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ORIGIN AND CHANGE

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NATURAL RETINAL IMAGE MOTION: ORIGIN AND CHANGE*

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It is generally accepted that "the function of the vestibulo-ocular reflex (VOR) is to maintain a stable retinal image during head rotations by generating appropriate compensatory eye movements."¹ There have been numerous expressions of enthusiasm for the effectiveness with which this reflex achieves retinal image stability, for example, "the remarkable fact emerges that the reflex produces virtually perfect compensation."²

We share this enthusiasm, but we believe that the true function of the VOR is more subtle than has been suspected. We believe that the VOR serves not simply to stabilize the retinal image of a fixated object during movement but, rather, to produce and maintain retinal image motion within each eye and between the eyes that is optimal for binocular vision.

It became possible for us to entertain this idea only recently because supporting evidence requires accurate measurement of binocular retinal image motion in freely moving human beings. When it became possible to make such measurements, we found that natural eye movement compensation was not virtually perfect and, furthermore, that compensation was different within each of the eyes.³ Subjectively, vision remained clear, fused, and stable under all but the most violent, active head rotations we studied despite such "imperfections" of oculomotor compensation.

The present experiments continue this line of research. First, we extended our results on natural binocular retinal image motion to a larger sample of subjects, making these observations with passive, as well as active, rotations. Second, we measured binocular retinal image motion with sinusoidal stimulation of fixed frequencies and amplitude, allowing estimates of retinal image speed at each of several frequencies. Third, we determined the degree and speed with which the VOR (in the dark and when supplemented by vision) could be modified by changing the correlation between the amount of retinal image motion and a given degree of eye rotation. These adaptation experiments were undertaken to determine whether the observed departures from virtually perfect compensation arose from limitations inherent in the compensatory subsystems or from the desire of the compensatory subsystems to maintain retinal image motion at some nonzero value that might be optimal for vision.

We will show that (1) compensation is rarely virtually perfect; (2) even when

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compensation is virtually perfect in one eye, it is not in the other eye, which leads to noncorrespondence of fixation positions between the eyes and high vergence velocities; (3) the degree of compensation in the light is the same with active and passive rotations; (4) the VOR in the light adapts completely within minutes (adaptation is complete in the sense that it reestablishes retinal image velocities observed prior to the introduction of novel optical arrangements); and (5) the VOR in the dark also adapts within minutes to as much as 90% of the required change.

METHODS

Recording

A revolving magnetic-field-sensor coil eye-movement monitor was used to record binocular eye and head rotations. Our instrument is based on the idea, suggested by Hartmann and Klinke, that Collewijn developed and used to measure eye movements on the horizontal meridian in the freely moving rabbit.^{4,5} Steinman and Collewijn subsequently used Collewijn's revolving field monitor with freely moving human subjects.³ Detailed descriptions of Collewijn's instrument are given in the prior papers. Here we will review only briefly its basic principle and then describe the Maryland instrument used in the present experiments.

Two horizontal a.c. magnetic fields of equal magnitude, in spatial and phase quadrature, generate a magnetic vector of constant magnitude rotating with uniform angular velocity through 360° during every period of the field frequency. The phase of the voltage induced in a sensor coil placed in the field varies linearly with the angular orientation of the sensor coil, and thus by phase detection the angular orientation of any object fitted with a sensor coil can be measured. It is crucial that the magnetic field be homogeneous in direction and magnitude and truly orthogonal in space and phase. The simple arrangement used by Collewijn and copied at Maryland for creating a uniform magnetic field was described by Rubens.⁶

The rotating field frequency of the Maryland instrument was 976 Hz. The orthogonality of the sinusoidal currents at this frequency and the strength of the magnetic field were maintained by a feedback loop receiving input from a (10-cm diameter) field-sensing coil located near the center of the magnetic chamber, which was 2.43 m on a side. The control accuracy of this magnetic-field servo loop was such as to compensate for departures from orthogonality (phase shift from 90°) smaller than 1°. The measured homogeneity of the magnetic field was within 1 part in 1,000 for translations of ± 24 cm, as expected from Rubens' analysis. The Maryland instrument is digital, and both magnetic field control and phase-detecting circuits were controlled by reference to a 200-MHz crystal clock. The bandwidth for phase measurement was 178 Hz (-3 dB). The noise level with the weak magnetic field used (0.278 gauss) and type of sensor coils attached to the eyes and head was $< 40''$. Phase indications were linear to better than 1% in 360°. The instrument was stable, i.e., the angular orientation of a fixed sensor coil drifted $< 6''$ during periods ranging from 1 second to 24 hours.

Eye movements were measured with the silicone-annulus sensor coils described by Collewijn, Van der Mark, and Jansen.⁷ These silicone annuli are shaped so as to suck onto the eye when they are inserted with the tool described by the inventors.⁷ The fidelity with which these annuli follow the eye was

determined originally by asking subjects to make a rapid series of twenty 20° saccades.⁷ No detectable differences in fixation position were observed following these saccades. We repeated this kind of experiment for two reasons. First, because the prior measurements had been made with an instrument less accurate than ours. Second, because we planned to elicit larger eye movements in our experiments and felt that the stability of the annulus should be verified under the conditions to be employed. Therefore, two of us (HC and AM) fixated a red diffraction-limited point target, located 12.2 m away, for 12.8 seconds with our heads supported on a bite-board. We then got off the bite-board and recorded while making large head and eye movements for an equal period of time. We then returned to the bite-board and recorded another fixation trial. HC recorded 30 pairs of such trials, and AM recorded 22 pairs. The annuli did not change position on the eye under these extreme conditions. The standard deviations of the mean fixation position were small (HC, standard deviation = 3.8' and AM, SD = 3.5'); both values are within the range of standard deviations of eye positions observed during fixation trials. These results—where the scatter around the mean fixation position is similar to the average scatter of the line of sight during periods of maintained fixation of the same target—show that a properly inserted annulus does not change its position with respect to the eye. Very occasionally, an annulus will lose its grip. Such occurrences are easily detected because the annulus no longer follows the eye and saccades, therefore, are no longer seen in the records. More often than not, a loose annulus falls out of the orbit. A properly inserted and seated annulus must be grasped with forceps and peeled off the eye at the end of each recording session. Ours typically lasted 20 to 45 minutes. Head movements were recorded from a sensor coil mounted on a contoured polycarbonate strip that was strapped and taped to the forehead.

Stimulation

The fixation stimulus was a colorful object (a yellow-orange polyurethane duck's-head hand puppet with red eyes) subtending 56' vertically and 42' horizontally. This target, located 12.2 m from the subject, was seen at the center of a 4.7° diameter circular field composed of a black and white random square array, each square subtending 2.8'. Subjects were required to fixate the duck's head while they sat either actively rotating their heads or while their heads were supported by a dental bite-board and their chair was rotated. The frequencies of the active rotations, which were paced by a metronome, were 0.33, 0.66, or 1.33 Hz. The passive rotations were provided by a motor-driven chair equipped with a cam and lever that produced approximately sinusoidal movements at 0.0, 0.33, or 0.66 Hz. The peak-to-peak amplitude of the passive rotations was set at 34°—the amplitude of head rotation that subjects felt was comfortable and natural, i.e., did not lead to neck strain when they attempted paced sinusoidlike active rotations.

Data Acquisition and Analysis

Digital eye position and head samples were acquired at 976 Hz. Four samples from each of three channels (right eye, left eye, and head) were averaged, converted to minutes of arc, and stored on tape at the end of each 12.8-second trial. The stored data, after averaging and scaling, describe eye and head position for successive 5-msecond periods, which means that our effective bandwidth was

100 Hz. The stored samples represent the positions of the eyes and head with respect to an earth-fixed framework. For a subject not wearing spectacles, these eye-position samples, which we will call "gaze," are equivalent to the position of the fixation target image on the retina. However, eye position measured with reference to an earth-fixed framework for a subject wearing spectacles must be corrected for the magnification factor of the spectacles before gaze (or retinal image position) is determined because, for example, a myope wearing a spectacle with a negative correction will have more retinal image motion for a given-amplitude eye rotation than will an emmetrope not wearing spectacles. Similarly, an individual wearing spectacles with a positive correction will have a smaller retinal image displacement for a given amplitude of eye rotation than will the person not wearing spectacles. Magnification factors for those of our subjects (HC, WC, and AM) who required and wore spectacles during the experiments were determined by a behavioral technique that will be described later. It should be noted, however, that whenever we speak of gaze or retinal image motion, the values reported or plotted incorporate appropriate corrections for the spectacle wearers.

Eye- and head-position samples served as the basis for the calculations of velocities and gains. These measures were calculated as follows.

A sliding-window technique was used to calculate velocity. The window—35 mseconds wide—contained seven position samples, and the slope of the line—fitted by least squares—through the seven positions provided a single estimate of "instantaneous" velocity. The window was then moved 5 mseconds later in time (one position sample), and the next velocity estimate was calculated. Velocity samples were then used to detect and remove saccades. Saccades were detected by an acceleration criterion, viz., each velocity sample was compared to the previous velocity sample and if it differed by more than $15\% + 300^\circ/\text{second}^2$, the velocity sample meeting this criterion was flagged as saccade onset. This criterion was checked against a large sample of eye-position records and listings of the velocities associated with these records. The criterion detected all saccades—the microsaccades occurring during maintained fixation and the large saccades occurring during high-velocity smooth compensatory eye movements. When a saccade was detected, 40 mseconds of data were removed, providing the saccade ended within this period. Most did. The determination of whether the saccade had ended was made by comparing eye speed at the end of the 40-msecond period during which samples were removed to eye speed preceding detection of the saccade. A saccade was judged to be over when eye speed was below the saccade-detection criterion. If the saccade had not ended, additional samples were removed until the criterion was met or 100 mseconds had elapsed.

Gain (35-msecond eye-in-head velocity/35-msecond head velocity) was calculated from the velocities determined with the sliding-window technique (described above) after saccades were removed and after the velocity of the eye in the head was determined by subtracting eye-in-space velocity from head-in-space velocity. Negative gains (periods during which the eye went in the same direction as the head) were not included in the summaries of gain (gain was negative in $< 2\%$ of the calculations). Negative gains were observed only near changes in direction of head rotation.

Subjects

We examined natural retinal image motion in seven subjects (four myopes and three emmetropes). Five of the seven subjects served in an extensive series of experiments, and only their data will be described in detail (the other two

subjects did not differ in any significant way). All three of the authors served as subjects, but only HC and RS had served in oculomotor experiments before. AM was completely inexperienced as an oculomotor subject. The other two subjects (EK and WC), whose performance will be described in detail, had served in prior oculomotor research, but neither had participated with free heads or the silicone annulus technique. Their experience was confined to contact lens optical lever and double Purkinje image tracker experiments. Subjects ranged in age from 21 to 64 years old. All had 20:20 Snellen acuity naturally or with their normal spectacle corrections.

RESULTS

Binocular retinal image motion was determined by recording positions of the eyes and head in space relative to an earth-fixed framework while the subjects maintained fixation of a distant target for 12.8 seconds. Recording sessions began

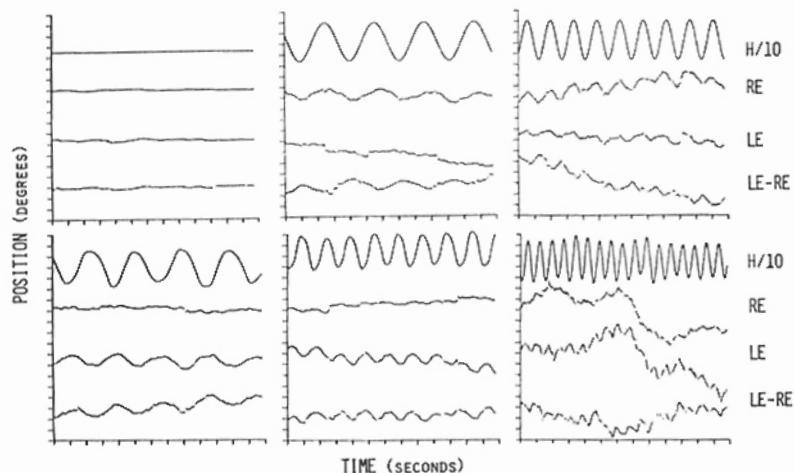


FIGURE 1. Six illustrative records of horizontal smooth compensatory eye and head movements of subject RS fixating a distant target while his head was passively or actively rotated. The top three records were made with the head supported by a bite-board while the body was rotated at three frequencies: 0.00 Hz (left), 0.33 Hz (center), and 0.66 Hz (right). The bottom three graphs were made during active head rotation paced by a metronome at three frequencies: 0.33 Hz (left), 0.66 Hz (center), and 1.33 Hz (right). The time-scale marks signify one-second intervals. The position-scale marks signify 1° distances. The head-position traces (H/10) show the position of the head scaled to 1/10 of its actual value. The gaze (retinal image position) of the right eye (RE) is shown just below the head trace, the gaze of the left eye (LE) is shown just below the right eye trace, and the vergence of the eyes (LE-RE) is shown at the bottom of each record. Upward changes in the head and eye traces signify leftward movements. Upward changes in the vergence traces signify divergence. Saccades have been removed from all eye traces. Saccades were detected by an acceleration criterion (see text), and the gaze 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.

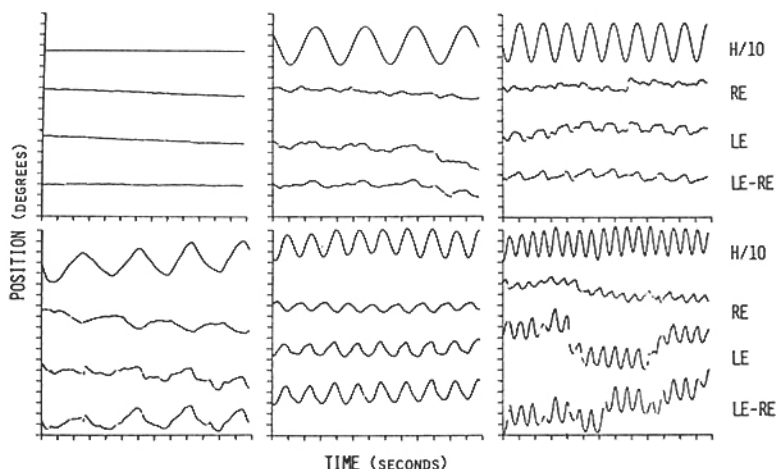


FIGURE 2. Six illustrative records of horizontal smooth compensatory eye and head movements of subject HC, a myope wearing his normal corrective spectacles, fixating a distant target while his head was passively or actively rotated. Gaze traces have been corrected for his spectacles. See FIGURE 1 for other details.

with the subject's head supported by a dental bite-board. This unnatural condition (0.00 Hz) permits examination of slow compensatory eye movements (VOR supplemented by vision) when head movement is minimal. Next, recordings were made while the subject's head remained supported by the bite-board as his chair was oscillated sinusoidally at 0.33 or 0.66 Hz with peak-to-peak amplitude set to 34° (peak velocities = 35° or 70° /second). The subject then removed his head from the bite-board, and a series of recordings were made during active head rotations whose frequencies were paced by a metronome (0.33, 0.66, or 1.33 Hz where peak velocity = 140° /second). Subjects tried to make sinusoidal movements and keep amplitude similar to the amplitude of the passive rotations. The results of these experiments are illustrated in FIGURES 1-5 and summarized in TABLES 1 and 2.

The retinal image of the fixation target moved very little only when the head was supported artificially. All five subjects, whose results are described in detail, performed similarly in this condition (the upper-left recording reproduced in each plate). Note, however, that the head movements, which did occur when the head was stabilized, were only modestly compensated by eye movements (see TABLES 1 and 2). The mean speed of these head movements on the bite-board was 31° /second (SD = 0.37). The mean oculomotor compensation for these small, relatively slow head movements was modest, i.e., only 30% (SD = 23). Now consider the illustrative eye- and head-movement records made during active and passive rotation. If compensation were virtually perfect, gaze and vergence traces would approximate horizontal straight lines—they do when the head is almost stabilized by the bite-board and vestibular compensation is not required to maintain gaze stability. There are very few instances, off the bite-board, during which it seems appropriate to speak of virtually perfect compensation, and even in these cases virtual perfection is achieved by only one eye. This causes considerable imperfection in the control of vergence. See, for example, subject

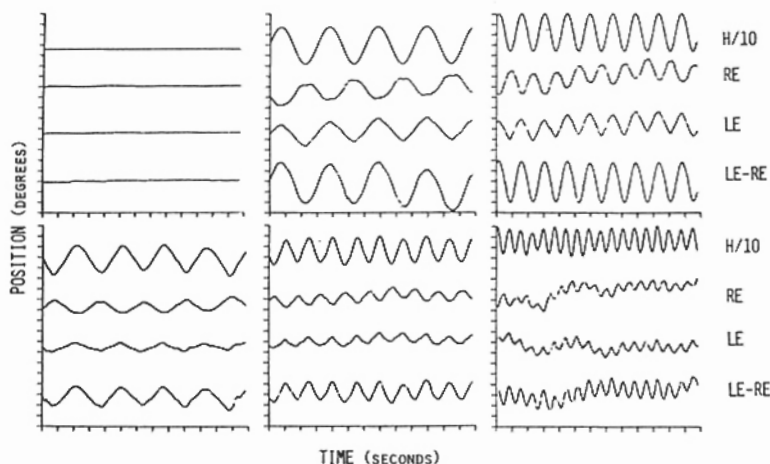


FIGURE 3. Six illustrative records of horizontal smooth compensatory eye and head movements of subject AM, a myope wearing his normal corrective spectacles, fixating a distant target while his head was passively or actively rotated. Gaze traces have been corrected for his spectacles. See FIGURE 1 for other details.

RS's gaze and vergence during passive rotation at 0.33 Hz (top center in FIGURE 1) and at 0.33 and 0.66 Hz during his active rotations (bottom left and center). Subject HC's right-eye gaze during passive rotation at 0.33 Hz (top center in FIGURE 2) and to a lesser degree at 0.66 Hz (top right) is almost as good as when his head is held. In all other instances (subjects and/or eyes), the differences

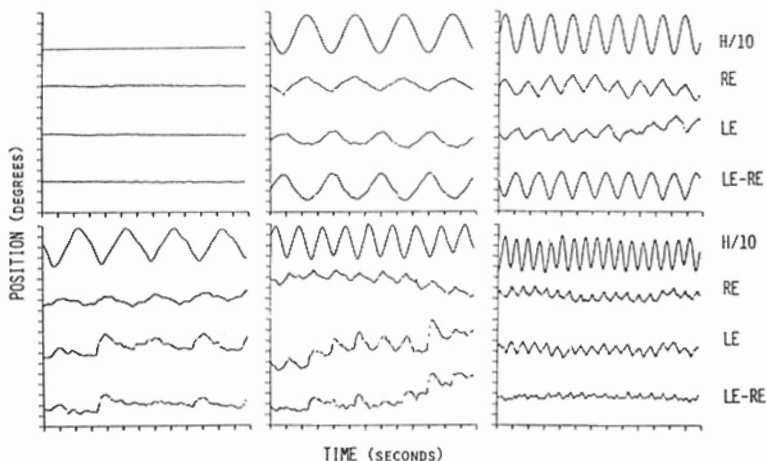


FIGURE 4. Six illustrative records of horizontal smooth compensatory eye and head movements of subject WC, a myope wearing his normal corrective spectacles, fixating a distant target while his head was passively or actively rotated. Gaze traces have been corrected for his spectacles. See FIGURE 1 for other details.

between compensation during head movement and during artificial head stabilization are striking. These "failures" in compensation arise from both overcompensation and from undercompensation. When the eye movement undercompensates, the gaze trace in these records moves in the same direction as the head. When the eye movement overcompensates, the gaze trace moves in the direction opposite to the head. See, for example, FIGURE 3. This subject, AM, undercompensates with his left-eye movements and overcompensates with his right-eye movements under all conditions. The other subjects show similar "failures," but they tend to vary with conditions of stimulation, e.g., WC in FIGURE 4 overcompensates with both eyes during active rotation, but his right eye undercompensates while his left eye continues to overcompensate during passive rotations. WC's performance in these records was idiosyncratic but consistent. He always

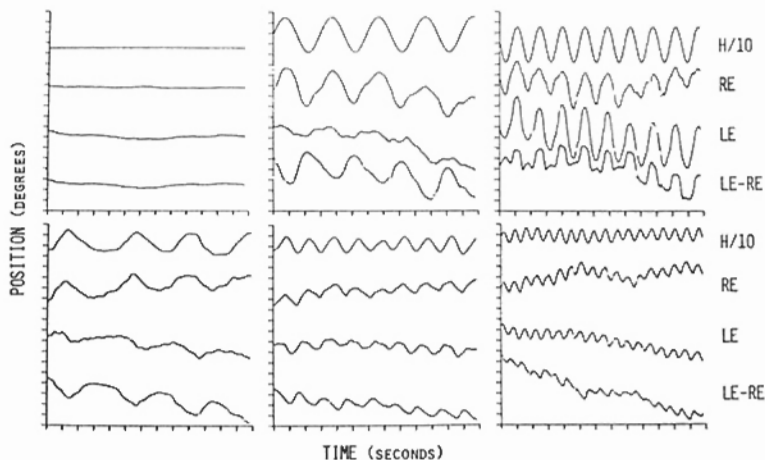


FIGURE 5. Six illustrative records of horizontal smooth compensatory eye and head movements for subject EK, a myope wearing her corrective corneal contact lenses, fixating a distant target while her head was passively or actively rotated. Gaze traces did not require correction. See FIGURE 1 for details.

shows these patterns, as do the other subjects, each of whom has his own binocular compensatory signature.

Despite these differences in gaze characteristics within and between individuals, there is considerable consistency in the overall pattern of data summarized in TABLE 2. The grand mean head-movement speed compensated under natural conditions (i.e., excluding measures on the bite-board) was 95% (SD = 2.1). Compensation was the same during active (mean = 95%, SD = 2.4) and during passive rotation (mean = 95%, SD = 1.9). Vergence speed increased very markedly once the head was allowed to move. The grand mean increase in vergence speed was 329% (SD = 249). The increase was greater under passive rotation for four subjects (mean = 429%, SD = 249) than under active rotation (mean = 178%, SD = 102). The opposite result was obtained with the other subject (HC), where active mean increase was 290% (SD = 164) and passive mean increase was 114% (SD = 59). These comparisons could be made only for

TABLE 1

MEAN BINOCULAR RETINAL IMAGE AND HEAD SPEED (MIN ARC/SEC) DURING ACTIVE AND PASSIVE HEAD ROTATION AT SEVERAL FREQUENCIES*

Condition		Head	LE	RE	LE-RE
Subject RS (n = 8000)					
Passive	0.00 Hz	25 (20)	24 (19)	21 (17)	30 (23)
	0.33 Hz	1,408 (650)	32 (37)	49 (36)	67 (44)
	0.66 Hz	2,999 (1,445)	79 (62)	103 (70)	124 (89)
Active	0.33 Hz	1,072 (760)	42 (34)	34 (35)	50 (49)
	0.66 Hz	2,281 (1,472)	62 (54)	43 (41)	68 (68)
	1.33 Hz	5,006 (2,742)	129 (119)	86 (80)	113 (97)
Subject HC (n = 4000)					
Passive	0.00 Hz	39 (29)	23 (21)	24 (21)	29 (23)
	0.33 Hz	1,361 (677)	55 (60)	44 (56)	50 (42)
	0.66 Hz	2,927 (1,472)	93 (76)	70 (55)	74 (63)
Active	0.33 Hz	908 (448)	58 (53)	43 (32)	76 (58)
	0.66 Hz	1,971 (1,010)	104 (76)	65 (44)	149 (87)
	1.33 Hz	3,862 (1,870)	257 (190)	113 (112)	313 (200)
Subject AM (n = 9000)					
Passive	0.00 Hz	43 (33)	20 (17)	25 (20)	31 (23)
	0.33 Hz	1,412 (656)	80 (40)	79 (53)	150 (80)
	0.66 Hz	2,947 (1,490)	168 (84)	154 (106)	307 (164)
Active	0.33 Hz	1,081 (483)	45 (32)	50 (18)	85 (49)
	0.66 Hz	2,042 (922)	83 (50)	83 (53)	157 (77)
	1.33 Hz	3,410 (1,796)	146 (82)	136 (93)	256 (137)
Subject WC (n = 4000)					
Passive	0.00 Hz	45 (34)	19 (16)	23 (19)	27 (20)
	0.33 Hz	1,424 (685)	58 (40)	57 (38)	98 (103)
	0.66 Hz	3,166 (1,531)	105 (74)	126 (66)	208 (101)
Active	0.33 Hz	1,207 (489)	76 (100)	47 (37)	65 (80)
	0.66 Hz	2,461 (960)	105 (100)	77 (52)	86 (80)
	1.33 Hz	4,584 (2,156)	149 (84)	131 (91)	107 (76)
Subject EK (n = 5000)					
Passive	0.00 Hz	22 (17)	23 (18)	21 (17)	30 (23)
	0.33 Hz	1,321 (652)	70 (56)	99 (77)	113 (83)
	0.66 Hz	2,807 (1,357)	340 (215)	213 (140)	184 (181)
Active	0.33 Hz	632 (359)	44 (35)	58 (43)	67 (47)
	0.66 Hz	1,106 (487)	73 (56)	82 (52)	79 (52)
	1.33 Hz	1,907 (919)	133 (97)	167 (93)	116 (73)

*Standard deviations are given in parentheses. Speeds are based on 35-msecond velocity samples after removal of saccades. The approximate number (n) of speeds contributing to the mean speeds is shown for each subject. The column labeled LE-RE represents the speed of vergence eye movements.

TABLE 2

PERCENT OF HEAD MOVEMENT SPEED COMPENSATED IN EACH EYE AND THE
PERCENT INCREASE IN VERGENCE SPEED DURING ACTIVE AND
PASSIVE ROTATIONS AT SEVERAL FREQUENCIES*

Condition		LE	RE	LE-RE
Subject RS (n = 8000)				
Passive	0.00 Hz	4	16	
	0.33 Hz	98	97	123
	0.66 Hz	97	97	313
Active	0.33 Hz	96	97	67
	0.66 Hz	97	98	127
	1.33 Hz	97	98	277
Subject HC (n = 4000)				
Passive	0.00 Hz	41	38	
	0.33 Hz	96	97	72
	0.66 Hz	97	98	155
Active	0.33 Hz	94	95	162
	0.66 Hz	95	97	414
	1.33 Hz	93	97	979
Subject AM (n = 9000)				
Passive	0.00 Hz	53	42	
	0.33 Hz	94	94	384
	0.66 Hz	94	95	890
Active	0.33 Hz	96	95	174
	0.66 Hz	96	96	406
	1.33 Hz	96	96	726
Subject WC (n = 4000)				
Passive	0.00 Hz	58	49	
	0.33 Hz	96	96	263
	0.66 Hz	97	96	670
Active	0.33 Hz	94	96	141
	0.66 Hz	96	97	219
	1.33 Hz	97	97	296
Subject EK (n = 5000)				
Passive	0.00 Hz	-4	5	
	0.33 Hz	95	93	277
	0.66 Hz	88	92	513
Active	0.33 Hz	93	91	123
	0.66 Hz	93	93	163
	1.33 Hz	93	91	286

*The percent compensation is based on the ratio of eye speed to head speed. The percent increase in vergence speed is based on the ratio of vergence speed during rotation to vergence speed at 0.00 Hz (head on bite-board).

0.33 and 0.66 Hz. It should be emphasized at this point that all subjects always saw the fixation field as fused, clear, and stable during the course of these experiments.

We conclude that virtually perfect compensation of head rotation by the VOR, supplemented by vision, is rarely observed when head rotations are within "the natural dynamic range of semicircular canal stimulation."⁸ The proportion of head speed that is compensated during natural head rotation is greater than when the head is artificially stabilized on a bite-board, which permits only very small, slow head rotations. The fact that compensation is particularly poor for very small rotations has been reported before by Skavenski, Hansen, Winterson, and Steinman.⁹ These authors proposed that incomplete compensation may aid vision by guaranteeing sufficient retinal image motion when bodily movement is very modest. Similar results were obtained subsequently in rabbit.¹⁰

Adaptation experiments were undertaken to determine whether the rather high retinal image speeds observed in all of our subjects during relatively large bodily movements arose from limitations of their oculomotor compensatory subsystems or from the teleologically attractive alternative suggested by Skavenski et al.⁹ Adaptation experiments can make it plausible to assert that the compensatory subsystems adjust their degree of compensation so as to guarantee some nonzero value of retinal image speed that subsequently might be shown in psychophysical experiments to be useful and perhaps essential to visual processing. This possibility becomes plausible if it can be shown that the amount of compensation preferred by a given subject remains the same when the VOR is forced to change its gain when a new correlation between the degree of head movement and the resulting displacement of the retinal image is introduced.

We knew from prior work that adaptation of the human VOR was possible but likely to be both slow and incomplete. Gauthier and Robinson reported that Gauthier partially adapted to a $2\times$ telescope, which he wore continually for 5 days.¹² Gonshor and Melvill Jones produced adaptation by using mirrors or dove prisms to reverse the direction of eye movement to head movement.^{8,13} Sixteen minutes of adaptation with the mirror on 3 consecutive days led to a modest cumulative reduction in VOR gain (VOR gain in the dark started at about 0.75 and went down to about 0.5). Adaptation of 14 days with continuously worn dove prisms led to complete elimination, and possibly to the beginning of reversal, of the VOR. Complete adaptation would be evidenced by negative gains of 0.75. Research with the rhesus monkey gave similar expectations of slow and incomplete adaptation.^{1,14} Monkeys fitted with $2\times$ telescopes required 3 days to reach 60% of the required increase in VOR gain and stayed at this level during 5 subsequent days. Monkeys fitted with $-0.5\times$ telescopes required 24 hours to achieve their stable level at 54% of the required reduction in VOR gain.

We began our experiments in this context and proceeded accordingly, viz., we measured VOR baselines in the dark and in the light, fitted magnifying or minifying spectacles, measured VOR performance with these spectacles, and then wore them continually for 24 hours, after which we once again measured the VOR both in the light and in the dark. When, after about a month of such experiments, it became possible to determine what had been happening, we found a great deal of adaptation of the VOR within minutes of fitting our magnifying or minifying spectacles. It did not change during the next 24 hours. This unexpected observation led to specific experiments on short-term adaptation, which will now be described. (The data obtained over longer periods of adaptation will be described elsewhere.)

Three of the subjects (the authors) served in these experiments. Two (HC and

AM) are myopic and had worn their normal negative corrective spectacles during the earlier experiments in which their natural retinal image motion was measured. The technique we use to make the correction for spectacle wearers when we describe or plot their gaze will be described here because the rationale underlying these corrections is the same as that used when altering the normal relation between rotations of the head and movements of the fixation target on the retina. There are two ways to determine the magnification factor required to convert eye in space to gaze for an individual wearing spectacles. First, the power of the spectacle and distance to the center of the eye's optics can be measured. This distance is difficult to determine accurately. The second method, the one employed, is behavioral. It permits an accurate determination because measurements are limited only by the stability of the fixating eye, which in all of our subjects was better than 5'.

Our behavioral measurement proceeded as follows. The subject's head was supported on a bite-board attached to his chair. The chair could be rotated through a known angle. The subject's task was to maintain monocular fixation of a distant target while wearing his normal spectacles. Fixation was recorded while the head faced the target and the subject looked through the center of his spectacle. The spectacles were secured to the head by tape during these measurements and during all subsequent experiments. The head was then rotated, to the right or to the left, 17°, and recordings were made while the subject once again fixated the same target monocularly. Now his eye was looking at the target, but the line of sight passed through an off-center portion of the spectacle lens. The amount of rotation of the eye required to place the line of sight on the fixation target depends on the power of the spectacle and its distance from the eye. If no spectacle is worn, the required rotation of the eye in the head will be equal in size, but opposite in direction, to the rotation of the head, i.e., the magnification factor equals one. If a negative spectacle is worn, the rotation of the eye in the head will be less than the rotation of the head and the magnification factor will be less than one. Positive spectacles will give magnification factors greater than one. This behavioral technique was reliable, i.e., the magnification factors for a given subject's left and right eye and particular pair of spectacles were highly reproducible. The validity of the technique was determined by making similar measurements for an emmetrope (RS) whose magnification factor for each of his eyes, when no spectacles were worn, was within 1% of unity and also for EK, a myope wearing corneal contact lenses concurrent with sensor-coil annuli who also had, as she should, a magnification factor of one.

The same behavioral technique was used to calibrate the spectacles that were used to encourage adaptive changes in the VOR. Subjects HC and AM, whose normal spectacles incorporate about -5 D corrections, were fitted with +5 D spectacles and then calibrated behaviorally in the manner described above. We determined that both subjects, wearing the +5 D spectacles, would have to increase rotations of their eye in space by 33% if they wished to maintain the same stability of gaze they prefer when they wear their normal negative spectacles. Requiring a myope to wear a positive spectacle, however, introduces considerable visual blur. It was for this reason that we used a relatively large colorful fixation target. This target, even when grossly defocused, provided a discriminable chromatic region that was clearly visible within what was now seen as a fuzzy grey background.

Following the calibration of the novel noncorrective spectacles, the short-term adaptation experiment was done as follows. A sensor coil was fitted to the right eye, and the positive spectacles were fitted. The subject was placed in

darkness and required to move his head sinusoidally in pace with a metronome set at 0.66 Hz. Very shortly after he began to move, a 12.8-second recording was made. The subject was instructed to imagine that he was looking at the distant fixation target while he moved his head in darkness. This record provided an estimate of VOR gain before adaptation. The blinds then were opened, and the subject continued moving at 0.66 Hz while he viewed the distant defocused fixation target. A 12.8-second trial in the light was recorded at this time. The subject continued adapting by fixating the defocused target while moving his head for 40 minutes thereafter. At 5-minute intervals, he was placed in total darkness and a recording was made followed immediately by a recording of his eye-movement pattern while fixating the visible target. HC continued wearing the positive spectacles for 24 hours, and recordings were then made both in the light and in the dark.

RS, a presbyopic emmetrope, served in an analogous experiment. He, however, was fitted with a -5 D pair of spectacles that required him to reduce his compensatory responses by 9% (measured behaviorally). We chose this experiment for this subject because, although RS does not require spectacle correction for normal distance vision, he has in recent years found it necessary to use a variety of magnifiers to read and to perform other close work. We wished to avoid any contamination of his adaptation results by such prior exposures to positive adaptations and therefore required him to reduce, rather than increase, his compensatory responses. RS's data were obtained last in a brief experiment in which we only examined the adaptation of his VOR in darkness because we already knew from our measurements of HC and AM that adaptation with a visual stimulus was almost instantaneous. We also expected that a 9% change would be completed very quickly.

The results of these experiments are summarized in FIGURE 6. The preadaptation gain of the VOR of HC and AM, the myopic subjects who will be fitted with

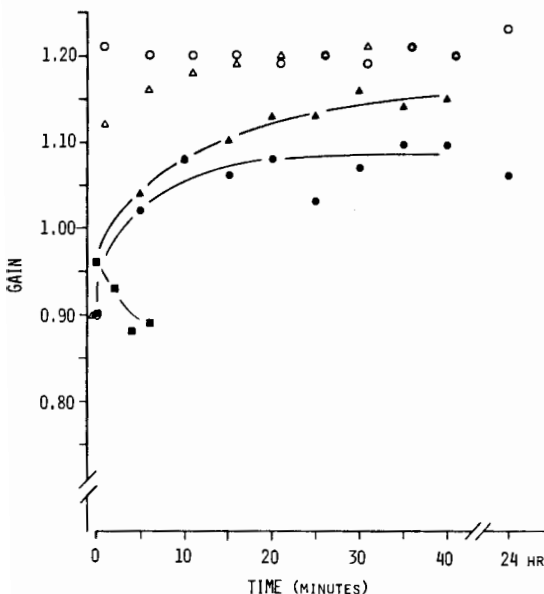


FIGURE 6. VOR gain (35-millisecond eye-in-head velocity/35-millisecond head velocity) in the light (open symbols) and in the dark (closed symbols) as a function of adaptation time. Subject HC's performance is shown by circles, AM's by triangles, and RS's by squares.

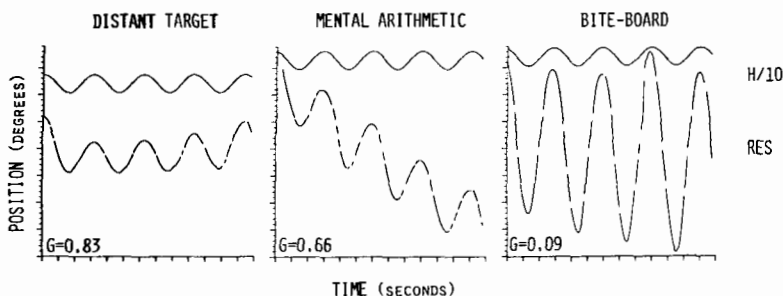


FIGURE 7. Three representative records of subject AM imagining a distant target (left), doing mental arithmetic (center), or imagining a target attached to his bite-board holder (right). Recordings were made in total darkness while AM's head was supported by a bite-board and his chair was rotated at 0.33 Hz. The time-scale marks signify one-second intervals. The position-scale marks signify 1° distances. 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. Gaps in the eye traces show when saccades have been removed. Mean gains (G) are also given.

positive spectacles, is shown at time zero. Both fail to compensate completely with their right eyes in the light as well as in the dark—both gains = 0.90. Exact compensation for the introduction of the positive spectacles would require their gain to increase to 1.21. Both HC and AM accomplished this adjustment very rapidly in the light; HC attained this level within 1 minute of starting the experiment. AM required only 11 minutes to reach asymptote. Adaptation of the VOR working alone in the dark was slower and less complete. Both subjects, however, achieved a great deal in only 40 minutes. AM's VOR accomplished about 90% of the required change in this time, and HC's about 70%. The circles at the right show HC's gains in the light and in the dark after 24 hours during which he continued to wear the positive spectacles. These values fall within the range observed during the later portion of the initial period of adaptation. RS's adaptation to the negative spectacles, requiring a 9% reduction in gain, is also reproduced in this figure (filled squares). His baseline gain shown at time zero was 0.96, the highest natural VOR gain observed in the dark in any of our subjects under these conditions. RS accomplished about 85% of the required reduction within 6 minutes.

Some comment about the gain of the VOR in the dark is both necessary and possible at this time. It has been claimed on the basis of behavioral, but never absolute, calibrations made with insensitive eye movement monitors (EOG) that the average gain of the VOR in the dark can be as high as 1.00. Unity gain was observed very rarely in our experiments except when gain was forced up by artificial optical arrangements. The average gain of the natural VOR in the dark was less than 1.00. Similar observations were made previously in a smaller series of experiments in Rotterdam and also in Boston.^{3,9} It also has been claimed that the gain of the VOR in the dark can be altered markedly and systematically by giving specific instructions to the subject.¹¹

We undertook to examine this second claim, also based on behavioral calibrations of EOG, now that we knew that the first was fallacious. AM participated in this experiment. He was chosen because of his relative inexperience as an oculomotor subject and researcher. The results are summarized in FIGURE 7 where his VOR in the dark is shown under three instructions: imagining

the distant fixation target mounted on the wall, during the course of mental arithmetic, and while imagining a target attached to the front of his bite-board holder.

We recorded five trials under each condition. Their mean gains are included in the illustrative analog records. Instructions clearly make a systematic difference. Distraction in the form of mental arithmetic will reduce gain noticeably, and almost complete cancellation of the VOR can be obtained by asking a subject to imagine a target moving with his head. Note, however, that imagining a distant target attached to the wall gave a mean gain of 0.83 not 1.00. The highest right-eye average gain observed for this subject imagining a distant stationary target was 0.90. His left-eye average was slightly higher, 0.92.

We have shown quantitatively in FIGURE 6 that the gain of the VOR can exceed one, but this unnatural state required adaptation with appropriate stimulation. By appropriate stimulation we mean novel optical arrangements that forced the compensatory subsystems to increase their response in the effort to reduce the retinal image slip of the fixation target. FIGURES 8 and 9 illustrate the changes in the oculomotor pattern of the myopic subjects (HC and AM) during the course of adaptation with +5 D spectacles that required them to increase gain well beyond unity.

All of these records show head position in space and the position of the right eye in space (RES). The top records, which illustrate performance in the light, also show the gaze of the right eye (RE) after correction for spectacles. The first pair of records in each plate illustrate preadaptation performance in the light (top) and in the dark (bottom). These baselines are typical of the right eyes of

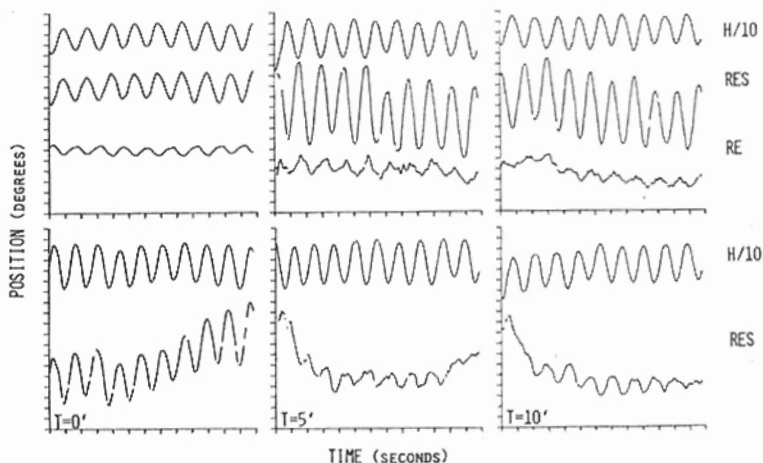


FIGURE 8. Six records of a myopic subject's (HC) short-term adaptation to +5 D spectacles. The upper three records were recorded in the light and the lower three records in total darkness while the subject actively rotated his head at 0.66 Hz. The time (T) these records were obtained relative to the start of adaptation ($T=0$) is indicated. The time-scale marks within each record signify one-second intervals. The position-scale marks signify 1° distances. 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 magnifying spectacles. Gaps in the eye traces show when saccades were removed.

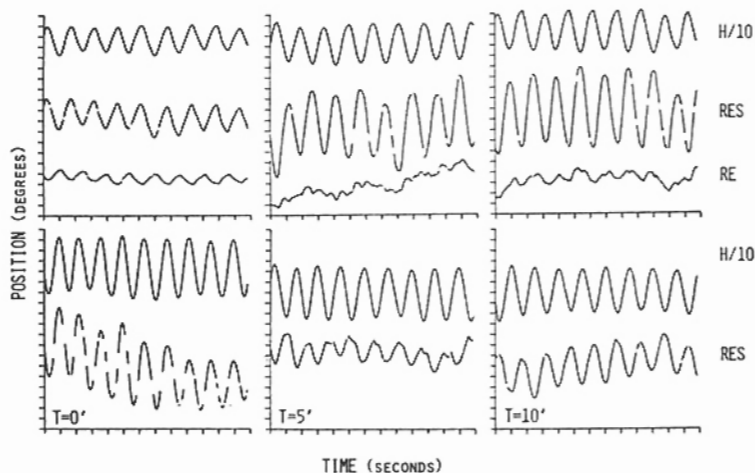


FIGURE 9. Six records of a myopic subject's (AM) short-term adaptation to +5 D spectacles. See FIGURE 8 for other details.

these subjects, namely, both overcompensate head movement [i.e., the eye in space trace (RES) moves opposite to the direction of the head] and both show considerable retinal image motion. (The mean head speed compensated by HC was 97% and by AM was 96%.) The middle records in these plates show performance after about 5 minutes of adaptation. Gain at this time had already exceeded 1.00; the eyes in space both in the light (top) and in the dark (bottom) are now moving *opposite* in direction to movements of the head (see RES traces before and after adaptation). Adaptation was almost over in the records shown on the right, which were made about 10 minutes into the adaptation period.

The gaze traces (RE) are of particular interest because they show the retinal image motion that the compensatory subsystems chose as optimal before and after adaptation. Note that marked changes in gain produced by novel optical arrangements reestablished the pattern of retinal image motion preferred before adaptation. The mean head speed compensated in the light after adaptation, when gain had increased 33%, was 95% for HC and 97% for AM—values very similar to the compensation shown by these subjects when they wore their normal corrective spectacles before adaptation. It is important to realize that when we pushed the compensatory subsystems from their natural low gain to an unnatural high gain, gain moved through values that would have allowed virtually perfect stabilization of the retinal image. Had virtually perfect stability been the goal of the compensatory subsystems, they should have stopped adapting at this time. They did not. This result permits us to conclude that the compensatory subsystems seek some appreciable nonzero retinal image speed rather than virtually perfect image stability.

DISCUSSION

We report two kinds of observations. Some extend our prior work on natural binocular image motion and others begin to examine its origin and change.

We confirmed, in additional subjects, our observations initially made in the Netherlands that natural binocular retinal image motion is appreciable,³ and extended the observations to show that this is equally true with active and passive rotations. We also confirmed that the gain of the VOR in the dark can be changed by instructions.¹¹ We did not find that instructions can produce natural average unity gain of the VOR in the dark. This last observation does not seem to require discussion beyond calling attention to the fact that we, unlike all others, used a sensitive instrument for measuring eye movement that is calibrated absolutely rather than behaviorally.

Our other observations were completely unexpected. Our demonstration that the slow compensatory subsystems adjust their gain very rapidly and almost completely in the dark to novel visual demands conflicts with prior reports both for man and infrahuman primates.^{1,8,12-14} If, for the sake of discussion, we take these prior EOG measurements at face value, we can discuss two more-or-less plausible explanations.

Perhaps we obtained such rapid and almost complete adaptation because we challenged the vestibular system only modestly. Prior authors generally required much larger changes in oculomotor compensation: $2\times$ in Gauthier and Robinson and complete reversal in Gonshor and Melvill Jones.^{8,12,13} It is only in the infrahuman primate literature that we have data on adaptation to a relatively modest change—in line with the demands we made. Miles and Eighmy required their monkeys to reduce VOR gain by 50%.¹ We required 33% increases in gain. Miles and Eighmy observed that adaptation proceeded faster when they required a 50% change than when they required a 100% change. However, their monkey's adaptation in the dark to 50% minification was only 54% complete after 24 hours and showed no signs of going further over 8 days. We obtained 70% changes for one subject and 90% changes for the other subject when we required a 33% increase. Our changes, which were accomplished within 40 minutes, were stable for periods as long as 24 hours. This difference in results may arise simply from the species difference. If this proves to be the explanation, rhesus would seem to be a poorer animal model for the human than most physiologists would like to believe.

There is another difference between our experiments and prior human and animal work. Namely, we used simple spectacles to change magnification factors both upwards and downwards. This optical arrangement is cost effective, but it has severe adverse effects on the clarity of vision. It is possible, although it seems unlikely to us, that our failure to provide a sharply focused visual world allowed the vestibular system to be more plastic than it would be when the clarity of vision is preserved. This explanation, as well as the possibility of slower vestibular adaptation to larger challenges than we have tried thus far, must be tested empirically.‡ Despite the desirability of examining these possibilities, the fact remains that a small, blurred foveal stimulus is sufficient to promote rapid and marked adaptation of the VOR.

We proposed at the beginning of this paper that the goal of compensatory eye movements might be to establish nonzero gaze velocities (retinal image motions) that are optimal for vision. We have added plausibility to this idea by demonstrating that the compensatory subsystems rapidly adapt to some nonzero value of gaze velocity. We now must study individual visual capacities with known gaze

‡Note added in proof: We found in subsequent research that rapid adaptation occurs when clear vision is preserved.

velocities and show that the gaze velocities preferred by an individual are optimal for that individual's visual requirements.

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