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The Precision of Gaze*

A Review

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Summary: This paper reviews advances in our knowledge about the stability of the human being's line of sight while fixating objects stationary with respect to himself. Recent technological developments made it possible to measure gaze with a high degree of accuracy when the head was free of artificial support. Measurements made with the head free while the subject sat, as still as possible, show that gaze is half as stable as when the head is held rigidly. Precision deteriorates by an additional factor of five when the head is moved actively or passively within a range of natural physiological frequencies and amplitudes. Fixation errors and retinal image motions associated with such imprecision of gaze under natural conditions would not be expected to degrade monocular vision in light of current psychophysical evidence. Binocular fixation errors and differences in retinal image motions in each of the eyes, associated with imprecision of vergence under natural conditions, cannot, however, be reconciled with current psychophysical knowledge of binocular vision attained thus far only under artificial conditions.

Key words: Compensatory eye movements – Fixation stability – Vestibulo-ocular response – Plasticity – Vergence

The Role of Eye Movement

The human oculomotor system has been studied for many years. There are good reasons for such interest. In foveate animals, such as ourselves, changes in eye orientation are required to fixate, i.e., bring an attended detail to the center of the fovea. Changes in eye orientation are also required to keep fixated objects relatively stationary when we move and also to maintain fixation of moving objects when we sit still. For reasons such as these, human eye movement characteristics and their functional significance must be understood if we wish to understand how a human being sees clearly, knows where things are, knows whether they are stationary or moving, and knows where he is in relationship to them.

It only became possible to study human oculomotor characteristics accurately about 30 years ago when recording techniques were developed which allowed the measurement of small rotations of the eye free from confusion with translations of the head, provided that the head was supported on a well-constructed dental bite-board. During the ensuing years human oculomotor performance has been under intensive study and the results of these studies have been reviewed frequently (the most recent general review can be found in Carpenter 1977). The present review describes the status of current knowledge about only a single aspect of human oculomotor system performance: The precision with which a human being can maintain his line of sight on an object stationary with respect to himself. This characteristic of human oculomotor performance is being re-examined because recent technological advances now allow accurate measurement of the precision of gaze in subjects free from artificial supports. Measurements made under such natural conditions show gaze to be much less precise than had been expected. These new findings raise questions about how we perceive a clear, stable, and fused world under natural conditions. It is now clear that this perceptually significant achievement does not result simply from the virtual perfection of human compensatory eye movements as had been generally believed. The new results and their significance will be described following a brief review of the results obtained in prior research. In all prior research the precision of gaze was studied under unnatural conditions.

The Importance of Precision of Gaze: Traditional View

Precise gaze is quite important for effective vision because of the high degree of heterogeneity in functional properties of the human retina. It is only the foveal floor, a region about 1.5° in diameter, that is capable of providing good resolution of visual input. The keenest vision is obtained only when the attended detail falls near the center of the foveal floor in the "foveal bouquet" (LeGrand 1957) – a region of high receptor density which has a diameter of about 20′.

The first accurate demonstration of the precision of human gaze was provided by Ratliff and Riggs (1950) who used a contact lens optical lever to measure fixation stability of subjects whose heads were stabilized in space by means of a tightly-fitted bite-board. They reported that the standard

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deviation of the line of sight on the horizontal meridian was of the order of 5′. Three kinds of eye movements were observed while the subject maintained fixation with such precision, namely, physiological nystagmus, microsaccades, and slow drifts. Physiological nystagmus (also called high frequency tremor) has a frequency of 20 Hz to 100 Hz and a median amplitude of about 20″. Such tremors are too small to be of visual significance because the cone to cone separation in the foveal bouquet is equal to the amplitude of the tremor. This means that the retinal image of the fixation target cannot be displaced significantly by these minuscule tremors. Microsaccades are much larger and could, therefore, have significant visual consequences. Microsaccades, which occur once or twice each second, have an average amplitude of about 5′. The line of sight drifts slowly during intersaccadic intervals with velocities on the order of 5′/s to 15′/s.

Cornsweet (1956) explored the functional significance of the microsaccades and slow drifts observed during maintained fixation by recording horizontal eye movements with a contact lens optical lever. He proposed, and supported experimentally, the idea that slow drifts arose from instabilities in the oculomotor control system. Slow drifts allowed the line of sight to wander away from the fixation target. Resulting fixation errors were corrected periodically by microsaccades which returned the line of sight to the target. Many features of Cornsweet's results were confirmed by Nachmias (1959, 1961) who made 2-dimensional recordings of the fixation eye movement pattern. Nachmias discovered that slow drifts could also serve a corrective, as well as an error-producing function. Subsequently, Fiorentini and Ercoles (1966) and Steinman et al. (1967) showed that microsaccades, characteristic only of adult human fixation, can be eliminated by simple instructions and that when microsaccades are eliminated, precise control of the line of sight is accomplished entirely by smooth eye movements. Steinman et al. (1973) called such low velocity fixation "slow control". This low velocity "field-holding reflex" (Walls 1962) typically shows standard deviations of position of the line of sight of 2′ to 4′. (See Steinman et al. 1973, for a review of research on fixation. See Ditchburn 1980, and Kowler and Steinman 1980, for a recent review and controversy concerning the functional significance of the various fixational eye movements.)

Natural Gaze is Not Precise

It is important to remember that the head was stabilized artificially in all of this work on the precision of gaze. It is easy to understand how clear and stable vision can be maintained under this condition because, once the head is stabilized artificially, the attended fixation target rarely moves far from the preferred fixation position and the velocities with which it moves on the retinal surface are very modest – less than 0.25°/s. Does this mean that clear and stable human vision can only be obtained by supporting the head on a rigid metal structure? Subjectively, this does not seem to be necessary. We all maintain our capacity to function visually during a wide range of bodily activities. But once a human being removes his head from an artificial support, he must move his eye to maintain his line of sight on a stationary detail if his head moves. There are compensatory eye movements which can be used to stabilize the line of sight when the head is free. These compensatory eye movements are generated in part by signals from the semicircular canals which initiate the vestibulo-ocular reflex (VOR). The operation of the VOR, working alone, is best studied in total darkness while a subject imagines he is fixating a stationary distant target. This is, of course, only a laboratory convenience. In natural conditions the VOR can be supplemented by vision because the slip of the image of the fixation target on the retina generates signals that can initiate smooth pursuit eye movements. Smooth pursuit, like the VOR, serves to stabilize the target image. It is these compensatory eye movements (the VOR supplemented by smooth pursuit or the optokinetic response) which have

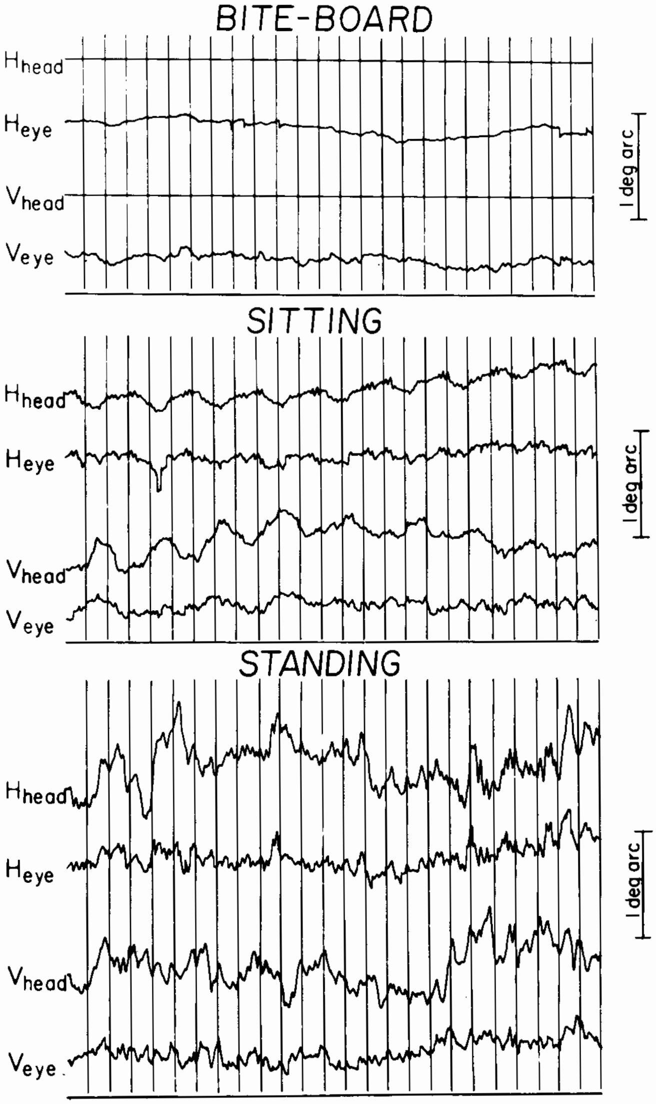

Fig. 1. Representative simultaneous recordings of horizontal (*H*) and vertical (*V*) head position and gaze (retinal image position) of subject *AS*, fixating a target at optical infinity, while his head was supported by a bite-board or while sitting or standing as still as possible without artificial support. Time began on the right and repetitive vertical stripes indicate 1 s intervals. The length of the vertical bars on the right corresponds to a 1° arc rotation on either meridian. Upward changes in head and image traces signify rightward movements in (*H*) and upward movements in (*V*). (From Skavenski et al. 1979)

traditionally been assumed to underlie our ability to see clearly when our heads are not stabilized artificially. Note, however, that it had been assumed and not demonstrated that these compensatory eye movements are "virtually perfect" (Wilson and Melvill Jones 1979), providing the oculomotor equivalent of a mechanically stabilized platform.

It is here that we encounter the problem which inspired our recent work on the precision of gaze under natural conditions. The only basis on which compensatory eye movements are believed to be virtually perfect is the fact that the visual world remains clear, stable, and fused over a wide range of bodily activities. This belief, although based on very compelling subjective perceptual experiences, could be unfounded. It is equally plausible that compensation for bodily movements by the oculomotor system is only partial and our ability to see a clear, stable, and fused world arises from visual processing of moving retinal images. We studied this problem and found that the clarity, stability, and fusion of the visual world cannot be based on the perfection of compensatory eye movements. Natural gaze is not precise.

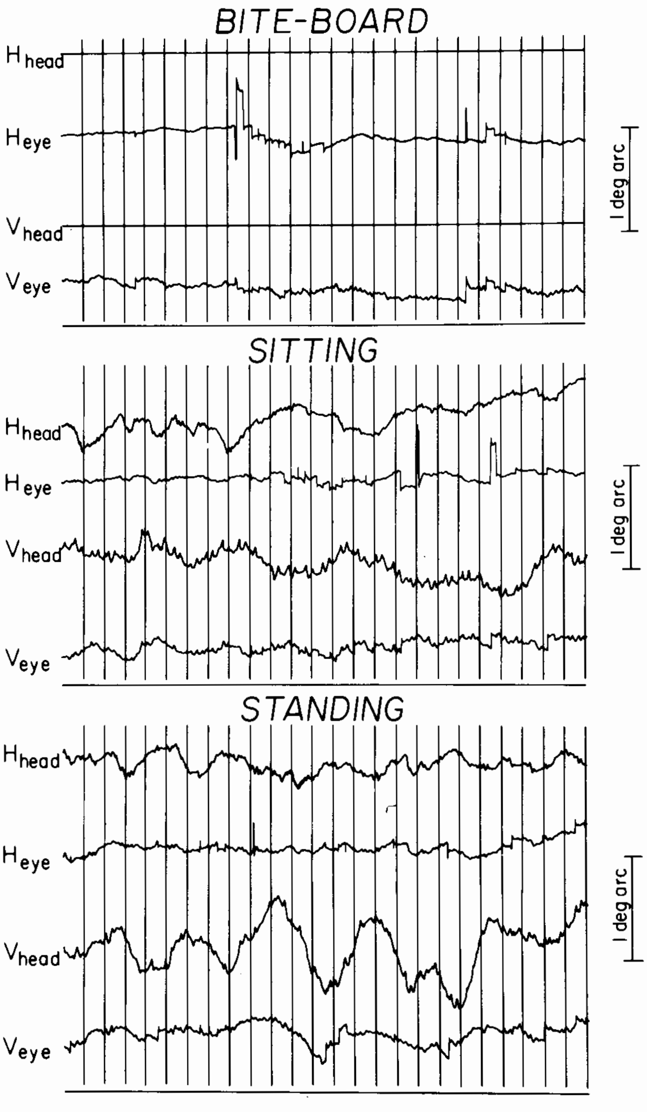

Fig. 2. Representative simultaneous recordings of horizontal (*H*) and vertical (*V*) head position and gaze (retinal image position) of subject *RS*, fixating a target at optical infinity, while his head was supported by a bite-board or while sitting or standing as still as possible without artificial support. See Figure 1 for other details. (From Skavenski et al. 1979)

The first step was made by Skavenski et al. (1979) who measured 2-dimensional monocular eye movements of two subjects fixating a target at optical infinity. Figures 1 and 2 show representative recordings of horizontal and vertical head and eye movements when their head were supported on a bite-board or when they sat or stood *as still as possible* with their heads free. These recordings were made relative to an earth-fixed framework so the eye position traces represent retinal image motion of the fixation target. (See Ratliff and Riggs 1950, for a justification for inferring retinal image motion from eye rotation with targets at optical infinity. See below for a justification with nearer targets.)

There was relatively little retinal image motion when the head was supported on a bite-board as would be expected from previous research. However, when the subjects sat or stood with unsupported heads, retinal image motion increased by a factor of 2 to 4. Remember that these subjects were sitting or standing *as still as possible*.

Skavenski et al. (1979) were limited by technical considerations to recording only one eye and that eye had to remain with a 1 cm^2 area to avoid artifacts introduced by translations of the head. Two questions remained. What happens to the precision of gaze when we allow ourselves to move, and what happens when we view the fixation target binocularly? Steinman and Collewijn (1980) began to answer these questions by examining horizontal binocular retinal image motion during natural active head rotations. They found that oculomotor compensation was incomplete, which meant that there was extensive retinal image motion in each of the eyes (average velocities of about 4°/s). Furthermore, they found that the amount of compensation was different in each eye which meant that vergence velocities were high (about 3°/s). These results are shown in Figure 3.[1]

In subsequent experiments with a more accurate instrument, Collewijn et al. (1981a) confirmed that retinal image motion is appreciable during passive, as well as active, head rotation and extended the observations to a larger sample of subjects. Figures 4, 5, 6, and 7 and Table 1 illustrate these results.

Modest retinal image motion was only observed in the unnatural condition when the head was stabilized by a bite-board. Off the bite-board, there were few instances where head motion was completely compensated. In these instances compensation was achieved by only one eye. In all of the experiments described so far the visual world remained clear, stable, and fused. The precision of gaze is summarized for 5 subjects in Table 1. First consider gaze when the head was supported on a bite-board and the subject remained stationary in space (frequency 0.0 Hz). Gaze was as stable (~ 3′) as would be expected from the large body of prior research

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[1] Records reproduced for subject HC in Figure 3 exaggerate gaze displacement (retinal image motion). This came about because of the failure to use an appropriate correction for the magnification factor of this myopic subject's spectacles. This error was corrected in subsequent research and his true gaze displacement is shown in Figure 4. See Collewijn et al. (1981a) for the behavioral technique used to obtain accurate estimates of magnification factors

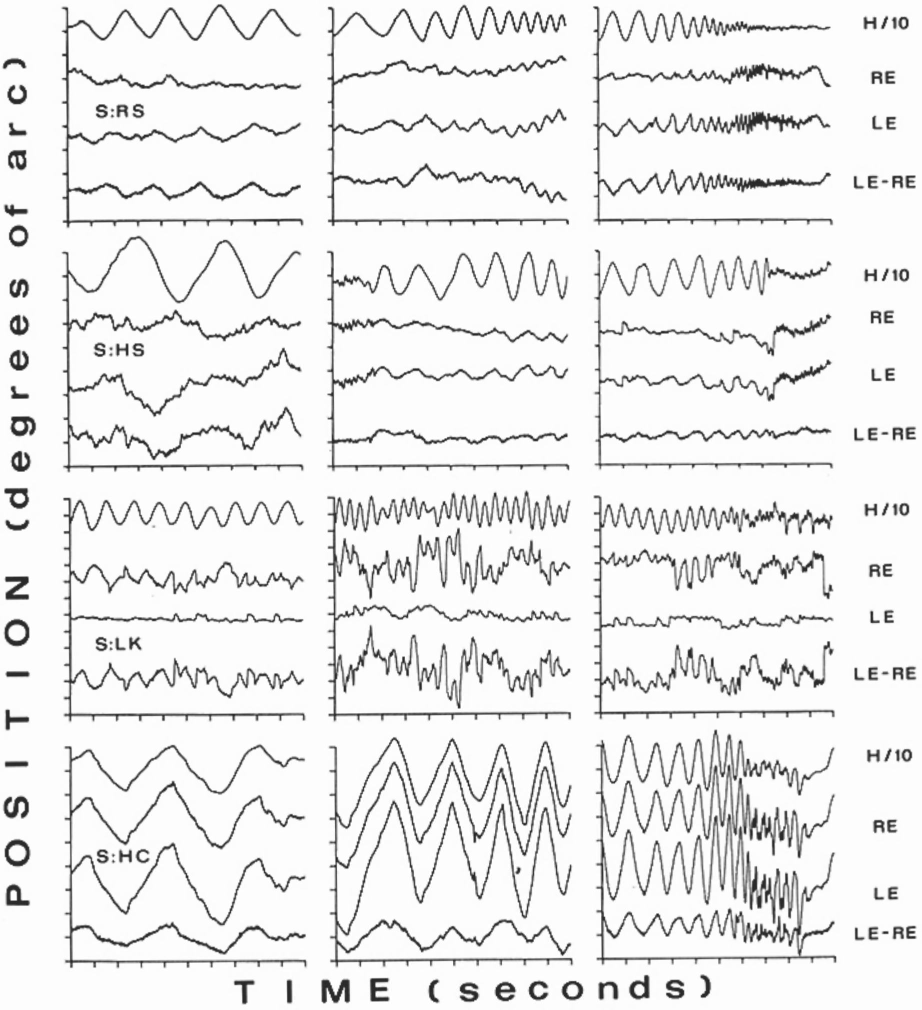

Fig. 3. Representative recordings of horizontal head position and gaze (retinal image position) of 4 subjects (*RS, HS, LK* and *HC*) while they fixated a distant object and actively moved their heads. Each of the 12 records begins on the left. The time scale-marks signify 1 s intervals. The position scale-marks signify 1° rotations. 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. (From Steinman and Collewijn 1980)

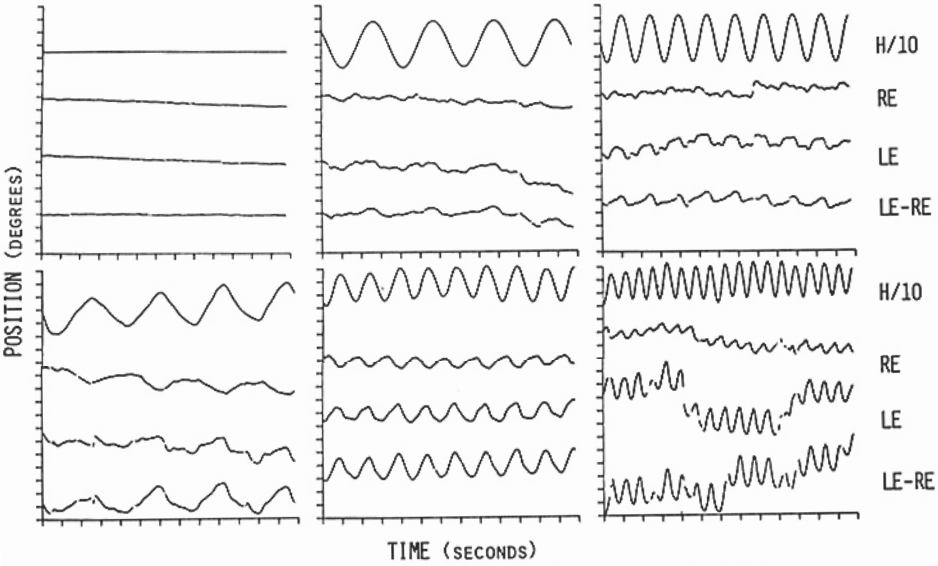

Fig. 4. Six representative records of horizontal head position and gaze (retinal image position) of subject *HC* fixating a target while his head was passively or actively rotated. The top 3 records were made with the head supported by a biteboard while the body was rotated at 3 frequencies, 0.00 Hz (left), 0.33 Hz (center), and 0.66 Hz (right). The bottom 3 graphs were made during active head rotation paced by a metronome at 3 frequencies, 0.33 Hz (left), 0.66 Hz (center), and 1.33 Hz (right). Each record begins on the left. The time scale-marks signify 1 s intervals. The position scale-marks signify 1° rotations. The head position traces (*H/10*) show the position of the head scaled to 1/10 of its actual value. Gaze of the right eye (*RE*) is shown just below the head trace, the gaze of the left eye (*LE*) just below the right eye trace, and the vergence of the eyes (*LE-RE*) at the bottom of each record. Upward changes in the vergence traces signify divergence. Saccades have been removed from all eye traces. These traces were corrected for the changes in position introduced by saccades by assuming that smooth compensatory eye movements continued during the saccade at the velocity present just prior to saccade-onset. Small gaps in the traces signify when saccades occurred and were removed. (From Collewijn et al. 1981a)

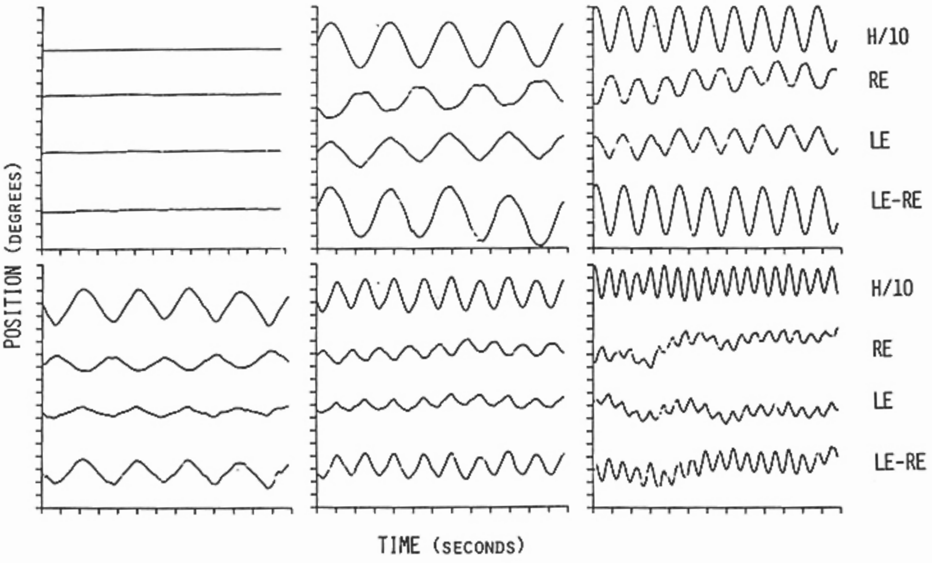

Fig. 5. Six representative records of horizontal head position and gaze (retinal image position) of subject *AM*, fixating a target while his head was passively or actively rotated. See Figure 1 for other details. (From Collewijn et al. 1981a)

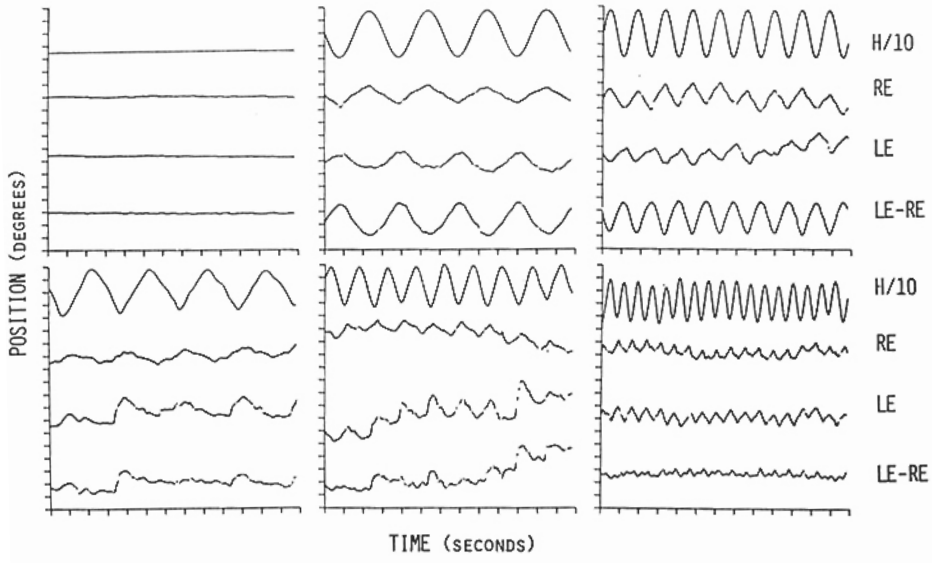

Fig. 6. Six representative records of horizontal head position and gaze (retinal image position) of subject *WC*, fixating a target while his head was passively or actively rotated. See Figure 1 for other details. (From Collewijn et al. 1981a)

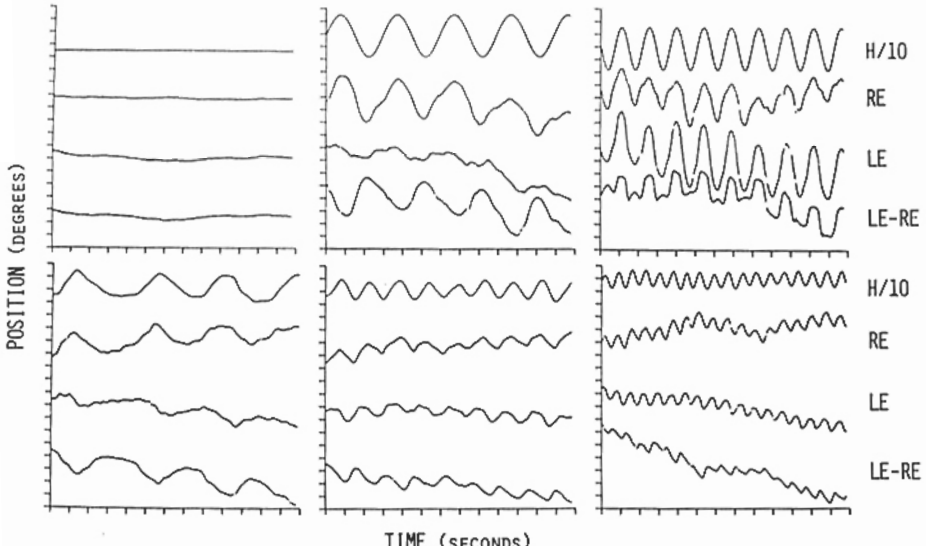

Fig. 7. Six representative records of horizontal head position and gaze (retinal image position) of subject *EK*, fixating a distant target while her head was passively or actively rotated. See Figure 1 for other details (From Collewijn et al. 1981a)

Table 1. Composite binocular precision of gaze during active and passive head rotation at several frequencies. Precision of gaze and head rotation are shown as standard deviations (min arc)

		Passive			Active		
	Frequency (Hz)	0.0	0.33	0.66	0.33	0.66	1.33
	Subjects						
Head	RS	3	741	770	644	636	818
	HC	3	744	769	537	521	508
	AM	2	750	779	533	529	470
	WC	2	757	786	595	613	608
	EK	1	701	711	373	298	257
Overall		2	739	763	536	519	532
LE	RS	4	11	16	20	19	31
	HC	2	20	21	35	31	41
	AM	2	39	41	20	20	19
	WC	2	26	25	46	31	21
	EK	6	62	94	40	37	43
Overall		3	32	39	32	28	31
RE	RS	1	22	34	7	9	24
	HC	3	14	12	28	19	19
	AM	2	41	42	24	23	22
	WC	3	26	29	20	18	18
	EK	3	74	55	69	36	43
Overall		2	35	34	30	21	25
LE-RE	RS	4	16	26	20	17	19
	HC	1	16	15	38	39	45
	AM	2	79	81	40	40	36
	WC	2	49	50	30	18	11
	EK	6	60	55	47	27	29
Overall		3	44	45	35	28	28

Standard deviations are based on at least 2557 five msec position samples. *LE-RE* represents the precision of vergence eye movements. The noise level of the recording instrument with bandwidth of 0–100 Hz (–3 dB) was less than 40 sec arc. "Composite" refers to the fact that saccades, as well as smooth eye movements, are included in the standard deviations

on maintained fixation when the head was supported artificially and the subject was stationary with respect to space. Gaze deteriorated by an order magnitude when oculomotor compensation of bodily movement was required. The precision of vergence was affected as much as precision of gaze within each eye. If we make the reasonable assumption that the mean position of the retinal image of the fixation target falls in the center of the foveal bouquet in each of the eyes, then oculomotor compensation for bodily movement was sufficient to keep the target image on the foveal floor a good deal of the time because the foveal floor has a diameter of about 90′ and the standard deviation of gaze during movement was about 31′. Given such values the target image would fall in the foveal floor about 86% of the time. When the head was on a bite-board and the subject was stationary, the target image would remain in the foveal bouquet (20′ diameter) more than 99% of the time because the standard deviation of gaze was about 3′. (See Steinman (1965) for a similar discussion and test of the assumption that eye position samples are normally distributed.)

Consider next the precision of vergence. When the head was held and the subject was stationary, there was very little change in the position of one eye relative to the other. The situation changed once the subject began to move. If we use the standard deviations of vergence to estimate Panum's area, which seems reasonable because fusion was maintained throughout this series of experiments, Panum's area during movement would be 118′ in diameter with 95% confidence was compared with 10′ when Panum's area is estimated from the precision of vergence observed when the head is held on a bite-board.[2] These differences in the precision of gaze and vergence between artificial and natural fixation may have significant consequences for understanding vision. Possible consequences will be described below.

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[2] Panum's area is the region in which binocular fusion will be maintained as disparity between the retinal images in each of the eyes is increased optically from the natural vergence established when a single scene is viewed binocularly. Panum's areas were not measured experimentally in these experiments. Their size on the bite-board and during movement is being inferred from the perceptual facts, namely, diplopia was not seen either on the bite-board or during movement. This result may mean that fusion was maintained. An alternative possibility will be discussed later

In the experiments just described the fixation target was stationary while the head was free to move. The head, deprived of artificial support, always moved appreciably even when the subject was asked to sit or stand as still as possible. Head movements were only paritally compensated by the oculomotor system, thus appreciable retinal motion was always present. Retinal image motion increased markedly when active or passive oscillations of the head were introduced. So, the precision of gaze of the fixating eyes, when the head is not supported artificially, is relatively poor when the target is stationary and the head moves. How does gaze fare when the target moves *with* the moving head? We know that when both the head and the target are stationary, gaze is precise. We know that when the head moves and the target is stationary, the precision of gaze deteriorates. Will precision of fixation upon the target improve if the head moves and the target is stationary with respect to the head as both move in space? Precision could improve, providing the vestibulo-ocular reflex could be attenuated. If VOR could be cancelled completely, gaze would be as precise as when both the head and the target are fixed in space.

We are not the first to examine this question. Dodge (1923) asked ". . . what would happen if the visual data conflicted with the vestibular data . . ." (p. 177) and found that

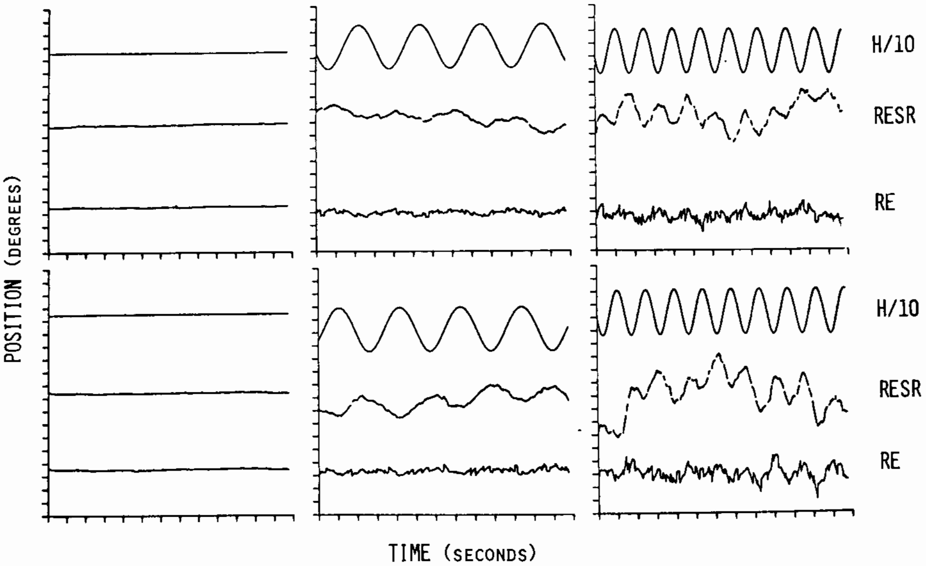

Fig. 8. Representative records of horizontal head position and gaze (retinal image position) of subject *AM* fixating a small red light attached to a biteboard supporting his head. The two left records were made while *AM*'s body and the target were stationary in space. The four remaining records were made during oscillation at 0.33 Hz (center) and 0.66 Hz (right). The upper three records were made while the target was seen in front of a stationary structured background. The lower three records were made while the target was viewed in darkness. Each record begins on the left with the time scale-marks signifying 1 s intervals. The position scale-marks signify 1° rotations. The traces labeled *H/10* show the position of the head scaled to 1/10 of its actual value. The traces labeled *RE* plot the composite gaze pattern of the right eye which includes saccades and therefore represents absolute retinal image position. The traces labeled *RESR* plot gaze of the right eye after saccades have been removed. The changes in position introduced by saccades were corrected by assuming that smooth eye movements continued during the saccade at the velocity present just prior to saccade onset. Upward changes in the head and eye traces signify leftward movements

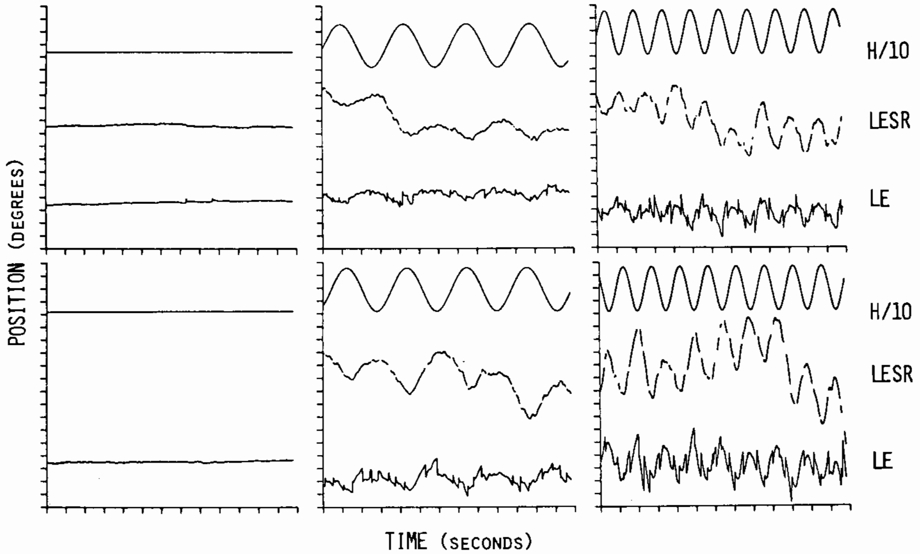

Fig. 9. Representative records of horizontal head position and gaze (retinal image position) of subject *RS* fixating a target attached to a bite-board supporting his head. See Figure 8 for other details. The *LESR* trace is not plotted in the lower left record because saccades were not made during the trial

". . . rotation always produced vestibular deviations in spite of the effort to fixate a motionless field" (p. 179). We reexamined this question because Dodge's measurements were made with a primitive instrument (corneal reflection). We did not anticipate a contradictory result because Dodge has proved to be virtually infallible in his interpretation of necessarily ambiguous recordings (see for example, Murphy et al. 1975). However, we felt that an accurate estimate of these vestibular deviations might be of value for understanding the precision of gaze under a variety of stimulating conditions.

Two of the authors (*AM* and *RS*) were asked to maintain binocular fixation of a 26′ diameter red-light target attached to their bite-board holder which was mounted on a chair that could be oscillated sinusoidally about a vertical axis. Movements of one eye relative to an earth-fixed framework were recorded by the silicone annulus revolving magnetic field technique (Collewijn et al. 1981a). The red disc target was seen either in complete darkness or in front of a highly structured pattern of randomly positioned squares. The pattern filled the entire visual field horizontally and 42° vertically. The red disc was 0.62 m from the eye and the patterned field was 0.85 m from the eye – the details of both could be seen clearly at these distances. The experiment was performed with these different visual arrangements because it is generally believed that visual input supplements the vestibular compensatory reflex. If this is true, then we should observe more "vestibular deviations" when the red disc is seen to move against the objectively stationary patterned field than when the red disc is seen in darkness. More deviations would be expected because retinal slip signals provided by the patterned field would, like the vestibular reflex, cause the eye to rotate in the direction opposite to the passive rotations of the subject's body and head. Fixation of the red disc in darkness does not provide such retinal slip signals and only the vestibular reflex need be overcome to improve the precision of gaze.

We confirmed Dodge's observations. Vestibular deviations were always produced when the subject was required to maintain fixation of a target stationary with respect to his head while both head and target oscillated horizontally with respect to the environment. Surprisingly, the expected supplementation of these vestibular deviations by visual input were not observed. The slipping patterned field *facilitated* fixation of the attended red disc. Gaze was more precise. These results are illustrated in Figures 8 and 9.

These figures, like those appearing earlier, plot the direction of gaze relative to the target while attempting to maintain fixation of the red disc which was mounted on the bite-board holder and therefore moved with the head. Under such conditions gaze is shown by plotting the position of the eye relative to the head rather than relative to an earth-fixed framework as was appropriate in the earlier experiments when the target was fixed with respect to the earth and the head was free to move. The records on the left show gaze when the chair was stationary with respect to space. Both subjects show the precision of gaze typically observed when the head is supported by a bite-board and the fixation target and subject are stationary. The other records were made while the subjects were oscillated horizontally at 0.33 Hz and 0.66 Hz through 34° (peak to peak).

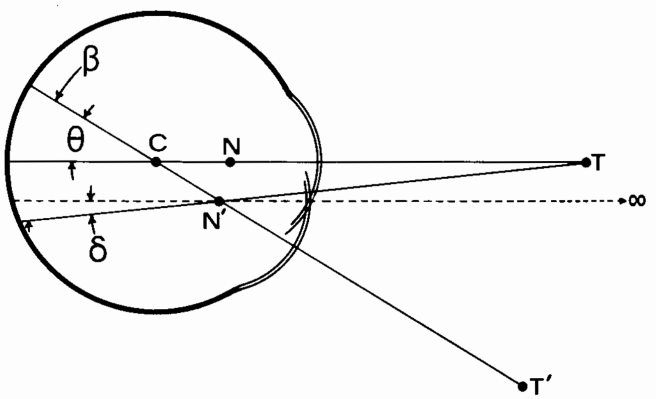

Fig. 10. The displacement of the retinal image of a stationary target produced by rotating the eye about its center. The text describes how the angle formed by an eye rotation, θ, and the angle subtending the displacement of the retinal image, β, are related. In calculating δ (the difference between θ and β) the distance of the center of rotation to the nodal point *CN* was 6.2 mm, and the distance of the center of rotation to the apex of the cornea 13.5 mm. Distances are taken from Bennett and Francis (1962) and Alpern (1962). (After Ratliff and Riggs 1950)

Consider first the bottom traces in each record that plot the composite gaze pattern which includes saccades, as well as smooth compensatory eye movements. Gaze was not very precise when fixation was attempted while the subject and target were mounted on a moving platform. *AM*'s standard deviation of horizontal gaze when stationary was 3′. It increased to 10′ at 0.33 Hz and to 26′ at 0.66 Hz. *RS*'s standard deviation of horizontal gaze when stationary was 5′. It increased to 20′ at 0.33 Hz and to 48′ at 0.66 Hz. Saccade rates, as well as the scatter of gaze, increased markedly when the subjects were moved (*AM*'s stationary saccade rate = 0.2 saccades/s, 0.33 Hz saccade rate = 3.3 saccades/s, and 0.66 Hz saccade rate = 3.5 saccades/s; *RS*'s stationary saccade rate = 0.1 saccades/s, 0.33 Hz saccade rate = 2.4 saccades/s, and 0.66 Hz saccade rate = 3.4 saccade/s). These high saccade rates are typical maxima, corresponding to rates observed during reading. Note that the sizes of the saccades increased as chair frequency increased. The reason subjects increased saccade frequency and size (when frequency was at its maximum) can be seen in the middle traces in each record. These middle traces plot smooth compensatory eye movements after saccades were removed. It is clear that the smooth eye movements did not maintain gaze on the red disc as well as they did when the subjects were stationary. Rather, gaze moved smoothly in the direction opposite to movements of the head as would be expected if these smooth eye movements were generated by vestibular signals.

So, vestibular deviations are, as Dodge suggested, not completely eliminated. Note, however, that vestibular deviations were smaller in the top records when the patterned visual field was visible than in the bottom records when the red disc was seen against a dark background (*AM*'s smooth gaze velocities: stationary dark = 21′/s, light = 21′/s; 0.33 Hz dark = 64′/s, light = 56′/s; 0.66 Hz dark = 176′/s, light = 185′/s and *RS*'s smooth gaze velocities: stationary dark = 24′/s, light = 25′/s; 0.33 Hz dark = 112′/s, light = 81′/s; 0.66 Hz dark = 323′/s, light = 202′/s). *AM*'s results show only a tendency to smaller vestibular deviations with visual supplement than in darkness. *RS*'s results, however, show clearly that the visual input, which should supplement his

VOR, actually *reduced* his vestibular deviations appreciably.

These records and descriptive statistics slightly ($< 1\%$) underestimate actual retinal image motion. Underestimation occurs because the principal nodal point of the optics of the eye lies anterior to the center of rotation of the eye. When an eye rotates relative to a stationary target, the angle of eye rotation is not exactly equal to the angle subtending the displacement of the retinal image of the target unless the target is at optical infinity. When the target is closer than optical infinity, the angle of image rotation will be greater than the rotation of the eye relative to the target. This difference is shown in Figure 10.

If the eye rotates about its center, C, so that the nodal point, N, is displaced to N', an angle δ is formed which must be added to the angle θ (the angle of eye rotation) to describe the angular displacement of the retinal image of target T. The relationship between the angle δ and the angle of eye rotation relative to the target θ may be calculated as follows:[3]

$$\delta = \tan^{-1} [\sin\theta/(CT/CN) - \cos\theta] \approx (CN/NT) \cdot \theta$$

where CT and CN are distances of the target and the nodal point from the center of rotation respectively. In the case where the target is located at optical infinity, the angle δ reduces to zero and angles β and θ are equal.

In the initial monocular experiments on natural image motion during which the subject sat or stood as still as possible (Skavenski et al. 1979), the target was at optical infinity and therefore no correction was required. In the binocular experiment in which subjects actively moved their heads (Steinman and Collewijn, 1980), the nearest target was 5000 m from the eyes which means that eye rotations underestimate retinal image motion by less than 0.0002%. In the binocular experiments in which the subject's head was actively or passively oscillated (Collewijn et al. 1981a) the target was 12.2 m from the eyes. The underestimation of retinal image motion by estimates of eye rotation in these experiments is less than 0.05%.

Thus, our examination of the significance of the error in estimating retinal image motions from the change in orientation of the anterior surface of the eyes shows that it would only be necessary to make corrections for very near targets. The error introduced by a fixation target located at 0.1 m, perhaps the nearest visually-useful working distance for an adult emmetropic eye, is less than 5.6% for any eye rotation. It is important to remember that these small corrections are always in the direction of increasing retinal image motion.

Two larger potential sources of error in estimating retinal image motion from eye rotation arise when the head is free to translate and rotate. If the head translates relative to the position of the target in space, the eye must rotate to maintain the target image in the same retinal position. If the head rotates, the eye must counter-rotate through a slightly larger angle than the angle of head roation to compensate more completely for the head rotation. This difference between eye and head rotation results from the non-coincidence of their centers of rotation; the center of eye rotation lies anterior to the center of head rotation. The additional angle of eye rotation can be calculated with the same trigonometric relationship expressed in Eq. 1. In this case, θ represents the angle of head rotation and CN the distance of the center of head rotation from the center of eye rotation. (See Collewijn et al. (1981c) for a complementary derivation.) So, both head translation and rotation produce overestimates of retinal image motion. These errors, however, are significant only in one set of experiments described in this paper (Collewijn et al. 1981a, b). Here the target was 12.2 m from the eyes and not at optical infinity as in the prior work. In these experiments one centimeter translations of the head would require 2.8 min arc eye rotations. A given head rotation would require at most a 1% increase in eye rotation when the target is 12.2 m away.

The three errors just discussed relate retinal image motion to eye rotation. See Collewijn (1977) for a discussion of an additional source of error which arises when eye rotation is measured during horizontal head rotation (yaw). The head may not rotate exclusively about its vertical axis. It can roll and pitch as it yaws. Such compound rotations may lead to inaccurate estimates of retinal image motion. The significance of this potential error cannot currently be evaluated because it requires accurate measurement of 3-dimensional head rotations.

Retinal Image Motion is the Goal of Oculomotor Compensation

Bodily motion, whether it be active or passive, increases retinal image motion. This result raises an interesting question. Is the failure of the oculomotor system to achieve virtually perfect compensation of bodily movement a limitation inherent in this biological control system? There is an alternative hypothesis. Perhaps the goal of oculomotor compensation of bodily motion is to establish some non-zero value of retinal image motion which is perceptually beneficial. This second hypothesis has some support.

Skavenski et al. (1979) reported that the quality of compensation of head rotation was related to the amplitude of head rotation. Very small head rotations were not compensated as completely as larger head rotations. This finding led Skavenski et al. (1979) to suggest "that the gain of the compensatory machinery is tuned to guarantee some appreciable retinal image motion". These authors pointed out that retinal image velocities during natural bodily motion tend to be low enough ($< 100'/s$) to permit excellent visual acuity (Westheimer and McKee 1975) and contrast sensitivity (Murphy 1978) and, at the same time, to be high enough to guarantee sufficient retinal image motion ($> 14'/s$) to prevent visual fading when head movement is kept to a minimum. From this point of view oculomotor compensation is in the service of vision, and vision requires appreciable, but not excessive, retinal image motion. Skavenski et al. (1979) made this suggestion plausible by pointing out that the gain of the VOR is known to be plastic and the VOR could.

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[3] In Figure 10 gaze has been specified by the optical axis, a line joining the nodal point and center of rotation of the eye. This line is not the same as the visual axis, a line joining the object of regard, the nodal point and the foveal center. In most eyes the optical axis intersects the retina 4° to 5° to the nasal side of the foveal center and about 1° to the superior pole. This angle formed by the visual and optical axes, commonly referred to as angle α, has been ignored in the present description because both axes rotate through the same angle when the eye rotates about its center.

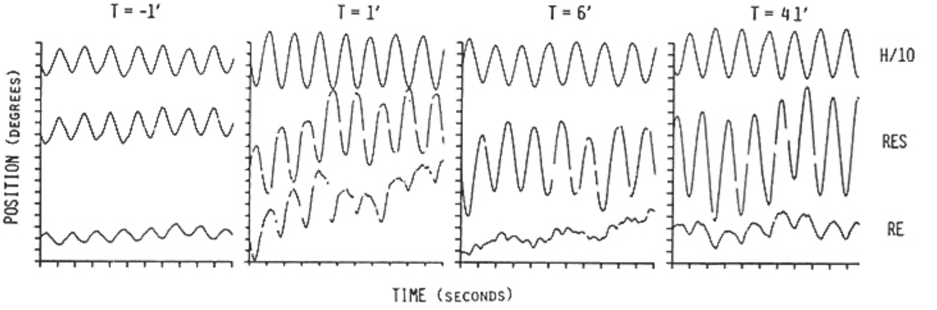

Fig. 11. Records of a myopic subject's (*AM*) adaptation to +5D spectacles while fixating a target and actively rotating his head at 0.66 Hz. The time (*T*) these records were obtained relative to the introduction of the novel spectacles is indicated. The time scale-marks within each record signify 1 s intervals. The position scale-marks signify 1° rotations. The trace labeled *H/10* shows the position of the head scaled to 1/10 of its actual value. The trace labeled *RES* shows the position of the right eye in space. The trace labeled *RE* shows the gaze (retinal image position) of the right eye after correction for the magnification of the spectacles. Gaps in the eye traces show when saccades were removed. Upward changes in position signify leftward movements

therefore, adjust its response so as to minimize retinal image motion if minimal motion were the goal of oculomotor compensation.

Recently, Collewijn et al. (1981a, 1981b) provided experimental support for this idea by showing that rapid plastic changes of the VOR tend to re-establish non-zero retinal image velocities even when the required plastic changes force the compensatory response through a region where virtually perfect compensation of bodily movement was obtained.

These experiments rest on the fact that the *VOR*, supplemented by vision, can adapt to changes in the normal relationship between rotations of the head and movements of a target image on the retina. To illustrate, if an emmetrope wears the spectacles of a myope, he will reduce the amplitude of his eye rotations in order to compensate his head rotations. He does this because negative spectacles minify the visual scene and therefore produce more retinal image motion for a given eye rotation. Compensation of head rotation in this case requires relatively small eye rotations. Conversely, positive spectacles magnify the visual world, produce less image motion for a given eye rotation, and therefore require relatively large eye rotations to compensate head rotations.

Collewijn et al. (1981b) required two myopes, whose normal corrective spectacles incorporate about −5D, to modify their compensatory eye movements by wearing +5D spectacles. Figure 11 illustrates the results of this experiment for one of the subjects. Each of the four eye movement records contains 3 traces. The top traces, *H/10*, show active sinusoid-like horizontal oscillations of the head at approximately 0.66 Hz. The subject attempted to oscillate his head through 34° (peak to peak). He was reasonably successful (these head traces are scaled to one-tenth of their actual value). The middle traces, *RES*, show the movements of the eye in space relative to a distant fixation target. The bottom traces, *RE*, show gaze (retinal image motion). These gaze traces are obtained by correcting the eye in space measurements for the magnification of the spectacles (−5D and +5D) worn by this subject (See Collewijn et al. (1981b) for the behavioral technique used to measure magnification factors). The left hand record, *T = −1'*, shows the subject's normal compensation. This record was made with his normal corrective spectacles one minute before they were replaced with the magnifying spectacles. The magnifiers required him to increase compensation by 33%. In other words the rotations of his eye will have to be larger than the eye rotations he normally makes if gaze is to be as stable with the magnifying spectacles as it is with the minifying spectacles he normally wears. The trace, *T = 1'*, shows extensive adaptation to the magnifying spectacles after the first minute during which the subject made about 30 head oscillations as he attempted to maintain fixation of the target. Adaptative changes can be seen by comparing the rotations of the eye in space, *RES*, in the first two records. Note that in the left hand record this subject's eye rotations in space were in the same direction as the movements of his head. This record shows compensation, that is, the eye rotated in the direction opposite to rotations of the head. But, these compensatory rotations were inappropriate to keep the target image stationary on the retina. The degree and origin of this failure of complete oculomotor compensation can be seen in the bottom gaze trace, *RE*, in which rotations of the eye in space have been corrected for the −5D magnification factor of the subject's normal spectacles. If eye rotations compensated head rotation completely after allowance for the optical arrangements, the gaze trace would be a horizontal straight line. It is not. Rather, gaze moves in the direction opposite to the direction of the head. This direction of gaze displacement arises when this subject over-compensates his head rotations. In other words his normal gain, although less than 1, is too high to stabilize the retinal image. Now look at his response only one minute after his spectacles were changed. The phase relationship between eye movements, *RES*, and head movements have changed – originally they were in phase now they are out of phase. This means that the eye is still compensating by rotating in the direction opposite to the head but larger eye rotations are required because of the magnifying spectacles. Eye rotations are beginning to adapt after only one minute but adaptation is not complete. The bottom trace, *RE*, shows the degree to which the partial adaptation has stabilized the retinal image. Note that this gaze trace is moving appreciably. The retinal image is less stable than normal. Also note that the movements of the retinal image are in the same direction as the head.

Now look at *T = 6'*. Compensation has increased and after only 6 minutes compensation was sufficient to produce a relatively stable retinal image. Compare gaze, Compensation is now excessive, causing the gaze trace to move in the direction opposite to movements of the head. This compensatory relationship was originally found in *T* = *−1′* when the subject wore his normal corrective spectacles[4]. Performance shown at *T* = *41′* was stable. It was the same 24 hrs later. These results offer experimental support for the idea introduced by Skavenski et al. (1979). The goal of oculomotor compensation has been shown to be some non-zero value of retinal image motion. When this subject's compensatory responses approached virtual perfection at *T* = *6′*, the oculomotor compensatory subsystems were not satisfied. They preferred more retinal image motion and continued to adapt until retinal image motion reached this subject's preferred level.

Implications of the New Results for Understanding the Role of Eye Movement in Visual Perception

We began this review by considering the significance of eye movement for visual perception and emphasized that compensatory eye movements are necessary to maintain a clear, stable, and fused visual world. Until recently, these significant visual accomplishments were believed to reflect the virtually perfect operation of the oculomotor compensatory subsystems. However, recent measurements of the precision of gaze with the head free to move naturally make it clear that the clarity, stability, and fusion of the visual world cannot be explained so simply. Faced with these new results and still convinced that we see a clear, stable, and single world when our heads are free of artificial support, some speculation about the origin of these perception, seems appropriate.

Consider first the question of how we see visual detail clearly with a single eye in the presence of the retinal image motion observed when the head is free from artificial support. When a subject sits or stands as still as possible, the standard deviation of the position of his line of sight on a single meridian is on the order of 15′ – two to five times greater than the standard deviation observed when the head is supported artificially. When the head is supported artificially and the standard deviation is only about 3′ on a single meridian, the retinal image of the target object will fall in the 20′ diameter foveal bouquet more than 99% of the time. But even without artificial support the target image will fall in this region of best visual acuity about 50% of the time which might be sufficient for most visual tasks requiring keen vision. Next consider how fast the retinal image is moving while fixation is maintained within this relatively circumscribed area. When the head is supported by a bite-board, retinal image speed is on the order of 15′/s and only rises to about 27′/s when the head is free and the subject sits or stands still[5]. We know from psychophysical experiments that retinal image speeds as high as 100′/s do not have adverse affects on detail vision (Westheimer and McKee 1975; Murphy 1978). So, as long as we sit or stand still vision should remain clear despite insufficient oculomotor compensation.

Now consider the relationship between oculomotor compensation and the clarity of vision when a subject is encouraged to move naturally. The standard deviation of the position of the line of sight on a single meridian is about 30′ under such conditions. This means that the retinal image of the target object would remain in the foveal bouquet 25% of the time. Mean retinal image speed increases to about 96′/s (S.D. = 58) when the mean head speed is 37°/s (S.D. = 19). So, during bodily movement, the precision of gaze with respect to both position and speed is sufficient to permit clear vision, particularly once we consider modern acuity measurements which show that the diameter of the isoacuity area is as large as 50′ (Millodot 1972), twice as large as the foveal bouquet.

Next consider conditions in which an objectively stationary visual world is perceived as stationary when the head moves. The recent results show that perceptual stability cannot be explained by the perfection of oculomotor compensation. A perceptually stable world is normally perveived in the presence of appreciable retinal image motion. A particular amount of retinal image motion is characteristic of a given individual's compensatory performance – his world looks stationary when somewhere between 90% and 97% of his head motion is corrected by ocular movements. We also know that when compensatory movements are forced to change by the introduction of novel optical arrangements, the adjustments re-establish the degree of retinal image slip normally observed in the free-headed performance of the same subject (Collewijn et al. 1981a). There are two previously unmentioned observations made during the course of these adaptation experiments that are significant for understanding perceptual stability in the presence of retinal image motion. First, our subjects, like everyone else, perceived a stable world when they moved. But, when they were first fitted with magnifying or diminishing spectacles, the visual world was no longer perceived as stable. It moved as the head moved. When the compensatory oculomotor responses adapted, the visual world was once again perceived as stable. At this time the compensatory eye movement for a given head movement was different from what it had been originally. This observation is significant because it means that the perceived stability of the visual world depends on the amount of retinal image motion a given subject expects and not on the particular compensatory eye movement pattern which produces such motion.

Second, we observed that perceptual stability, not visual clarity, controls adaptation of the compensatory responses. The adaptation experiments were done with simple magnifying and minifying lenses and an adapting field that filled less than 5 degrees of visual angle. Under these conditions the small foveal adapting stimulus was defocussed and remained

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[4] Gaze was displaced more in the right record than in the left record. This difference in retinal image motion, before and after complete adaptation, is due to differences in head velocity. While the frequencies of oscillation were similar (~ 0.66 Hz), amplitudes differed appreciably. In the left record the head oscillated through 30° peak to peak. In the right record the head oscillated through 45° peak to peak. The percent compensation, however, before and after adaptation, was the same (96%)

[5] Here only smooth eye movement speed is being considered because visual processing is attenuated during saccades. See Matin (1974) for a review of "saccadic suppression"

blurred throughout the course of adaptation. Adaptation proceeded rapidly and the visual world appeared stable within a few minutes. This observation suggests that the goal of oculomotor compensation is not to facilitate detail vision because vision could not be clear with the particular adaptive procedure used[6]. This result suggests that the goal of oculomotor compensation is to restore perceptual stability of an objectively stationary world by adjusting new and unaccustomed retinal image velocity to the value normally present for a given subject. In short, the perceived stability of the visual world seems to be naturally correlated with a particular degree of retinal image motion. For most people the world looks stable when retinal images move as fast as 1° to 2°/s. The amount of retinal image motion that can be associated with perceptual stability can be very much higher. For example, individuals with congenital nystagmus can have retinal image velocities ten or more degrees/s without experiencing oscillopsia.

Perhaps the most provocative aspect of the recent results on precision of gaze under natural conditions is the degree to which compensatory activity in each of the eyes is different. This guarantees appreciable vergence velocity and large differences between directions of the line of sight fixating a single distant target. It should be noted that these failures of Hering's Law are only observed when vision supplements vestibular compensation during bodily movement. Eyes are yoked very well when the vestibular response, working alone, is measured in total darkness. So failures in Hering's Law arise from visual-vestibular interactions. It is surprising that these failures occur. We know that they do not degrade vision because in all the experiments reviewed in this paper only a single visual world was perceived. The subjects did not see double when the eyes compensated differently. What is the significance of this result? It could mean that the binocular visual system uses such mismatches in visual input to generate the perception of depth. It might mean, on the other hand, that when the head is not artificially stabilized and vergence becomes imprecise, we see a single world by suppressing input from one of the eyes – perhaps alternating the eyes so that we do not lose the full extent of the visual field. We have no hard evidence that rules out this last possibility. However, there is some suggestive evidence that binocular depth perception persists and can be established when a subject moves. MacLeod (private communication) looked at this when he became familiar with the recent work on natural binocular retinal image motion. He used Julesz color-coded displays and wore red-green spectacles. Stereodepth was maintained when he oscillated his head. He also reported that he could establish stereodepth when the red-green spectacles were slipped on while the head was moving. MacLeod could not measure binocular retinal image motion. But, if it is assumed that his oculomotor performance resembled one of the nine subjects whose natural binocular retinal image motion has been studied thus far, it seems likely that the single world observed in the presence of bodily movement does not arise from monocular alternation but rather from the processing of concurrent binocular input.

To Summarize

1. When the precision of gaze, both with respect to position and speed, is compared to known functional properties of the heterogeneous human retina, clear monocular vision should be possible during the course of natural bodily movement. In other words our subjective binocular visual impressions seem to be consistent wich knowledge of monocular visual physiology.
2. An objectively stationary visual world is perceived when its binocular retinal images move appropriately. Appropriate retinal image motion is idiosyncratic. It is different for each subject and each eye. When retinal image slip exceeds the accustomed value, the world appears to move, forcing the oculomotor compensatory subsystems to adjust their responses and re-establish the accustomed values in a matter of minutes.
3. Binocular vision is maintained despite gross failures of Hering's Law in the presence of natural bodily movement. This result cannot be explained at present.

In Conclusion

Recent developments in research on the precision of gaze contain a number of unexpected and provocative results. An explanation of these results should lead to advances in our knowledge of visual and oculomotor physiology. Explanation will require studies of vision in the presence of natural bodily movement. Such studies will provide a basis for selecting visual, perceptual, and oculomotor models which, until now, have been tested in unnatural experiments based on what we now know to be untenable assumptions about the relative stability and binocular yoking of retinal images.

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[6] The rapid adaptive process does not depend on having a defocused visual scene. Adaptation is as fast and has the same characteristics when visual clarity is maintained in the presence of novel optical arrangements (Collewijn et al. 1981a)

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