

Vision in the presence of known natural retinal image motion

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Previously we reported that failures of compensatory eye movements led to appreciable binocular retinal image motion during head rotation. Subjectively, the visual world appeared clear, fused, and stable under these conditions. The present experiments examined these impressions psychophysically. The spatial modulation transfer function of subjects with known retinal image motion was measured during head rotation. We found that contrast sensitivity was reduced for gratings over 6 cycles/degree and was increased for lower spatial frequencies. Our results, when compared with Kelly's [*J. Opt. Soc. Am.* **69**, 1340-1349 (1979)] measurements made with artificially moving stabilized gratings, show that natural retinal image motion is less harmful to contrast sensitivity at high spatial frequencies and more beneficial at low spatial frequencies. Furthermore, we had previously found that natural retinal image motion was different in each eye during head movement but no diplopia was noticed. We confirmed this subjective impression by measuring forced-choice stereoacuity thresholds concurrent with binocular head and eye recordings. Stereoacuity was not disturbed by large fixation disparities or high vergence velocities. Recordings also were made while a fused Julesz stereogram was viewed during attempts to break fusion with violent head movements. Fusion could not be broken. Stereograms turned on during violent head movement fused rapidly. We conclude that vision is better with natural retinal image motion than expected from experiments done with stabilized heads.

INTRODUCTION

Human beings, deprived of bite boards and chin rests, must use compensatory eye movements to maintain the retinal-image position of attended visual targets. These compensatory eye movements use both visual and vestibular information to move the eye so as to reduce motion of the retinal image when the head moves. Healthy human beings, except during quite violent movements of their heads, are under the impression that they see a single clear visual world as they move about. This widespread subjective impression had, until recently, encouraged oculomotor investigators to believe that oculomotor compensation for bodily movement was virtually perfect.¹ The world was seen as clear because compensatory eye movements prevented appreciable retinal image motion in each eye. The world was seen as single because the compensatory movements of the eyes were yoked, preventing appreciable vergence changes as long as the distance between the attended target and the observer did not change.

We began to question these assumptions about 5 years ago when it became possible to measure retinal image motion accurately and precisely when the head was free from artificial restraints. In our first, monocular, experiment we found that subjects, sitting or standing as still as possible, had retinal image speeds two to four times greater than retinal image speeds observed when their heads were stabilized with a bite board.² Subsequent technical advances made it possible to look at binocular oculomotor compensation while the head moved in a range of frequencies and amplitudes similar to those encountered in much normal human activity.³ We

found that binocular oculomotor compensation of head movement was rarely virtually perfect. Even when compensation was virtually perfect in one eye, it was not in the other eye. This led to appreciable noncorrespondence of fixation positions between the eyes and to high vergence speeds. Subjects, in all of this prior research, reported that the world remained perceptually clear and single as they moved their heads. These observations encouraged us to begin to study visual processing in the presence of natural retinal image motion. We found that vision was better with natural retinal image motion than would be expected from experiments done with moving targets and stabilized heads.

SPATIAL MODULATION TRANSFER FUNCTION DURING ACTIVE HEAD OSCILLATION

Three subjects (two of the authors, HC and RS, and subject EK) served in this experiment. Their natural retinal image motion was known because all three had previously served in experiments during which an extensive series of measurements were made of their compensatory eye movements during head movement.⁴ The subjects were required to adjust the contrast of a sinusoidal grating display, produced by conventional techniques, either while their heads were supported by a chin rest or while they oscillated their heads horizontally at $\frac{1}{3}$ or $\frac{4}{3}$ Hz through peak-to-peak amplitudes of about 34° . Their sinusoidal-like head movements were paced

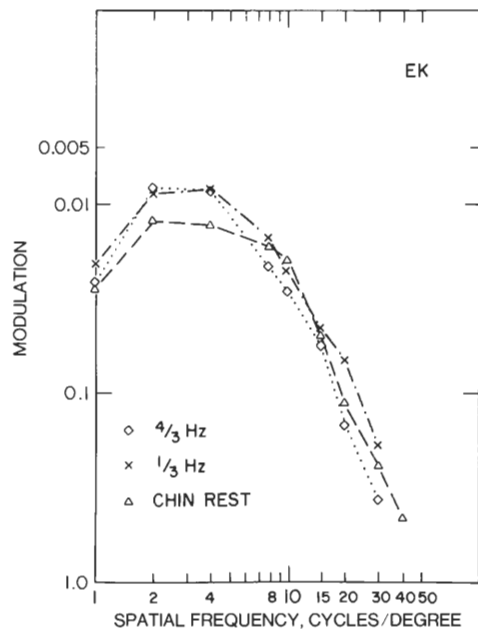


Fig. 1. Threshold grating contrast-modulation settings of subject EK as fractions of 100% contrast at various spatial frequencies. Three voluntary-head-movement conditions were used, as described in text.

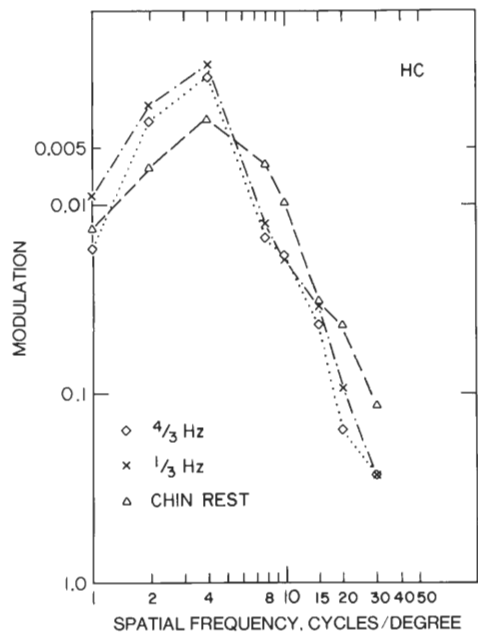


Fig. 2. Threshold grating contrast-modulation settings of subject HC as fractions of 100% contrast at various spatial frequencies. Three voluntary-head-movement conditions were used, as described in text.

by a metronome, as had been done previously in the above eye-movement experiments. All subjects were experienced psychophysical observers as well as eye-movement subjects. A verbally controlled method of adjustment was used to measure contrast thresholds because the subjects found it difficult to keep time with the metronome, control the amplitude of head movement, and simultaneously manipulate a potentiometer controlling the contrast of the display. Instead, the subject directed the experimenter verbally to increase or to decrease contrast until threshold was obtained.

Average threshold contrasts were not noticeably affected by this procedure, but their precision was improved. A high criterion was used, viz., the subjects set the display to a just-visible pattern of bright and dark bars. During head movement the subjects were careful to make their threshold determinations while the head was in the middle of its oscillation, where head speed and, therefore, retinal image speed would be at its maximum. This was in accord with their previous practice. The stimulus display, located 5.8 m from the eye, subtended 1° of visual angle and was surrounded by a 4° by 5° diffusely reflecting homogeneous white field of the same space-average luminance. The luminance of the display was 119 cd/m². Measurements were repeated until the experimenter (author JL) felt that a reliable estimate had been made of the spatial modulation transfer function (MTF) for each subject under each of the three conditions.⁵⁻⁷

Results are summarized in Figs. 1-3. The results for all three subjects were qualitatively similar. Head movement, with its concomitant retinal image motion, produced a need

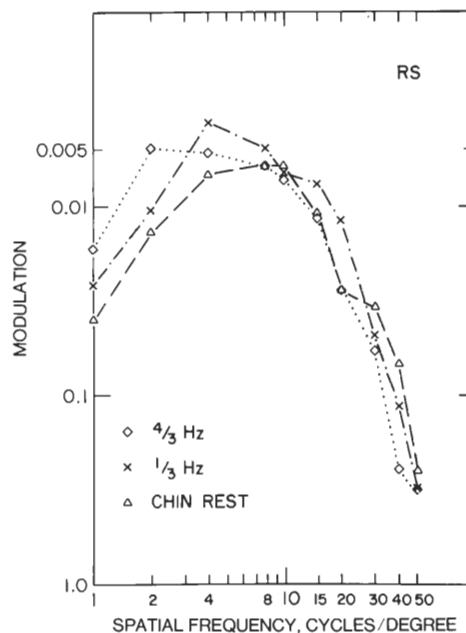


Fig. 3. Threshold grating contrast-modulation settings of subject RS as fractions of 100% contrast at various spatial frequencies. Three voluntary-head-movement conditions were used, as described in text.

Table 1. Mean Retinal Image Speed during Active Head Oscillation^a

Subject	EK			HC			RS		
	0	1/3	4/3	0	1/3	4/3	0	1/3	4/3
Head frequency (Hz)									
Image speed (arc min/sec)	22	51	150	24	50	185	22	38	108
Standard deviation	18	39	95	21	42	151	18	34	100
	Average of the Three Subjects								
Head frequency (Hz)	0			1/3			4/3		
Image speed (arc min/sec)	22.7			46.5			147.5		
Standard deviation	19.0			38.3			115.3		

^a Retinal image speeds, based on data obtained in a previous experiment,⁴ are the means of the combined right-eye and left-eye image speeds.

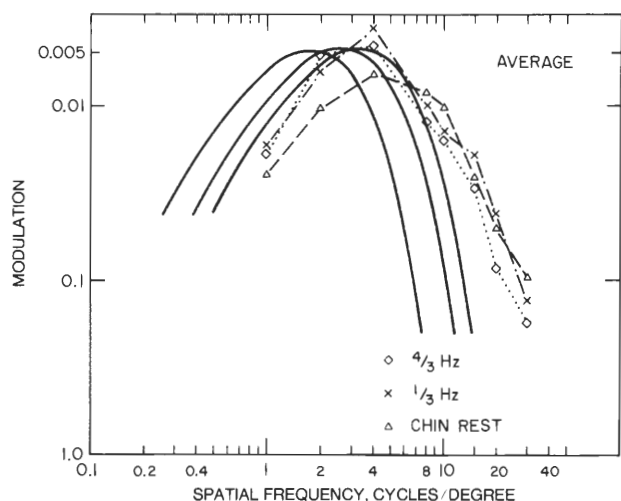


Fig. 4. Averages (geometric) of threshold contrast settings of three subjects under the three conditions of head movement. Solid curves are from Kelly⁸ for equivalent grating velocities with stabilized viewing.

for more contrast at high spatial frequencies and reduced the need for contrast at low spatial frequencies. The crossover in the functions (where moving the head causes high-frequency attenuation and low-frequency enhancement of contrast sensitivity relative to the function obtained with the head on a chin rest) occurred at about 10 cycles/degree for subjects EK and RS and at about 6 cycles/degree for subject HC. Note, however, that the deleterious effects of image motion on high spatial frequencies were modest for all three subjects, the differences in all cases being less than a factor of 2 of contrast. Also note that the extrapolated high-frequency cutoffs for each of the subjects under all the conditions would be well above 30 cycles/degree.

Table 1 summarizes smooth-eye-movement retinal image speeds (absolute velocities) associated with these kinds of head movements. The tabled speeds were measured in a prior experiment.⁴ Retinal image speeds were calculated with a sliding-window technique applied to eye position samples obtained at 5-msec intervals. The window, 35 msec wide, contained seven eye-position samples, and the slope of the line, fitted by least squares, through the seven position samples provided a single estimate of instantaneous retinal image speed. The window was then moved 5 msec later in time (one position sample), and the next speed estimate was calculated. Speed samples were also used to detect and remove saccades.

Figure 4 compares our results with those obtained by Kelly,⁸ who used an SRI double Purkinje image tracker to stabilize sinusoidal gratings upon which constant velocity motions were then imposed. Our results, shown by broken lines connecting data points, show the averaged results (geometric means) of our three subjects whose mean 35-msec smooth-eye-movement retinal image speeds are summarized in Table 1. The solid functions are derived from Kelly's spatiotemporal surface for the same retinal image speeds.

There are several differences. First, his extrapolated high-frequency cutoffs would lie between about 9 and 18 cycles/degree. Ours all fall above 40 cycles/degree—a difference of more than a factor of 2. Second, Kelly's crossover points occur below 3 cycles/degree. Ours crossover above 6 cycles/

degree—once again a factor of at least 2. We conclude that despite a superficial qualitative similarity there are interesting differences in our and Kelly's results.

There are a number of potentially important differences between our experiments that could contribute to the difference in results. Kelly imposed constant-velocity displacements of the gratings—his stimulus moved continually in only one direction. Kelly's relatively low-contrast sensitivity at high spatial frequencies and his relatively low crossover frequencies may reflect the effects of retinal velocity adaptation caused by continually moving the stimulus in the same direction.⁹ In other words, his constant-velocity technique could prevent normal processing by the visual system.

Our free-head movements were periodic, resulting in retinal image motions of approximately the same frequency as the head. These periodic oscillations are the normal inputs to the visual system, which, even with the head restrained on a bite board, occur, more or less sinusoidally, at frequencies predominantly in the range of 2 to 5 Hz. Even such small-amplitude (<10' peak-to-peak) oscillations are sufficient to prevent fading of targets located in the central fovea.^{10,11} Increasing the oscillation amplitudes by head movements improves contrast sensitivity at low spatial frequencies. But, of course, large-amplitude oscillations cannot but degrade the visibility of high-spatial-frequency gratings. The loss in acuity that we have found for image motion obtained with oscillatory head movements should be compared with the loss found with comparable oscillatory image motion imposed on a stabilized display. We intend to do this in the near future.

It is, of course, also possible, but much less interesting, that the differences shown in Fig. 4 (wherein we find the average curves of our three subjects, each of whom performed similarly, were different from the curves reported by Kelly) merely reflect the fact that Kelly's measurements are based exclusively on his eye, which is atypical in the general population. Other uninteresting possible reasons for the differences in our results include the fact that we made measurements binocularly, whereas Kelly's were monocular. Probability summation would not seem sufficient to predict the kind of differences we observed. Similarly, luminance differences in the two experiments do not seem likely to be sufficient to offer an explanation. We worked at 119 cd/m². Kelly reports 300 Td (pupil diameter unspecified). It is likely that our retinal illumination was essentially the same as his.

Finally, yet another explanation—a speculative but tempting one. Suppose the compensatory-eye-movement subsystems, which do not correct eye position perfectly, achieve perfect correction for head motion at the visual neural level. Julesz has postulated a "neural remapping" for retinal disparity in stereopsis.¹² Why should not a horizontal shift in the neural representation of the image on the retina also be produced by compensatory-eye-movement signals? The vestibularly driven compensatory subsystem seems a particularly promising candidate because it knows what the head is doing and could also know its customary preferred percentage of compensation for each eye.⁴ Of course, before following this speculation further, the other above-mentioned explanations must be ruled out.

Arend's¹³ experiments on sensitivity to gratings when the subject tracks a spot oscillating across the grating (at two speeds, 0.5 and 5 deg/sec) are very relevant here. Low-spa-

tial-frequency sensitivity is enhanced, and high-frequency sensitivity is reduced. At frequencies above 5 cycles/degree "there was no apparent detrimental effect of tracking the 0.5 deg/sec target, but the effect was very strong in the 5 deg/sec condition; the dropoff of sensitivity increased rapidly as the spatial frequency increased, reflecting the linear increase of temporal frequency on the retina with increasing spatial frequency." A tracking speed of 5 deg/sec is only about twice the greatest image speed in our experiments. Even so, Arend, like Kelly, found greater acuity losses than those reported here. But, like Kelly, in Arend's experiments the head was not moved. Only the eyes moved. This still leaves the possibility that a vestibular contribution enhances acuity when the image motion is produced by head motion. Something has to get around "the linear increase of temporal frequency on the retina with increasing spatial frequency." Further speculation had better wait for further experimentation.

STEREOACUITY

Understanding the effects of retinal image motion on contrast sensitivity would be only a partial step toward understanding visual processing. The visual system does more than abstract the presence of variations in contrast. It is also exquisitely sensitive to the relative position of details within the visual array presented to a single eye and to the relative differences in position of elements presented independently to both of the eyes. These accomplishments, vernier acuity and stereoacuity, have been called examples of visual "hyperacuity" by Westheimer.¹⁴ They are called hyperacuties because resolution of relative position differences is smaller than the cellular separation within the densest part of the receptor mosaic where separation is on the order of 20". We already knew from the experiments of Westheimer and McKee¹⁵ that vernier acuity would be preserved in the presence of appreciable retinal image motion. Their findings are consistent with our subjective impressions that relative positions of details are seen clearly in the presence of head movement, which our recent work has shown produce appreciable monocular retinal image slip. The situation was not so clear, however, for stereoacuity because stereoacuity is believed to require relatively stable binocular yoking.

Stereoacuity, like vernier acuity, suffers little when the target pair moves laterally together as fast as 2 deg/sec in the frontal fixation plane, but, when stereoacuity is measured with the test targets moving at various distances in front of or behind the fixation plane, stereoacuity deteriorates by a factor of 4 when the test plane and the frontal fixation plane differ by as little as 10'.¹⁶ We, therefore, studied stereoacuity thresholds concurrent with measurements of natural binocular retinal image motion because we knew that large oscillatory changes in vergence (>30') would be common during head movement.^{3,4} Our observed changes in vergence imply that the frontal fixation plane moves continually toward and away from the observer when the head oscillates. Vergence changes also imply that the relative retinal positions of the stereo test-target details change as the head moves. We had no idea from the previous work how stereoacuity would fare under these previously unexplored but natural conditions.

Stereoacuity thresholds of three subjects (one of the authors, JV, and two other young emmetropes) were measured while horizontal head and binocular eye movements were

recorded with the revolving magnetic-field-sensor coil technique.³ This instrumentation, as used in the present experiments, had a bandwidth, after digital filtering, of 0–40 Hz and a noise level of 3' peak to peak.

The stereoacuity stimuli were red–green color-coded anaglyphs made by photographing a black bar mounted on a micrometer movement in front of a transilluminated screen upon which a number of haphazardly positioned black paper rectangles had been mounted (the rectangles subtended about 0.5° near the center of the display and increased in size to about 5° in the periphery). High-contrast photographic negatives obtained with the movable bar at different lateral positions with respect to the screen, paired with a negative of the display with the bar in the center of the screen, were used as the stereo stimuli. These negatives provided no depth cues of any kind other than disparity. The screen, on which the pair of stereo slides was projected, was located 5.45 m from the subjects' eyes. The red–green filters, used for presenting each slide to a different eye, allowed only about 0.5% cross talk. The subject wore a pair of spectacles, containing one red and one green filter. A movable filter wheel permitted the experimenter to exchange silently the filters in front of each of the slide projectors, permitting the bar, which appeared bright in the negative, to be presented in a stereo view that would, after fusion, appear either in front of or behind the plane of the projection screen that contained the pattern of bright and dark rectangles. The entire stereoacuity stimulus was 17.5° wide and 11.1° high. The bright vertical bar test stimulus, which was the full height of the test field, was 0.44° wide. Ten pairs of slides were available, covering a range of disparities from 11.4" to 58.6". The stereo test stimuli, therefore, consisted of 20 pairs because each pair could be presented with the red–green filters arranged so as to cause the bar to be seen either in front of or behind the plane of the projection screen.

Measurements were made in the following manner. There was an initial practice session during which the subject's stereoacuity threshold was measured by a forced-choice method of constant stimuli under each of four conditions, viz., sitting still or oscillating the head approximately sinusoidally at 1/3, 2/3, and 4/3 Hz through a peak-to-peak amplitude of about 20°. The subject, either sitting still or oscillating his head in time with a metronome, opened his eyes and viewed each stereo-target pair chosen randomly so that the bright bar appeared either in front of or behind the plane of the display. The subject responded either "front" or "back" on each trial. The experimenter then informed the subject of the correctness of his response. During his practice session, trial length was not restricted, and we observed that all three subjects responded within 1 or 2 sec after the test stimuli came into view. Following this practice session, measurements were made by mounting a sensor coil on the head and a silicone-annulus sensor coil on each of the eyes.¹⁷ The experimental sessions were run in essentially the same manner as the practice session except that trial length was fixed at 3 sec. The subject, who typically saw the fused test stimulus near the beginning of the trial, refrained from responding until the 3-sec trial was over. This was done in order to exclude head and eye movements associated with talking from being included in the recordings.

Typical eye and head movement records for each of the subjects are reproduced in Fig. 5. These records were taken

from trials in which the subjects responded correctly to disparities as small as 11.4". These recordings show the position of the head and eyes with respect to the position of the stereotargets in space. If oculomotor compensation of head movement had been perfect, the eye traces (RE and LE) would be horizontal straight lines. As we have reported before, compensation is rarely perfect.²⁻⁴ There is appreciable retinal image motion in each of the eyes. Furthermore, compensation is different in each of the eyes, leading to appreciable changes of vergence (LE-RE) despite the fact that the target distance was fixed at 5.45 m from the subject. If the eyes had been perfectly yoked, the change of vergence trace would also be a horizontal straight line. The change of vergence trace is of particular interest in this experiment because it shows that vergence changes as large as $\frac{1}{2}^\circ$ to 1° are common in the records of each subject, particularly when the head moved at $\frac{4}{3}$ Hz. The stereoacuity target was correctly detected and continued to be visible throughout these trials.

It should be noted that if vergence and disparity were to provide the primary perceptual cues underlying the perceived distance of the display, the display should appear to move toward and away from the observer as vergence changes when the head moves. Such changes in perceived depth were not perceived. Rather, the percept was veridical. After fusion, a single bar, relatively near or far from the plane of projection,

was perceived. The bar's relative perceived position, determined by the absolute disparity of the test slide pair, remained stable in the presence of the vergence changes illustrated in Fig. 5. It is also apparent in these records that saccades, made during head movement and while sitting still, were occasionally dissimilar in direction and size in each of the eyes—an observation that we reported previously in other subjects.³

The vergence speeds (absolute velocities) obtained for these subjects under the various conditions are summarized in Fig. 6. These speeds are based on successive saccade-free periods of 100 msec in which a linear regression was calculated over the 33 data points that were obtained during such periods. Mean vergence speed when the subjects were sitting still was about 20"/sec. Mean vergence speed rose to more than 1°/sec when their heads were moving at $\frac{4}{3}$ Hz.

Psychophysical performance is summarized in Fig. 7. Clearly, we measured only the upper limb of the psychometric stereoacuity function. Subjects were correct on more than 85% of the trials even when the stimulus had a disparity of only 11.4". Differences between data obtained while sitting still and while moving the head were not large or statistically reliable, nor were there reliable correlations between retinal image speed and incorrect responses.

All subjects claimed that it was easier to fuse the stereograms and see the bar while they were moving than when they kept their heads still. The psychophysical data do not sup-

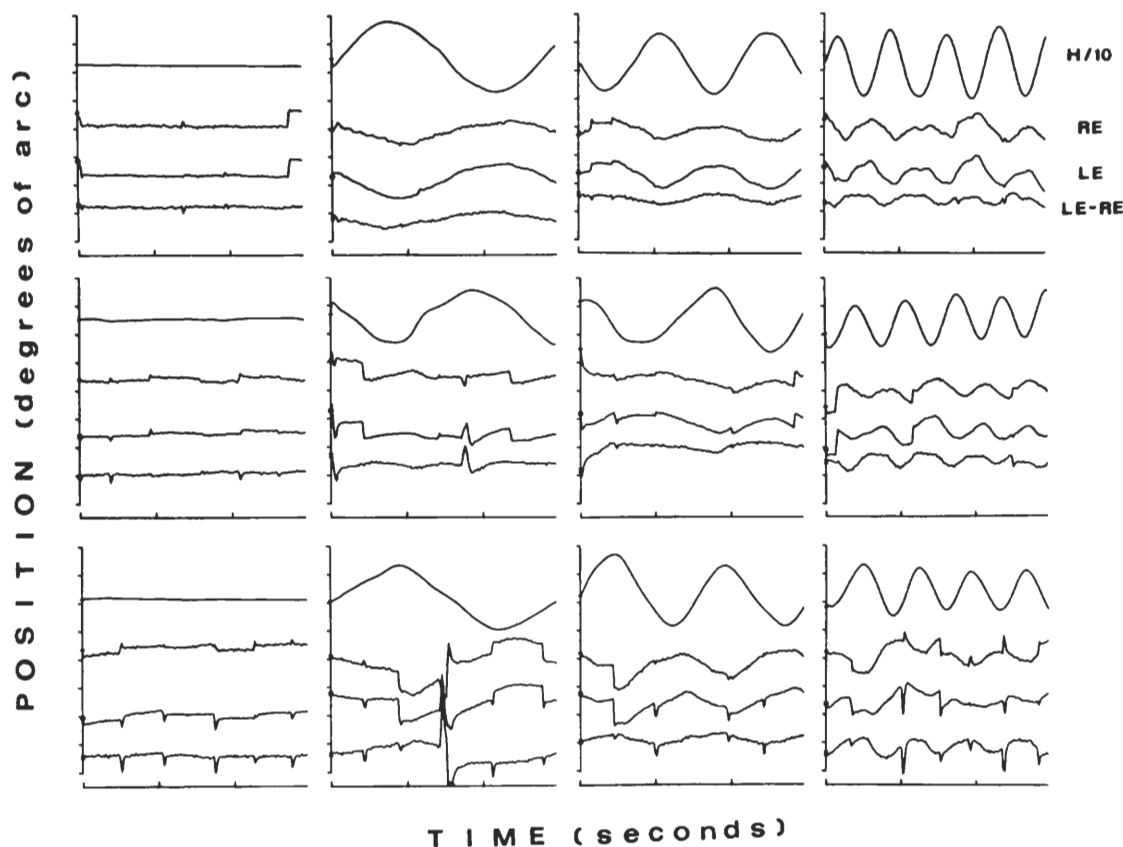


Fig. 5. Average head and eye movements of three subjects with respect to an earth-fixed framework. Recordings were made under four conditions from left to right: Head still; $\frac{1}{3}$ -, $\frac{2}{3}$ -, and $\frac{4}{3}$ -Hz left-right oscillations per second. Head rotations are reduced in scale by 10. Eye rotations, RE and LE, show considerable, but certainly incomplete, and variable, compensation when the head moved. If compensation had been perfect, the eye traces would be horizontal straight lines, i.e., the target image would not move on the retina. These residual eye rotations, then, represent retinal image motion in each of the eyes. The trace labeled LE-RE represents changes of vergence resulting from different degrees of compensation in each of the eyes. Methods are described in the text.

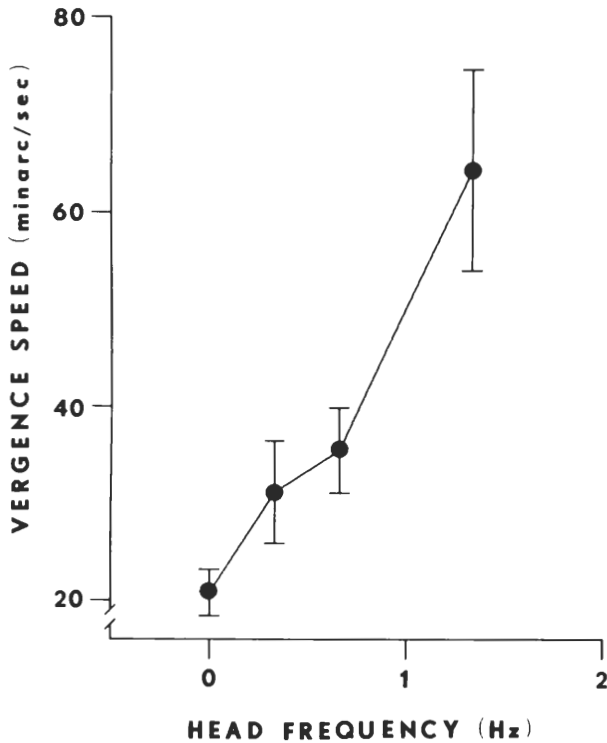


Fig. 6. Mean vergence speed (absolute velocity) as a function of head frequency for three subjects. The error bars (standard deviations) show intersubject variability.

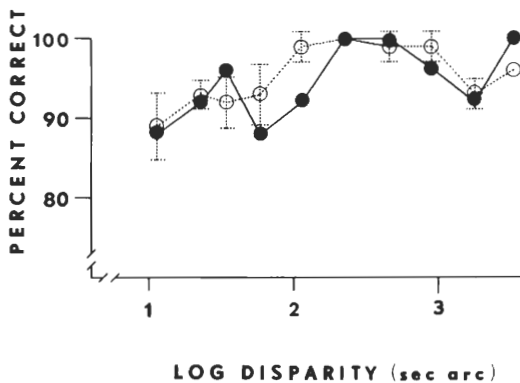


Fig. 7. Accuracy of report of target position (percent correct) as a function of disparity of the stereostimuli. The data points represent the average of three subjects. The closed circles show average performance when the subjects kept their heads still (0 Hz). The open circles show average performance when they moved their heads at 1/3, 2/3, and 1 Hz. The error bars (standard deviations) show the variability associated with moving the head at three different frequencies.

port these subjective reports, but we cannot rule out their claim, which might be supported when actual thresholds are measured with a finer set of test stimuli. Our results show that stereoacuity is preserved in the presence of fast and large changes of vergence. This result could not have been predicted from previous work, which restricted head movement and tested acuity in or near the relatively stable frontal fixation plane that is observed under such restricted conditions. The fact that our subjects encountered little difficulty in fusing stereograms with large image separations—separations greater than 1/2°—led us to the next experiment, in which we examined the effect of natural vergence changes, arising from

mismatches in oculomotor compensation, on random-dot stereograms.

ESTABLISHMENT AND MAINTENANCE OF FUSION OF RANDOM-DOT STEREOGRAMS DURING HEAD MOVEMENT

The observations to be reported confirm objectively subjective observations made by MacLeod when he first heard about our previous work in which we reported appreciable perturbations of vergence during head movement. MacLeod viewed chromatically coded fused Julesz stereograms¹² and shook his head, noticing that he was unable to break fusion despite rather violent head movements. He also noticed that if he had his head in motion and then viewed the stereoplates, fusion occurred rapidly. We repeated these experiments, this time measuring binocular eye and head movements. We used an easily fused random-dot Julesz stereogram, a triangle, with the colored filters arranged to make it appear in front of the plane of projection that was 5.45 m from the subject. The projected stimulus pair was about the same size as the stereoacuity display described above. Disparity was 22.7'. First, we recorded attempts to break the fusion. Results of this experiment are illustrated in Fig. 8.

The subject (author RS) made the most violent head movements he could while keeping their amplitude within our useful recording range, about 25° peak to peak. As expected, compensation in each eye was not complete and was different

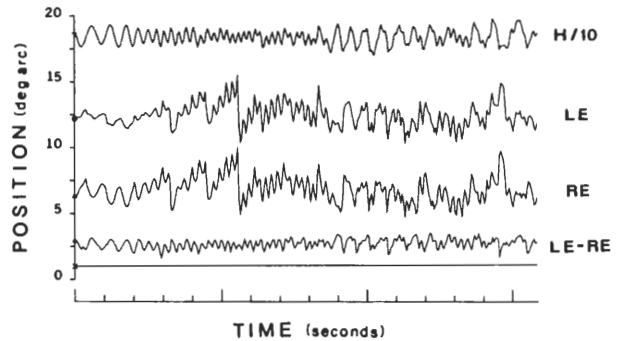


Fig. 8. Subject RS's head and eye movements with respect to an earth-fixed framework while attempting to break fusion. Head swings, about 25° peak to peak, were made as rapidly as possible. See Fig. 5 for the significance of the labeled traces. The bottom line, a psychophysical indicator, would have dropped to zero had fusion been broken.

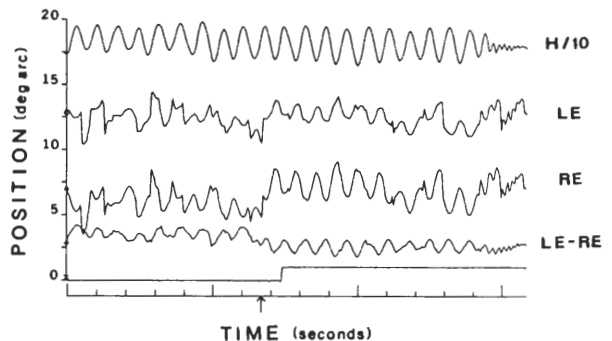


Fig. 9. Acquisition of fusion on presentation of display (arrow) during head rotation. Upward deflection of bottom line indicates fusion, less than 1/2 sec after display onset. The significance of the labeled traces is the same as those reproduced in Fig. 5.

in each of the eyes, leading to changes of vergence. The solid line at the bottom of Fig. 7, the psychophysical trace, indicates that fusion was maintained throughout the 16-sec trial illustrated in this record. Mean change of vergence speed on this trial was $5.5^\circ/\text{sec}$ (standard deviation, 3.74). Trials with mean change of vergence speeds as high as $8.2^\circ/\text{sec}$ (standard deviation, 8.24) were recorded. All efforts to break fusion were unsuccessful. The triangle appeared to move slightly from side to side but always remained clearly visible and fixed in depth well in front of the background. The mean standard deviation of vergence change was 0.38° . Clearly, Panum's fusional area during natural head movement is not only large it is also relatively insensitive to rapid changes of vergence.

The typical result of the second experiment is shown in Fig. 9. Here the head was in motion for 6.5 sec before the display was projected. The display was projected at the time indicated by the arrow on the abscissa. The moment of fusion and its persistence throughout the remainder of the trial is indicated by the upward deflection in the lowest psychophysical trace. The psychophysical trace shows that fusion occurred less than $\frac{1}{2}$ sec after the presentation of the display despite changes of vergence as great as 2.5° . The mean vergence speed on this trial was $2.7^\circ/\text{sec}$ (standard deviation, 1.75). Mean vergence speeds as high as $8^\circ/\text{sec}$ gave the same results. Five other members of the laboratory viewed the display during head movement and found it impossible to break fusion and easy to establish fusion while they moved their heads. Our results with the random-dot stereograms, once again, suggest that retinal image motions arising from the failure of the compensatory-eye-movement subsystems to perform virtually perfectly are not so detrimental to visual processing as would be expected from experiments in which motion was imposed on displays while the head was kept immobile. We will now review previous work in justification of this claim.

Fender and Julesz¹⁸ used a contact-lens optical-lever technique to stabilize stereotargets whose image separation could be varied. Two types of targets were used—a single line pair and a pair of random-dot stereograms. They found that the line pair, fused and seen in depth, would continue to be fused and seen in this manner as image separation was increased to about $60'$ where fusion was broken. Once fusion was broken, however, image separation had to be reduced to about $40'$ before the lines could be re-fused. The result with the random-dot stereogram pair was qualitatively similar but quantitatively very different. Fusion was maintained as image separation was slowly increased to be about 2° before fusion was broken, and, once broken, image separation had to be reduced to about $6'$ before the random-dot targets could be re-fused. They called this asymmetry (the persistence of fusion to large image separations in contrast to the requirement of small image separations to reestablish fusion) "hysteresis." Diner¹⁹ repeated this kind of experiment with line targets, elaborating the technique so as to make it possible to make convergent as well as divergent changes of image separation. He also obtained evidence for hysteresis, but the range of image separation over which fusion was maintained was less than half of the range reported in the original paper.¹⁸ Recently, Hyson *et al.*²⁰ studied these phenomena under what the authors considered to be more natural conditions. Stabilization was not used. The subject's natural eye movements

were recorded while the separation of a random-dot target pair was varied. They found that Panum's fusional area could be as large as 5° . Evidence for hysteresis was also obtained. Once fusion was lost, vergence saccades were required to re-establish fusion by realigning the stimulus pair to its initial image separation. In all of this previous work the experimentally introduced changes in the relative positions of the stimulus pair were slow— $2'/\text{sec}$ in the early work and only $10'/\text{sec}$ in the most recent report. Our experiment was quite different. When our subjects oscillated their heads, changes of vergence with concomitant changes of disparity of several degrees each second occurred naturally while fusion was maintained. Also, and even more important, fusion could be established within a simple reaction time in the presence of similar perturbations. This result is important because it implies that hysteresis may not be characteristic of natural stereopsis. We have no indication that establishing fusion required much smaller disparities than will be tolerated after fusion is established.

Furthermore, vergence saccades, essential to reestablish fusion in the study of Hyson *et al.*,²⁰ were relatively rare in our experiment (see Figs. 8 and 9). They were not required either to maintain or to establish fusion. In Fig. 9 we see only a very well-yoked pair of conjugate saccades (versions) in the period near the presentation of the stimulus pair and the subject's psychophysical report. Both eyes looked to the right, probably toward the center of the display where the subject saw, or expected to see, the triangle. It should be noted, however, that our experiment and the experiment of Hyson *et al.*²⁰ were quite different. They held the head still and changed image separation. This is equivalent to moving an object toward and away from the observer, requiring vergence changes to keep the stimulus fused or to re-fuse the stimulus if fusion breaks down. We did not change image separation experimentally. Our changes in image separation, which were fast as well as large, were the result of differences in the degree of compensation each eye showed in the presence of active head oscillations. In our experiment the visual system could use vestibular signals to tell it about the velocities to expect as inputs from each retina. The vestibular system knows how the head is moving. The visual system need only know the amount of compensation characteristic of each of the eyes for a given head movement. If it did, it could use this information for a neural remapping, which could, in this case, maintain or establish stereopsis. We introduced this speculation earlier when comparing our and Kelly's⁸ results on the effects of retinal image motion on the spatial MTF. We cannot add to this speculation at this time and conclude by claiming only that our results show that vision in the presence of natural retinal image motion, produced by failure to compensate completely for head movement, is more robust than could have been expected from previous work that stabilized the head and manipulated the visual stimulus. We are intrigued, however, by the possibility, and hope to be able to prove, that visual processing and oculomotor compensation operate synergistically under natural stimulating conditions. Put simply, the vestibular system helps us to see as we move about. The vestibular system does this not by its perfection of oculomotor control, which we know is beyond its capacity, but, more plausibly, by telling the visual brain about its quirks.

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