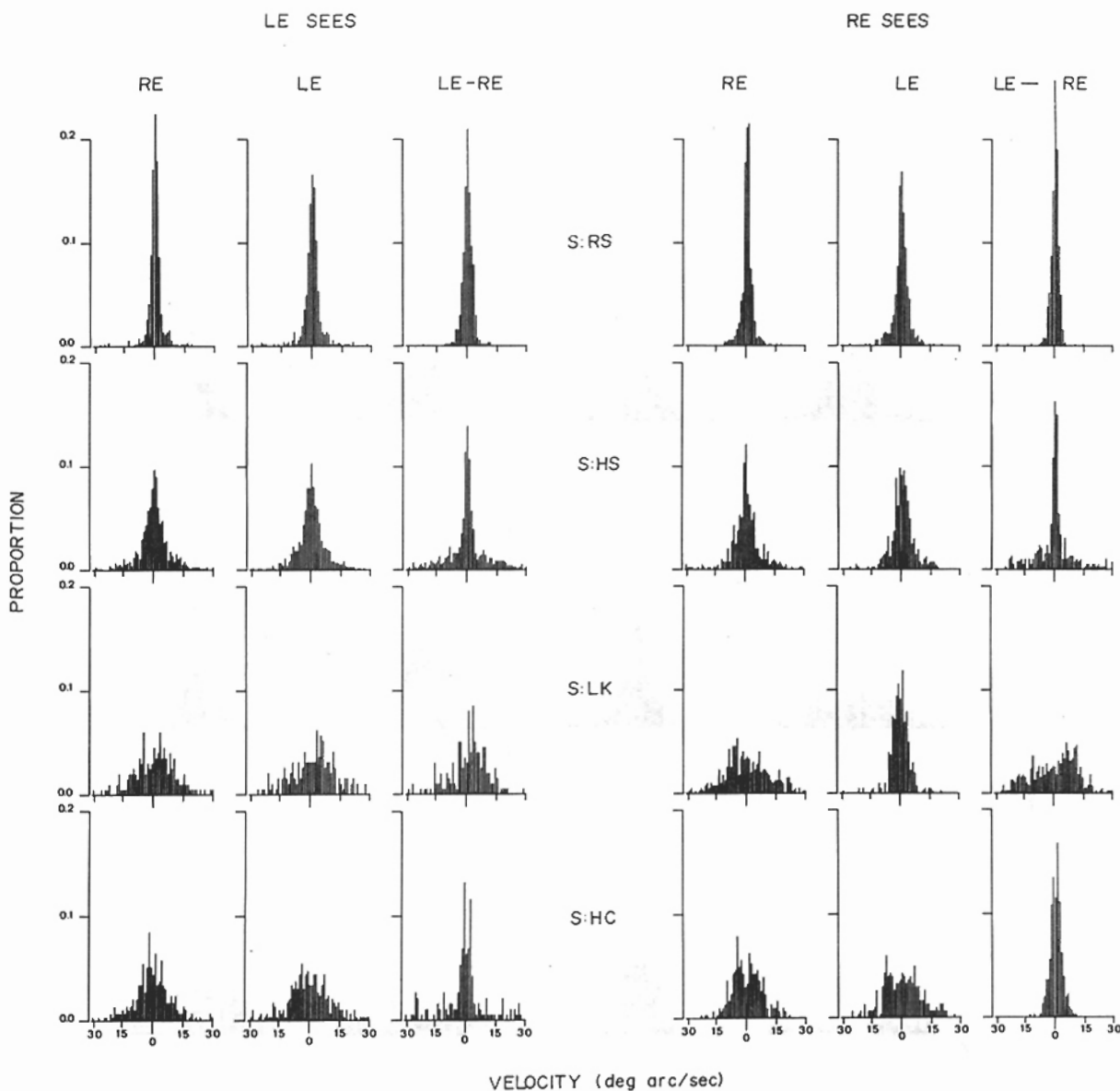


Fig. 3. Horizontal velocity histograms of 4 subjects (RS, HS, LK and HC) while they fixated a distant object with the right eye (RE SEES) or with the left eye (LE SEES) as they moved their heads. The histograms plot proportions of velocities. Leftward velocities are plotted to the left of zero, rightward velocities to the right of zero. Vergence velocities (LE-RE) to the right of zero signify convergence. Vergence velocities to the left of zero signify divergence. All velocities are grouped in 1 deg/sec bins.

Monocular viewing during head rotation

Figure 3 shows similar velocity histograms while the subject viewed the distant target with either his right eye or his left eye while we recorded from both eyes and the head. The head histograms are not included but the head velocities under these conditions were essentially the same as those observed in the initial experiment and plotted in Fig. 2. These histograms are a bit more jagged because fewer observations were made under these conditions. Each histogram contains about 500 velocities. For three of the subjects (RS, HS and HC) covering one or the other

eye did not have marked effects on the results, particularly when allowance is made for the smaller number of samples contained. Subject LK, however, behaved in a very interesting manner. Note, as is shown in Figs 1 and 2 that LK's left eye during binocular viewing compensated for head rotation relatively well. His right eye did not under binocular viewing and appreciable image motion resulted. Now look at Fig. 3. When LK's left eye, the good eye during binocular viewing, viewed the distant target, both eyes resembled his poor right eye. However when his poor right eye viewed the stimulus and the left eye was patched, LK performed, in both eyes, as he did

VOR in DARK

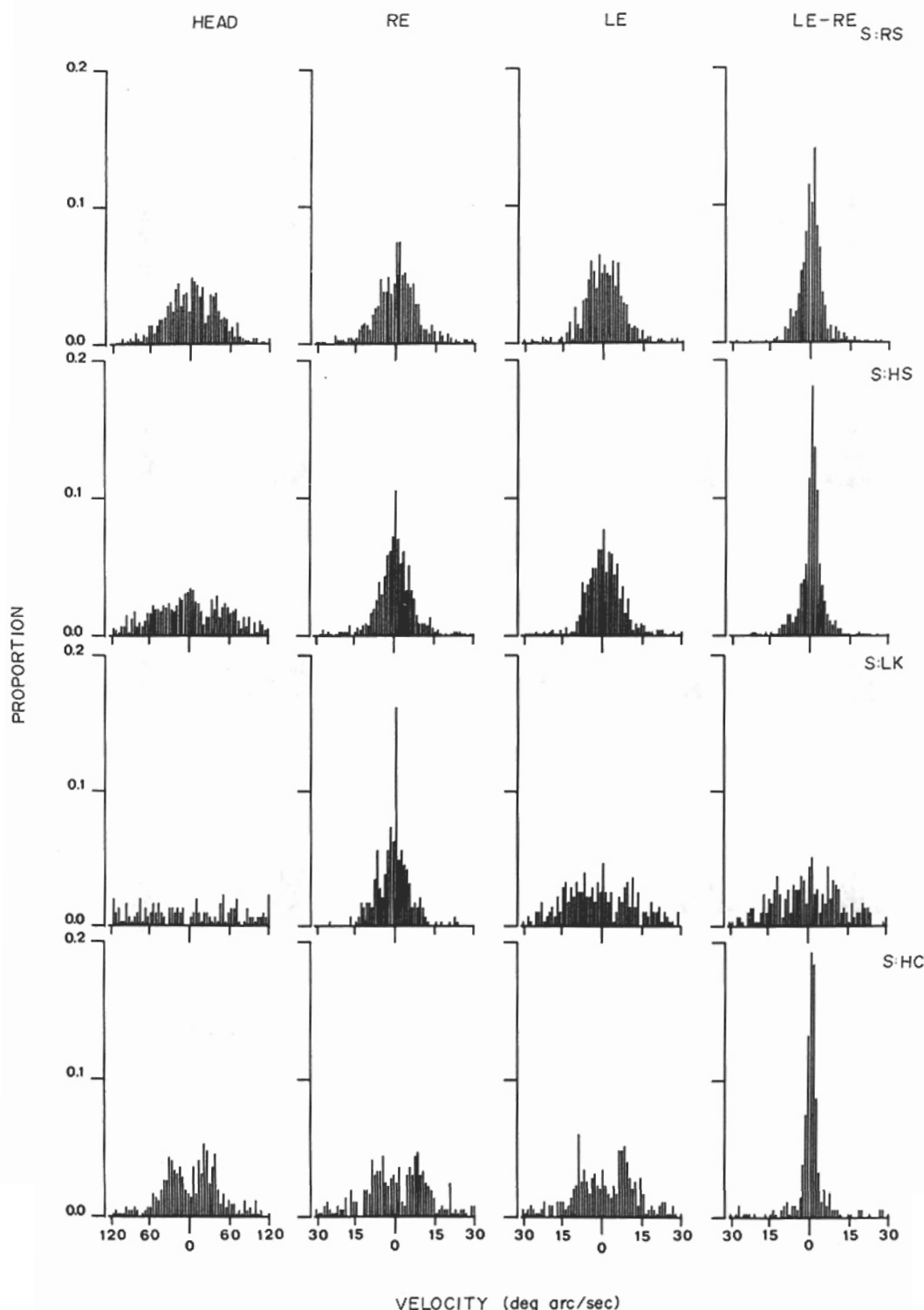


Fig. 4. Horizontal velocity histograms of the vestibulo-ocular response (VOR) obtained when 4 subjects (RS, HS, LK and HC) moved their heads in total darkness. The histograms plot proportions of velocities. Leftward velocities are plotted to the left of zero and rightward velocities to the right of zero. Head velocities (HEAD) are grouped in 4 deg/sec bins. Right eye (RE), left eye (LE) and vergence velocities (LE-RE) are plotted in 1 deg/sec bins. Leftward velocities are plotted to the left of zero, rightward velocities to the right of zero. Vergence velocities to the right of zero signify convergence. Vergence velocities to the left of zero signify divergence.

when he viewed binocularly. This result shows that visual-vestibular interactions can be maladaptive during compensation for natural head movements. This fact became even clearer when the vestibulo-ocular response was measured when no visual input was present. This result is summarized in Fig. 4.

Head rotation in darkness while imagining a distant target

The expected benefits to oculomotor compensation derived from visual input can be seen by comparison of Fig. 4 with Fig. 2. The histograms in Fig. 4 are based on about 500 samples and therefore are somewhat more jagged than those in Fig. 2. Subjects RS's and HS's retinal image velocities in the dark tend to be much higher than those observed when the distant object was viewed as the head moved. Subject HC, however, does not benefit as much from visual input. His histograms in Fig. 2 are not much sharper than those obtained in total darkness when HC was imagining, rather than seeing, the fixation stimulus. The most striking result, however, is found in subject LK's data. In the dark when visual input was not available, his right eye compensated for head rotations much better than his left eye compensated. This is opposite to what this subject did when he saw the stimulus (see

Fig. 2)! This reversal in LK's performance can be seen in the analog record reproduced in Fig. 5.

In examining Fig. 5 ignore the periodic large saccades and slow systematic drifts which are typically observed when human subjects fixate in total darkness. Slow control is under visual guidance and large saccades are required to maintain visual direction when the normal field holding reflex is absent (see Skavenski and Steinman, 1970). If, however, you confine your attention to low compensatory eye movements and compare this record with the records reproduced for this subject in Fig. 1 (both were made at the same recording session), it is readily apparent that the compensatory response of the right eye in darkness is better than it is when the compensatory response could benefit from visual input. More than 90% of the motions of the head were removed by appropriate motions of the eye in the dark. In the 7th and 8th sec of Fig. 5 we can see almost perfect compensation in the right eye produced by the action of vestibular signals operating alone. LK's left eye operating under only vestibular input, however, is typical of what was observed in the other subjects. Namely, compensation without visual input seldom exceeds about 80%. It seems, then, that when LK views the target binocularly while he moves his head, his right

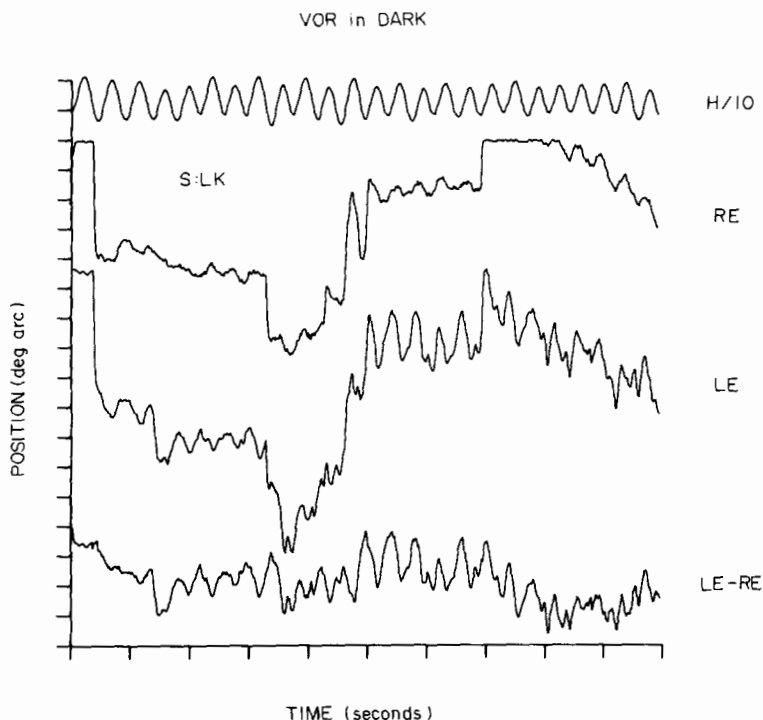


Fig. 5. Representative analog record of subject LK's horizontal vestibulo-ocular response (VOR) when he moved his head in total darkness. The record begins on the left. The time scale-marks signify 1 sec intervals. The ordinate shows position of the head and eyes in space. The position scale-marks signify 1° distances. The head position trace (H/10) shows the position of the head in space scaled to 1/10th of its actual value. The position of the right eye (RE) in space is shown just below the head, the left eye (LE) in space just below the right eye, and the vergence position of the eyes (LE-RE) is shown at the bottom. Position changes upwards in the head and eye traces signify rightward movements. Upwards changes in the vergence trace signify convergence.

eye, which gets a high degree of compensation from the vestibular system, is further driven by the visual input. This causes over-compensation of head motion which leads to instability and consequently very high and variable retinal image velocities in his right eye. LK's left eye, however, where vestibular responses are far less complete is effectively aided by visual stimulation and attains the high degree of compensation evident for this subject in Fig. 1 and summarized in Fig. 2.

In summary, we have seen so far that all 4 subjects show appreciable retinal image motion when they move their heads through relatively modest angles at generally moderate frequencies. We have also seen that there is appreciable relative motion between the images in each of the eyes—"corresponding points" often differ by a degree or more and the vergence

velocities can be as high as the retinal image velocities within each eye. We have also seen considerable individual variations in the way these results come about ranging from relatively good compensation in both eyes (RS and HS), to relatively poor compensation in both eyes (HC), including one subject (LK) with good compensation in one eye and appreciable over-compensation in the other eye. We have also seen that in at least one of the subjects (LK) visual-vestibular interaction can be maladaptive and we have also seen in subject HC that compensation with visual input is not appreciably better than compensation in complete darkness.

Binocular smooth pursuit

The last observation raises an interesting question. Namely, to what extent do the individual differences

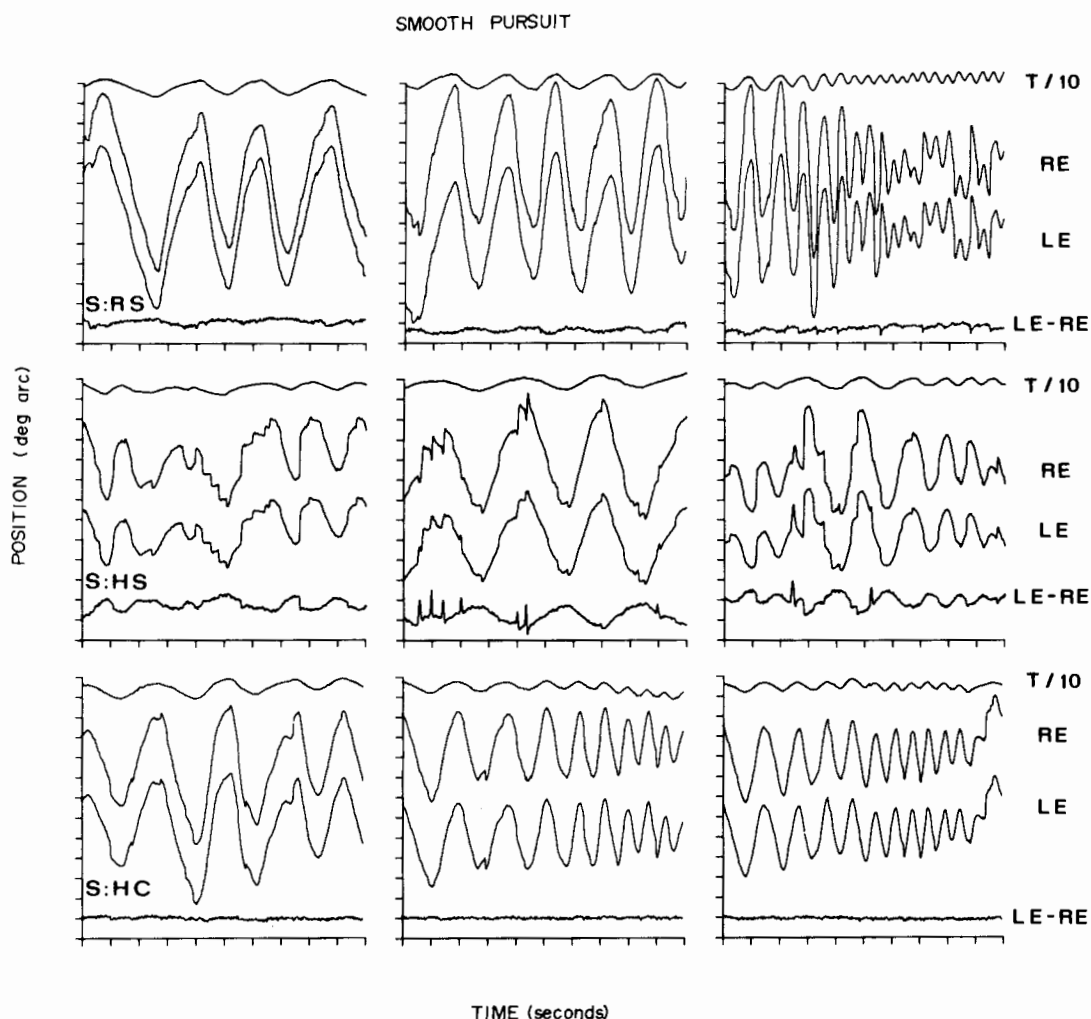


Fig. 6. Representative binocular smooth pursuit records of 3 subjects (RS, HS and HC) tracking a distant object reflected from a mirror moving horizontally. Each of the 9 records begins on the left. The time scale-marks signify 1 sec intervals. The ordinate in each record shows position of the target object and eyes in space. The position scale-marks show 1° distances. The target position trace (T/10) is scaled to $1/10$ th its actual value. The position of the right eye (RE) in space is shown just below the target, the left eye (LE) in space just below the right eye, and the vergence of the eyes (LE-RE) is shown at the bottom of each record. Position changes upwards in the target and eye traces signify rightward movements. Upwards changes in the vergence trace signify convergence.

observed in the basic binocular experiment result from differences in the way visual input to each of the eyes can be used by the several subjects when they move their heads? We looked at this for 3 of the subjects (RS, HS and HC) by measuring binocular smooth pursuit while they sat still and tracked the distant object which they now saw after reflection from a large moving plane mirror. The moving mirror was large enough and near enough to the subject that the entire visual field was seen to move—no stationary frames were visible. The mirror was moved so as to produce target oscillations that had similar frequency-amplitude characteristics to the head oscillations studied in the prior experiments. It should be noted that this technique produced a somewhat unusual stimulus for smooth pursuit because, although the subject was tracking a single moving distant target, the entire highly structured visual field was moving and seen to be moving. This means that the retinal slip signals available in our smooth pursuit experiment were similar to the slip signals produced previously when the subject rotated his head and the visual field remained stationary. The percepts in the two conditions were different, however. In the smooth pursuit experiment the world was seen as moving. In the head movement experiment the world was seen as stationary. It also means that input to drive OKN, as well as input for smooth pursuit, was available in the smooth pursuit experiment. This could be important if, as some believe, OKN and smooth pursuit are driven by different signals; OKN by slip of a structured display on large portions of the peripheral retina and smooth pursuit by slip of a detail on or near the fovea.

Representative binocular smooth pursuit records are reproduced in Fig. 6. Target position is scaled to $\frac{1}{10}$ of its value to make it possible to reproduce all of the records in a single plate. In this figure, unlike Fig. 1, we expect to see the eyes moving in the same manner as the target. Eye movements reproduced in these records would match target movements ($\times 10$) if pursuit were perfect. The yoking of the eyes can be seen in the vergence trace. A horizontal straight line would mean that the eyes were perfectly yoked during smooth pursuit.

The most striking result of this smooth pursuit experiment is shown in the bottom records of subject HC. His two eyes were almost perfectly yoked during smooth pursuit. This is a very interesting result because, as can be seen in Fig. 1, HC's compensation to head rotation was sufficiently different in each of his eyes to produce considerable changes in vergence as his head moved. This does not happen when his head stays relatively still as he pursues a moving target binocularly. This result suggests that retinal image slip, which is associated with concurrent vestibular signals, is handled differently by the oculomotor system than retinal image slip which is processed when vestibular input is very modest (sitting as still as possible is not the same as immobilizing the head, see

Skavenski *et al.*, 1979). The performance of the other two subjects RS and HS, with respect to the yoking of their smooth pursuit eye movements is not as interesting as the performance of HC. RS shows better yoking than HS but neither is as good as HC and their yoking during smooth pursuit is not clearly different from the yoking of their eyes during head rotation. HS does show somewhat poorer yoking during pursuit than during head movement but the difference is not striking. Smooth pursuit gains (eye velocity/target velocity) were what would be expected during tracking of more or less predictable target motion. Gain was calculated for 50 msec velocity samples, excluding samples between 50 msec before the target changed direction and 150 msec after it changed direction. Saccades were also excluded. Mean gain for subject RS's right eye = 1.04, left eye = 0.95; HS's right eye = 0.87, left eye = 0.66; HC's right eye = 0.82, left eye = 0.80. RS's superior performance probably arises from his extensive prior practice in tracking experiments (see Kowler *et al.*, 1978, for the effects of practice on smooth pursuit gain). The degree of yoking between the two eyes during binocular smooth pursuit is illustrated quantitatively in Fig. 7.

This histogram, like the prior histograms, does not include velocities associated with saccadic eye movements which occurred much more frequently in the smooth pursuit experiment than they did when the subjects moved their heads and the stimulus remained stationary. It is not surprising that saccades tended to be more frequent during smooth pursuit than when the line of sight was maintained on a distant target while the head moved.

The instruction to track a moving target has been shown to be interpretable by the subject either as keeping the moving target relatively stationary on the retina or as fixating the target accurately. The latter increases saccade rates (see Puckett and Steinman, 1969). The tendency, however, to have relatively frequent saccades in the smooth pursuit experiment makes it necessary to comment on the operation of Hering's Law with respect to saccades. We have already seen, although not described in such terms, the fact that Hering's law holds imprecisely with respect to direction, size and velocity of smooth eye movements. The story is not different with respect to saccades. We observed saccades that are very well yoked with respect to direction and size. We have also seen saccades that were badly matched for size. Very occasionally we have seen saccades in opposite directions in each of the eyes. Examples of failures of Hering's law for saccades can be seen in the smooth pursuit records reproduced in Fig. 6. Note particularly subject HS—the middle records. In his left hand record HS made a fair number of well-yoked saccades in the first 5 sec. In the 6th sec we can see two right going saccades which differed a bit in size followed by a burst of 3 saccades that were well-yoked. This was followed by an appreciable size mismatch in the 8th sec. In the middle plate and to a lesser extent in the

SMOOTH PURSUIT (LE-RE)

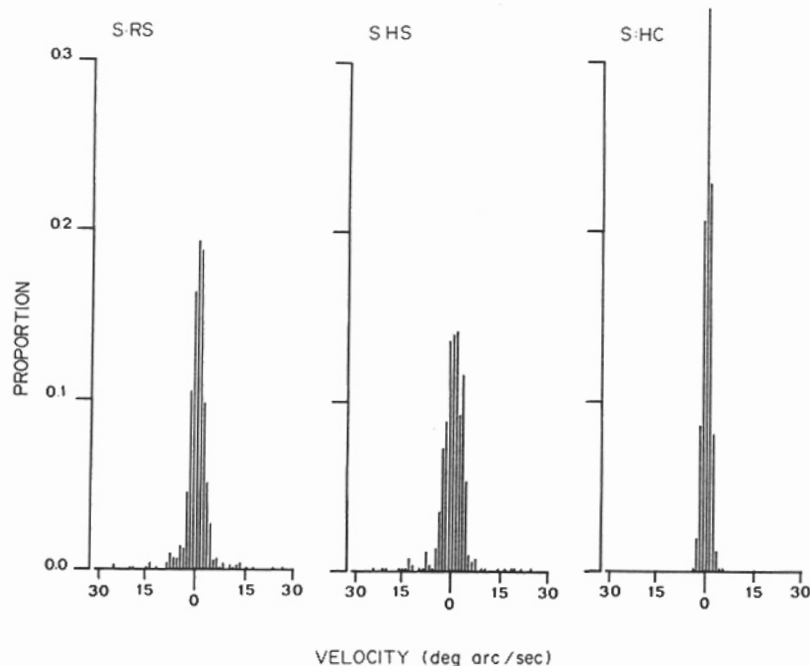


Fig. 7. Horizontal vergence velocity histograms of 3 subjects (RS, HS and HC) during binocular smooth pursuit. The histograms plot proportions of velocities grouped in 1 deg/sec bins. Velocities to the right of zero signify convergence. Velocities to the left of zero signify divergence.

right hand plate we see more striking mismatches. The other two subjects, who made saccades less frequently during smooth pursuit, show rather good yoking throughout. Notice, however, in the right hand plate for subject RS, where he is tracking a fairly high frequency target, there is a tendency for his saccades to be somewhat mismatched in size—saccades

in his right eye tending to be slightly larger than saccades in his left eye. Failures of Hering's law with respect to the size of human saccades have been known to occur for a long time (e.g. Krauskopf *et al.*, 1960) and have also been reported for the slow compensatory eye movements of a number of animals (Gavin, 1978).

VERTICAL

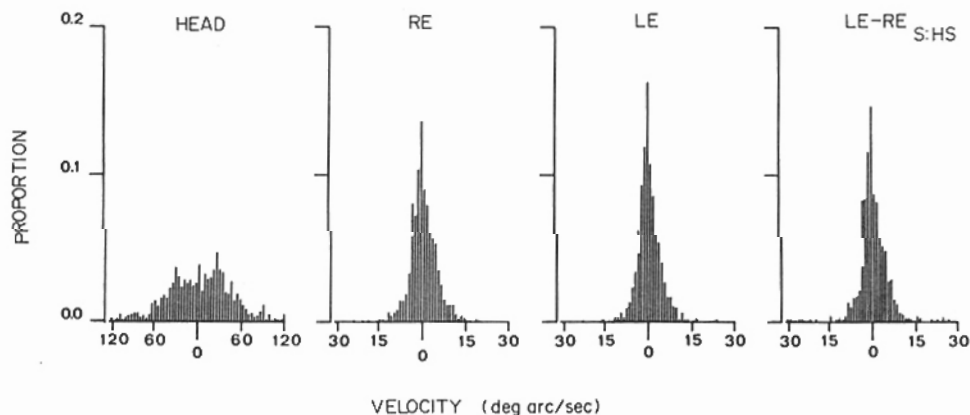


Fig. 8. Vertical velocity histograms of subject HS moving his head about a horizontal axis while he fixated a distant object. The histograms plot proportions of velocities. Downward velocities are plotted to the left of zero and upward velocities to the right of zero. Head velocities (HEAD) are grouped in 4 deg/sec bins. Right eye (RE), left eye (LE), and vergence (LE-RE) velocities are grouped in 1 deg/sec bins. Vergence velocities to the right of zero signify convergence. Vergence velocities to the left of zero signify divergence.

Table 1. Mean speeds of 4 subject's (RS, HS, LK and HC) retinal image motions (RE and LE), vergences (LE-RE), and HEAD motions when they fixated a distant object binocularly as they oscillated their heads horizontally. Speed is shown as deg arc/sec

SUBJECT	HEAD	RE	LE	LE-RE	N
RS	27.2 (22.5)	1.9 (2.0)	2.5 (2.6)	1.8 (1.7)	1583
HS	35.7 (29.7)	3.7 (4.6)	3.5 (4.0)	3.5 (4.0)	1160
LK	91.9 (66.1)	7.0 (6.2)	2.1 (2.1)	7.9 (6.8)	585
HC	52.5 (47.8)	6.6 (5.8)	7.8 (6.2)	2.5 (2.8)	880
Overall	43.8 (35.8)	4.1 (4.1)	3.8 (3.7)	3.3 (3.8)	4208

Standard deviations are given in parentheses. The number (*N*) of speeds averaged for each subject is also given. Speeds are based on 100 msec samples and the overall means shown have been weighted by the number of observations.

Vertical and passive head rotation

On the completion of these experiments we rearranged the field coils and one of the subjects (HS) participated in a complete session of the basic binocular head movement experiment while rotating his head about a horizontal axis. The results of this experiment are reproduced in Fig. 8 where it can be seen that the compensation of vertical head movement is essentially the same as compensation of horizontal head movement. We were only successful in recording from a single eye in two of the other subjects (HC and RS) and can report, not surprisingly, that the monocular vertical performance of these subjects also did not differ in any qualitative way from what had been observed when they moved their heads horizontally.

We also did a horizontal binocular experiment in which subjects HS's and HC's heads were oscillated passively as they fixated the distant object. Results were the same as when they actively generated their own head rotations.

Retinal image speed

Table 1 summarizes the speed of the retinal image and vergence motions observed for each subject in the binocular experiment in which they actively oscillated their heads horizontally as they maintained fixation on a distant object. Mean retinal image speed varied between subjects and between eyes. The subject with the best compensation in both eyes (RS) had a mean retinal image speed on the horizontal meridian of about 2 deg/sec. The mean speed of his vergence movements was similar. The other subjects showed higher mean retinal image speeds in at least one of the eyes and the mean speed of their vergence movements could be as high as 7.9 deg/sec. Note that RS's head rotations were, on the average, slower than the other subjects. He might not have done as well if he had moved his head faster. If these 4 subjects are representative of what is likely to be observed in other subjects with normal binocular vision, then the mean retinal image speed during modest natural head rotation would be on the order of 4 deg/sec on a single meridian. The mean speed of vergence changes on a single meridian during binocular viewing would be on

the order of 3 deg/sec. We have partial data showing that compensation is similar on the vertical meridian which means that a seated subject moving his head through angles smaller than 30° at frequencies from 0.25 to 5 Hz would have two-dimensional retinal image speeds on the order of 5 deg/sec—more than twice the retinal image speed which has been shown experimentally to be tolerated by the visual system and at least twenty-five times as fast as retinal image speeds observed when a subject's head is stabilized on a bite board.

DISCUSSION

It has been known for 30 years that the retinal image must move if vision is to be maintained. Demonstration of this fact required the development of instruments to stabilize retinal images. Once such instruments were available, it became possible to impose controlled motion on a display that was locked to the retina. This technique has been used in numerous visual psychophysical experiments to study how motion of the retinal image contributes to the generation and maintenance of vision. During the same period, instrumentation and analytic techniques were developed for the study of oculomotor system performance. These methods have been used to study how the oculomotor system compensates for bodily movement and how the line of sight tracks stationary and moving objects when the body is stationary.

In almost all of this research, vision and ocular motility were studied with subjects whose heads were immobilized as they looked at the test stimulus with a single eye. Until very recently there was no good alternative to this strategy. It is not easy to study binocular eye movements accurately in freely moving subjects or to stabilize retinal images under such conditions. Furthermore, it was not believed to be necessary to study freely moving subjects. Almost all investigators of visual and oculomotor processes believed that natural visual and oculomotor performance, and their interaction, could be understood despite the fact that their subjects' heads were immobilized.

Two assumptions underlie this belief. First, it is assumed that the oculomotor system compensates

almost perfectly for motions of the body when visual, as well as vestibular, stimulation is available to the subject as he moves. Second, it is assumed that compensatory oculomotor activities are almost perfectly yoked in two eyes. Once these two assumptions are made, the fusion, stability and clarity of the visual world during normal activity can be explained. These explanations, however, rest on what we now know is an idealized view of the operation of the oculomotor system.*

When it became possible to examine the quality of oculomotor compensation accurately in subjects who were not supported artificially, compensation was found to be far from perfect (Skavenski *et al.*, 1979). These authors discovered that the retinal image motion of a subject, sitting or standing as still as possible, was faster than the retinal image motion expected from prior oculomotor research in which the head was immobilized. This result, in itself, did not make serious difficulties, however, because the retinal image speed of subjects sitting or standing as still as possible fell in the range of retinal image speeds that had been shown to be optimal for vision in stabilized image experiments. Natural retinal image speeds were 2–4 times faster than speeds observed when the head was on a bite-board. However, stabilized image experiments had consistently shown that bite-board image speeds are too slow to be optimal for vision. (See Kowler and Steinman, 1980, for a discussion of this fact and its significance.) It was not possible, however, for Skavenski *et al.* (1979) to study natural bodily movements or to examine compensatory binocular eye movements.

When it became possible to do this, we found that natural retinal image motions were considerably faster than expected from prior research on stabilized images, and also that retinal image motions were quite different in each eye. It is important to realize that most of the head rotations described in the present paper were not violent. The subjects were seated and moved their heads through modest angles at generally modest frequencies. The reader should attempt these motions while viewing a distant target. Be careful to keep their peak-to-peak amplitude less than 30° and their frequencies similar to those illustrated in the analog records reproduced in Fig. 1. We believe that you, like ourselves, will see perfectly well until your head twitches violently. Your retinal image

and vergence motions will almost surely resemble those of 1 of our 4 subjects. We hope that you will now wonder, as we do, how the brain deduces a single, clear and stable world in the presence of the retinal image motions we now know exist within and between the eyes.

It does not seem profitable at this time to speculate about how normal vision is accomplished under such conditions. The role of oculomotor compensation in vision needs further study before such speculations are likely to be useful. All we know now is that the simple idea that the oculomotor system compensates almost perfectly for motion of the body is not correct. Further understanding requires that we make visual psychophysical measurements in the presence of measured natural binocular retinal image motions. We believe that this is necessary because there are intimations in our research that the vestibular and visual systems interact in more complex ways than has been previously suspected. We are particularly intrigued by the possibility that vestibular signals are monitored by the visual system and used to compensate for retinal image motion that accompanies bodily movement. Less interesting explanations are certainly possible. For example, we may simply find that vision under the conditions of retinal image motion described in the present paper is actually much less keen than our phenomenological observations suggest. This can be determined by measuring contrast sensitivity and visual acuity for distant targets in the presence of binocular retinal image motion resulting from natural head rotations.

This kind of experiment, however, does not seem to have the highest priority. It seems more important to examine 2-dimensional binocular retinal image motion while human beings manipulate objects within arm's reach. Man, and other prehensile animals, use vision most carefully under these conditions. Such experiments require accurate measurement of translations of the head, as well as accurate measurements of rotations of both eyes and the head, if we wish to know what is happening on the retina. These kinds of experiments have the highest priority because manipulative tasks demand more of the oculomotor compensatory subsystems than the experiments we have done thus far. Vergence must change appreciably and accurately when nearby objects are manipulated if fusion and stereopsis are to be maintained. Psychophysical measurements must also be made under these conditions if we wish to relate what we find out about natural binocular oculomotor compensation to prior experimental studies of human binocular vision. Instrumentation, which will make these experiments possible, is nearing completion at the University of Maryland.

* One particularly germane example of the prevalence and danger inherent in making these assumptions will be given. Collewin (1977) described oculomotor performance in the freely moving rabbit and concluded that the rabbit's eye was *stable* with respect to space as the animal moved about. However, a closer inspection of the relatively insensitive recordings provoked by subsequent research (Winterson *et al.*, 1979) revealed that retinal image speeds, ranging from 1 to 14 deg/sec, were common when the rabbit's head was free to move. Oculomotor compensation in rabbit, like oculomotor compensation in man, is far from perfect. It can be easy to neglect this important fact when it conflicts with prevailing beliefs.

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