THE TIME COURSE OF ADAPTATION OF HUMAN COMPENSATORY EYE MOVEMENTS

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A human being must make compensatory eye movements to maintain his line of sight on a stationary detail while he moves his head. 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 a stationary distant target. In more natural conditions the VOR is supplemented by vision, i.e., the slip of the image of the fixation target generates signals for smooth pursuit eye movements.

Traditionally, it has been assumed that these compensatory eye movements are virtually perfect *because* the visual world remains clear and stable during appreciable bodily activity. However, recent accurate measurements of natural retinal image motion during head and body movement showed that compensation is far from perfect (Skavenski, et al., 1979; Steinman, Collewijn, 1980; Collewijn, et al., 1981). This fact led these authors to suggest that the functional goal of oculomotor compensation is to maintain an amount of retinal image motion, within each eye and between the eyes, that is optimal for binocular vision. This suggestion seems plausible because the VOR is known to be plastic. If the goal of the VOR were virtually perfect image stabilization, it should, in principle, adjust its gain to achieve this outcome.

We undertook to study the plasticity of human compensatory eye movements as a step towards understanding the relationship between oculomotor and visual processes. Very little is actually known about plasticity of human compensatory eye movements. The few reports, which used inaccurate eye movement monitors (EOG), suggest that plastic changes are slow and incomplete (Gauthier, Robinson, 1975; Gonshor, Melvill Jones, 1976). If this were true, oculomotor system performance could impede effective visual function when visuomotor responses must change.

We found that: 1) adaptation to novel optical arrangements is virtually complete within minutes when the VOR is supplemented with visual input, 2) about 70% of the required change of the VOR, working alone in darkness, is obtained within 24 hours, 3) stimulation with defocused visual input is sufficient to produce these adaptive changes, 4) similar adaptive changes occur when clear vision is maintained and optical arrangements are changed by requiring a myope to adapt to corrective spectacles after removal of corrective corneal contact lenses, 5) a novel optical arrangement to one eye will adapt both eyes when one eye is patched, and 6) a single eye will determine the adaptation of both eyes when conflicting optical demands are imposed.

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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 (1976), which Collewijn (1977) developed and used to measure eye movements on the horizontal meridian in the freely moving rabbit. Steinman and Collewijn (1980) subsequently used Collewijn's revolving field monitor with freely-moving human subjects. Detailed descriptions of Collewijn's instrument are given in the prior papers. Here we will only briefly 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 (1945).

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 was maintained by a feedback loop receiving input from a (10 cm dia.) 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 1000 for translations of $\pm$ 24 cm as expected from Rubens' (1945) 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 (0.278G) 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 sec to 24 hours.

Eye movements were measured with the silicone annulus sensor coils described by Collewijn, et al. (1975). See Collewijn et al. (1981) for an experiment which shows that these annuli do not change position with respect to the eye under the conditions reported in the present paper.

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° dia. 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 equiped with a cam and lever that produced approximately sinusoidal movements at 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 sinusoidal-like active rotations.

Data Acquisition and Analysis: Digital eye position and head samples from each of 3 channels (right eye, left eye and head) were averaged, converted to min arc and stored on tape at the end of each trial which lasted 12.8 sec. The stored samples summarized 5 msec 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.

Eye and head position samples served as the basis for the calculations of velocities and gains. A sliding window technique was used to calculate velocity. The window, 35 msec wide, contained 7 position samples and the slope of the line, fitted by least squares, through the 7 positions provided a single estimate of "instantaneous" velocity. The window was then moved 5 msec later in time (1 position sample) and the next velocity estimate was calculated. Velocity samples were then used to detect and remove saccades. Periods in which saccades were removed were not included in any analyses.

Gain (35 msec eye in head velocity/35 msec 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 moved 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 adaptation of compensatory eye movements in 5 subjects (4 myopes and 1 emmetrope). All 3 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 2 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 53 years in age. All had 20:20 Snellen acuity naturally or with their normal spectacles.

Protocol: The experimental sequence began with measurements of the subject's pre-adaptation compensatory eye movements in the light and in the dark. The baseline measurements were made with the subject's normal optical arrangements, i.e., the myopes wore their corrective spectacles or in one case (EK) hard corneal contact lenses. The baseline measurements began with a calibration of the magnification factors of each subject's normal optical arrangements.

A behavioral technique was used. 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 and the magnification factor will be one. Positive spectacles will give magnification factors greater than one. Negative spectacles will give magnification factors less 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.

Next, compensatory eye movements were measured at the various frequencies during both active and passive rotations in the light and in the dark. These measurements were followed by a calibration of the magnification factors of the novel optical arrangement which would require each subject to modify his compensatory eye movements so as to reduce the now uncompensated retinal image motion resulting from head movement. The presbyopic emmetrope (RS) was fitted and calibrated with +5 D spectacles. HC, whose normal spectacles are about -5 D, was fitted with +5 D. AM, whose normal spectacles are about -5 D, was required to perform without any correction for his myopia. EK, who requires about -8 D correction, was first measured with her corneal contact lenses which were removed without disturbing the silicone annuli and replaced by her normal spectacles. The spectacles provide the same refractive correction but require her to reduce the gain of her compensatory eye movements.

Compensatory eye movements were measured immediately following fitting of the new optical arrangements and once again 24 hours later during which time the subjects went about their normal activities to the extent that this was possible in what was, in all but one case (EK), a highly blurred visual environment.

RESULTS

The main results of this experiment are summarized in Table 1 where the mean gains of the compensatory eye responses are shown. Consider first the gains of the myopic subjects wearing their normal spectacles which minify the visual scene and, therefore, require relatively small eye rotation for a given amplitude of head rotation. These subjects (*HC*, *AM* and *WC*) normally function, when they wear their negative corrective spectacles, with appropriate gains, i.e., their gains are less than unity. This was true in the dark as well as in the light. Compare these results with those of subject *RS*, the emmetrope performing without spectacles, and with subject *EK*, the myope wearing her -8 D corneal contact lenses. Both of these subjects showed approximately unity gain when their compensatory eye movements were provided with both visual and vestibular input. They also showed relatively high gains in the dark when they move actively.

Next consider the changes in gain both in the light and in the dark after the normal optical arrangements were changed. All of the subjects, except *EK*, were required to increase their gain either by the replacement of their negative spectacles with positive spectacles or by the removal of the normal negative spectacle correction (*AM*). *EK* was required to reduce gain when her contact lenses were removed and her normal negative corrective spectacles were introduced. The gains designated *Just After* in the table summarize measurements made during the period that immediately followed the introduction of the novel optical arrangements. During the first 20 min measurements were made while all of the subjects adapted by viewing the fixation target as they moved. Ten 12.8 sec adaptation trials were recorded (6 active at 3 frequencies and 4 passive at the 2 lowest frequencies). During the subsequent 20 min two of the subjects (*HC* and *RS*) were measured while they moved in total darkness. All of the subjects changed their gains in both eyes in the appropriate direction. Gains continued to change over the ensuing day but a large proportion of the required change was obtained shortly after the introduction of the novel optical arrangements. All of the subjects showed higher VOR gains in the dark when they actively rotated the head than when the head was supported on a bite-board attached to a chair which was oscillated sinusoidally.

The amount of adaptation of the compensatory eye movements required of each of the subjects and the degree to which they achieved this compensation just after and one day after the introduction of novel optical arrangements are summarized in Table 2. In all, 68 cases can be examined to evaluate the effects of optical re-arrangements on adaptation of compensatory eye movements. Of these in only one case, *AM*'s right eye measured in the dark during passive rotation, failed to show an appropriate adaptive change. Twenty-eight evaluations are possible if we consider only measurements made in the period just after the introduction of the novel optical arrangement. In all of these cases adaptation, both in the light and in the dark, was in the appropriate direction. The percent of gain change achieved varied considerably between subjects and between eyes. In some cases it was virtually perfect with 24 hours. In others, the gain change exceeded the requirement markedly (see AM). The most interesting condition for evaluating the nature of the adaptive change is the VOR in the dark. The average change for the two subjects (HC and RS) whose gain was measured in the dark after only about 130 sec of visual stimulation during movement was high (mean = 53%, S.D. = 12). The average gain change for the entire group of 5 subjects, measured in the dark one day after the novel optical arrangement was introduced, was also high (mean = 73%, S.D. = 30).

We conclude that adaptation of human compensatory eye movements proceeds rapidly and extensively. Subsequent experiments designed specifically to study short-term adaptation during continual active head rotation have shown that adaptation in the light will be complete within 10 minutes and adaptation in the dark will be 70% to 90% complete within 40 minutes (see Collewijn et al., 1981).

Figure 1 reproduces typical eye movement records for one of the subjects (HC) before and during the course of adaptation. The records show compensatory eye movements made in total darkness while imagining a stationary distant target. The left record shows performance before optical arrangements were introduced, requiring increased VOR gain. These records show the movement of the eyes and head in space. Therefore, gains less than unity show as eye rotations in the same direction as rotations of the head (unity gain would show as a horizontal straight line). HC's pre-adaptation performance shows less than unity gain. This is expected because HC is myopic and normally wears minifying spectacles which require him to make relatively small eye rotations in response to his head rotations. In the middle graph we see his performance after about 130 sec of adaptation produced by viewing a fixation target while moving his head. It is clear that gain has increased appreciably, i.e., the rotation of his eyes in his head was larger than before adaptation which means that the rotation of his eye in space (plotted in this graph) will be smaller than before adaptation. The record on the right shows performance 24 hours later. Note that now the eye in space is, once again, rotating appreciably but now it rotates in the direction *opposite* to rotations of the head. This shows that his gain has gone appreciably above unity.

We did additional experiments. First, we repeated the basic experiment with subject RS wearing a -5 D spectacle in front of his right eye and a patch in front of his left eye. Both eyes adapted. Next, we again repeated the basic experiment but this time RS wore a +5 D spectacle in front of his left eye and a -5 D spectacle in front of his right eye. These arrangements were disturbing inasmuch as diplopia, oscillopsia, as well as blur, persisted throughout the experiment. Adaptation was observed but both eyes adapted to the optical arrangement imposed on the right eye of this subject--his dominant eye in the pointing test. Adaptation was not the same during conflict as it was when one eye was patched or when both eyes had the same novel optical arrangements. Specifically, adaptation of the VOR in the dark was as fast and complete only during passive rotations. Just after beginning adaptation during passive rotation, the left eye adapted to 67% of the required change for the -5 D spectacle in front of the right eye. The right eye adapted to 53%. Twenty four hours later,

TABLE 1. Mean gain of slow compensatory eye movements during active and passive rotation in the light and in the dark. Gains were measured before, just after and one day after the introduction of novel optical arrangements which required the gain to change so as to reduce retinal image motion during head movement.

Subject HC:	Active		Passive	
	LE	RE	LE	RE
Before				
Light	0.87	0.90	0.87	0.86
Dark	0.82	0.82	0.72	0.67
Just After				
Light	1.12	1.24	1.17	1.16
Dark	0.93	0.96	0.90	0.86
One Day Later				
Light	1.15	1.24	1.19	1.22
Dark	1.04	1.06	1.00	0.97
Subject RS				
Before				
Light	1.02	1.01	1.01	0.98
Dark	0.94	0.94	0.76	0.74
Just After				
Light	1.18	1.19	1.21	1.17
Dark	1.03	1.02	0.91	0.86
One Day Later				
Light	1.22	1.21	1.16	1.19
Dark	1.07	1.08	0.92	0.89
Subject AM				
Before				
Light	0.90	0.90	0.89	0.91
Dark	0.88	0.88	0.83	0.86
Just After				
Light	1.00	0.98	1.04	0.99
One Day Later				
Light	1.00	0.99	0.98	0.97
Dark	0.96	0.94	0.87	0.85
Subject WC				
Before				
Light	0.97	0.91	0.98	0.87
Dark	0.91	0.90	0.92	0.85
Just After				
Light	1.13	1.11	1.19	1.12
One Day Later				
Light	1.23	1.17	1.24	1.19
Dark	1.16	1.13	1.09	1.08
Subject EK				
Before				
Light	1.03	0.95	1.00	0.94
Dark	0.96	0.89	0.73	0.68
Just After				
Light	0.90	0.79	0.86	0.74
One Day Later				
Light	0.86	0.81	0.90	0.75
Dark	0.80	0.71	0.71	0.57

Mean gains are based on from 8000 to 25,000 "instantaneous" 35 msec velocity samples with saccades excluded. Gains in the active or passive conditions did not differ across the frequencies studied. The mean gains, therefore, are reported as averages over the frequencies.

TABLE 2. The required gain change in the light and in the dark and the percent of gain change achieved just after and one day after the introduction of novel optical arrangements which required the gain to change so as to reduce retinal image motion during head movement.

	Active		Passive	
Subject HC	LE	RE	LE	RE
Required Change	0.28	0.32	0.28	0.32
		Percent Achieved		
Just After				
Light	89	106	107	94
Dark	39	44	64	59
One Day Later				
Light	100	106	114	112
Dark	79	75	100	94
Subject RS				
Required Change	0.20	0.20	0.20	0.20
		Percent Achieved		
Just After				
Light	80	90	100	95
Dark	45	40	75	60
One Day Later				
Light	100	100	75	105
Dark	65	70	80	75
Subject AM				
Required Change	0.06	0.14	0.06	0.14
		Percent Achieved		
Just After				
Light	166	57	250	57
One Day Later				
Light	166	64	150	43
Dark	133	43	67	-7
Subject WC				
Required Change	0.24	0.27	0.24	0.27
		Percent Achieved		
Just After				
Light	67	74	88	93
One Day Later				
Light	108	96	108	119
Dark	104	85	71	85
Subject EK				
Required Change	-0.17	-0.23	-0.17	-0.23
		Percent Achieved		
Just After				
Light	76	70	82	87
One Day Later				
Light	100	61	59	83
Dark	94	78	12	48

Required gain change for each eye is the difference between the behaviorally measured magnification factors with the subject's novel and normal optical arrangements. Percent of the gain change achieved is based on the ratio of the difference between the gain after adaptation and gain before adaptation to the required gain change.

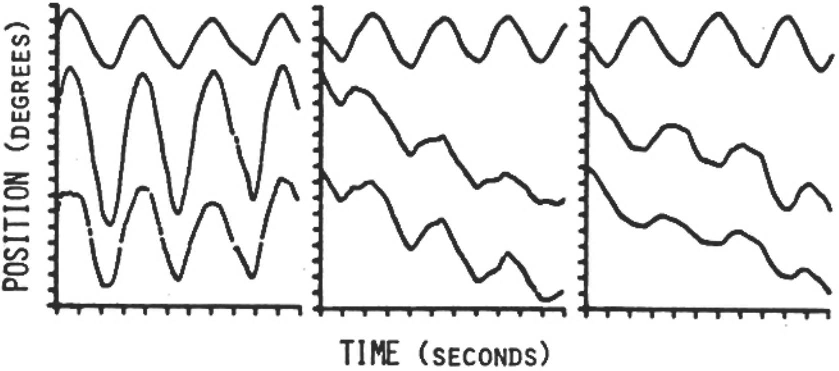

Fig. 1. XY plots of digital head and eye position samples of HC's horizontal eye and head rotations as he actively rotated his head in total darkness while imagining a stationary distant target.

The left record was made before adaptation to +5 D spectacles. The center record was made after the first 130 sec of adaptation to +5 D spectacles. The right record was made 24 hours after adaptation to +5 D spectacles.

The time scale-marks signify 1 sec intervals. The position scale-marks signify 1° distances. The top traces in each record show the position of the head in space scaled to 1/10 of its actual value. The center traces show the right eye in space and the bottom traces show the left eye in space. Upward changes in the traces signify leftward movements.

Saccades have been detected by an acceleration criterion and removed in all of the eye traces. Eye traces were corrected for the changes in position introduced by saccades by assuming that slow compensatory eye movements continued during the saccade at the velocity present just prior to saccade-onset. Small gaps in the eye traces signify when saccades occurred and were removed.

both eyes had adapted to 80% of the required gain change. Active rotations in the dark, however, showed only 40% of the required change in the left eye and 27% change in the right eye after 24 hours of adaptation.

DISCUSSION

We undertook this series of experiments anticipating that the VOR would adapt to novel visual arrangements, but we expected that adaptation would proceed very slowly and be partial at best. We would have done different experiments had we anticipated the results obtained. Specifically, our measurements made just after the introduction of the novel optical arrangements were planned to be pre-adaptation baseline measures. We did not expect to see adaptation during this brief early period. We expected only relatively modest changes after a single day. It seemed reasonable nevertheless, to undertake these experiments because we had a highly accurate eye position monitor which would allow us to see even small adaptive changes.

Consider why we had these expectations which we now know were false. Gauthier and Robinson (1975) reported that Gauthier only partially adapted to a 2.1X telescope which he wore continually for 5 days. Gauthier's gain in the dark had increased only 53% at the completion of the experiment. Gonshor and Melvill Jones (1976a) studied adaptation by using mirrors to reverse the direction of eye rotation to head rotation. Sixteen minutes of adaptation with the mirrors on 3 consecutive days led to only 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 continually worn dove prisms led to complete elimination and perhaps the beginning of reversal of the VOR in the dark. Zero gain means that only about 50% of the required adaptation had been accomplished in two weeks (Gonshor and Melvill Jones, 1976b).

We can suggest only a single explanation for the difference between our results and those of prior investigators. Namely, our challenges to the compensatory subsystems were modest. The novel optical arrangements we used required less than 50% changes in gain. Prior investigators demanded reversals of direction or increases in gain of more than 100%. Perhaps, rapid adaptation only occurs when the demands are relatively modest and physiologically natural. This possibility must be explored experimentally.

There are clinical implications of our discovery that human compensatory eye movements adapt rapidly. First, it explains why when we are fitted with a new pair of spectacles or borrow a pair from a friend, the world appears to move about. A few minutes, or at most an hour, is quite sufficient for the compensatory subsystems to adapt sufficiently to eliminate oscillopsia. Not surprisingly, the oculomotor system rapidly adapts back when the new spectacles are replaced by the original optical arrangements. We know that these perceptual observations, which the reader can easily confirm, are not news but the oculomotor basis on which these perceptual results are obtained is now clear.

The second clinical implication is less straightforward. It cannot be confirmed by the reader simply by putting on a strange pair of spectacles. We observed that all 5 of our normal subjects, who ranged in age from 21 to 53 years, made rapid oculomotor adjustments to novel optical arrangements. They adapted rapidly both in the light when smooth pursuit supplemented the VOR, and also in the dark when the VOR worked alone. This last finding raises the intriguing possibility that the loss of normal capacity for rapid adaptive change of the VOR, working alone, may be an early sign of impending neurological disease. This possibility must now be explored clinically.

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