

COMPENSATORY EYE MOVEMENTS DURING ACTIVE AND PASSIVE HEAD MOVEMENTS: FAST ADAPTATION TO CHANGES IN VISUAL MAGNIFICATION

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SUMMARY

1. Rotational eye and head movements were recorded with great precision with scleral and cranial search coils in a rotating magnetic field.
2. Compensatory eye movements were recorded in light and darkness during active as well as passive head movements in the frequency range 0.33–1.33 Hz.
3. From the recorded, nominal gaze movements the effective gaze was reconstructed taking into account magnification or reduction factors of corrective spectacles. Effective gain was calculated as the ratio between the velocities of the effective corrective eye movements and the head movements.
4. In the light, effective gain of compensatory eye movements during active head motion was mostly between 0.97 and 1.03. It was never precisely unity and differed systematically between subjects and between the two eyes of each subject.
5. During passive head motion in the light, gain was lower by about 3% than during active motion.
6. During active head movement in the dark, gain was mostly between 0.92 and 1.00; values were about 5% lower than during active motion in the light.
7. During passive head movement in the dark, gain was about 13% lower than during active motion, and the variability of the oculomotor response increased.
8. Adaptation of these base-line conditions was induced by fitting the subjects with magnifying or reducing spectacles for periods of 40 min to 24 h. The largest required change in amplitude of eye movements was 36%. When active head movements were made, the amplitude of compensatory eye movements in the light as well as in the dark adjusted rapidly. Most of the adaptation of the vestibulo-ocular reflex in the dark was completed in about 30 min. This rate is much faster than that found in previous experiments requiring larger adaptive changes.
9. Differential adaptation to unequal demands for the two eyes proved to be very hard or impossible. In a mild conflict situation the system adjusted to an intermediate level, distributing the error symmetrically between the eyes. When the discrepancy was large, the adaptive process of both eyes was controlled by the one eye which provided the most meaningful information.

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10. It is concluded that the system generating compensatory eye movements performs best during active rather than passive head movements, and that adaptation to moderate changes in optimal gain are made very rapidly.

INTRODUCTION

The pattern of displacement of gaze (the direction of the line of sight relative to the visual world) is distinctly different from that of the motion of the head. While head movements are mostly smooth, continuous and erratic, most of the displacement of gaze is done discontinuously in steps, called saccades. The difference between head and gaze movements consists of active, compensatory eye movements generated by the co-operative action of vestibulo-ocular (v.o.r.) and visual (optokinetic or smooth pursuit) reflexes. These reflexes eliminate most of the continuous components of head movements from gaze. Specifically, they restrict the velocity of retinal image slip between saccades.

Due to the dynamics and structure of the vestibular and visual subsystems, neither of the two alone is capable of ensuring effective stability for the full frequency range of head movements and over long periods; a symbiotic function is required (Robinson, 1977). Visual control of eye movements is restricted by a long delay and relatively low limits on velocity and acceleration (Lisberger, Evinger, Johanson & Fuchs, 1981). The v.o.r. is fast and effective through all but the very lowest naturally occurring frequencies, but being a feed-forward system it will by itself not maintain a correct gain in the presence of growth, degeneration and damage in the sensori-neuro-muscular system. Even the wearing of ordinary spectacles introduces a change of the required amplitude of compensatory eye movements of about 3% per dioptre, due to visual magnification factors. Therefore, there is a need for visual correction of the gain (and also the balance) of the v.o.r. In part this is an immediate, supplementary action of the visual pursuit subsystems, stimulated by the remaining image slip. However, as recognized long ago, (Rönne, 1923) and amply discussed more recently (Ito, 1972; Robinson, 1975), there is a need for continuous recalibration of the v.o.r. on the basis of systematically excessive slip of the retinal image. Over- or undercorrection by the v.o.r. will be detected by visual direction-selective elements, which will lead to an adaptive change in the parameters of the v.o.r., possibly through circuits involving the vestibulo-cerebellum. In foveate species, the activity of the smooth pursuit subsystem may have special significance (Miles & Lisberger, 1981).

Many experiments in recent years have indeed demonstrated adaptive changes in the v.o.r. (measured in darkness) due to altered relations between head motion and displacement of the visual world. In most of these experiments drastic dissociations between head and eye movements were imposed. The most frequently used procedure has been inversion of the visual correlate of head motion, a condition which ideally should induce a v.o.r. with near unity gain but inverted direction (i.e. a 180° phase shift for all frequencies). This result has not been fully achieved in any experiment and only rarely even approximated after extremely prolonged exposures. The general outcome of this type of experiment suggests that the adaptation of the v.o.r. is slow and incomplete.

For human subjects, Gonshor & Melvill Jones (1976*a, b*) reported a decrease of the

v.o.r. gain to 77% of the initial value after 16 min of tracking with an inverted retinal image motion, whereas a decrease to 25% required a week of continuous exposure to inverted vision. The beginning of inversion of the v.o.r. did not appear until the second week. After 27 days phase was lagging 130° relative to normal (at $\frac{1}{3}$ Hz) and gain was about 50% of the normal value. For the monkey, Miles & Eighmy (1980) calculated that the time constant of adaptation of the v.o.r. to inverted vision is 49 h. Comparable experiments in rabbits show a decrease of the v.o.r. gain to about 70% after 5 h of forced oscillation (Ito, Jastreboff & Miyashita, 1979; Collewijn & Grootendorst, 1979). In the cat, v.o.r. gain decreased to 7% at 0.05 Hz and 45% at 1.2 Hz after 8 days of continuously inverted vision, supplemented by 2 h daily of forced oscillation (Robinson, 1976), while true inversion of a cat's v.o.r. has been only observed for a limited stimulus range even after 200 days of exposure (Melvill Jones & Davies, 1976).

Most of these experiments show a fast, but limited change of gain during the first hours of the exposure. The excessive time required for a more complete adaptation might be a consequence of the extraordinary demand – inversion – on the v.o.r., the physiological or pathological equivalent of which is not easily conceived.

More limited demands have been introduced using telescopic spectacles with magnification factors 2 or 0.5. These were first used by Miles & Fuller (1974) in the monkey. In a later more extensive paper Miles & Eighmy (1980) reported for $\times 2$ spectacles a time constant of acquisition of 39 h with an asymptotic gain value of 1.7, compared to an initial value within a few percent of unity. The time constant for recovery was 9 h. For the $\times 0.5$ spectacles the time constants for acquisition and recovery were 8 h and 15 h, respectively, with an asymptotic gain value of 0.7. Repeated exposures did not accelerate either time course.

Gauthier & Robinson (1975) performed a similar experiment in a human subject, using telescopic spectacles with a magnification factor of 2.1. After 5 days of continuous exposure the v.o.r. had increased its gain from 0.81 to 1.24.

We felt that the paradigms used so far in studying the adaptability of the v.o.r. were highly, even extremely, demanding and therefore the results might not be representative of the more moderate adaptive requirements occurring in normal life. As our instruments allowed the measurement of head and eye movements with unprecedented precision and stability, we decided to study the effects of relatively small changes in the visual magnification factor, introduced by ordinary spectacles. The main points addressed in this report are the base line of v.o.r. function, the time course and completeness of adaptation, differences between active and passive rotation in the light and the dark and differences between the two eyes.

METHODS

Subjects

Five subjects (including the authors) served extensively in these experiments. R.S. was emmetropic and presbyopic. A.M., H.C. and W.C. were myopic and normally wore negative corrective spectacles. E.K. was myopic and normally wore negative contact lenses. All had 20/20 Snellen acuity in both eyes naturally or with their normal corrections.

Stimulation

The visual target was a brightly illuminated colourful object (a yellow–orange duck's head puppet with red eyes) subtending 56 min arc vertically and 42 min arc horizontally. It was located 12.2 m in front of the subject and surrounded by a circular random dot pattern (elements 2.8 min arc) with a diameter of 4.7°. Suitable masking prevented view of any other object. Subjects were instructed to fixate the duck's head or (if visual acuity permitted) some detail of it.

Subjects were seated on a motor-driven chair which could be oscillated sinusoidally at 0.33 or 0.66 Hz (amplitude 17°) around a vertical axis passing approximately through the centre of the head. The head was firmly locked to the chair by a dental bite-board. Alternatively, the subjects were instructed to make active, sinusoidal head movements at frequencies of 0.33, 0.66 or 1.33 Hz and at about the same amplitude (17°), on the rhythm of a metronome.

These active and passive rotations were executed in the light and also in total darkness. In the latter case subjects were instructed to continue looking at an imagined, stationary visual target.

Recording techniques

The revolving magnetic field – sensor coil technique was used to record absolute eye and head position in space. The principle of this technique has been described before (Collewiijn, 1977). Briefly, sensor coils are attached to the eye(s) and head and a homogeneous magnetic field rotating in the horizontal plane is generated around the subject. The phase of the a.c. potential induced by the field in a sensor coil is linearly related to the latter's angular orientation. In the present experiments generation of the field and phase detection of the induced signals were digitally controlled. The field frequency was 976 Hz. The noise level was < 40 s arc, linearity was better than 1% over 360°. Stability was better than 6 s arc (for a fixed sensor coil) over periods from 1 s to 24 h. The instrument was not sensitive to linear displacements of the coil within the range occurring in our experiments. Coils embedded in a self-adhering silicone annulus as described by Collewiijn, Van der Mark & Jansen (1975) were used to measure the position of one or (usually) both eyes simultaneously. The stability of these coils, when properly inserted, was documented by the inventors and confirmed for the present experimental apparatus (see Collewiijn, Martins & Steinman, 1981*a*). Head position was recorded by a sensor coil mounted on a contoured polycarbonate strip which was strapped and taped to the forehead.

Conditioning

After the base line of compensatory oculomotor performance had been measured, the refraction of the subjects was changed to introduce a new visual magnification factor with which the system had to cope. Several myopes changed their negative spectacles for positive spectacles (+5 D), a change of 6–10 D. In addition to magnifying the visual image these spectacles also blurred it considerably. This was our reason for using a large visual target rather than a small point-target. The colour of the large target could be distinguished even when acuity was reduced.

E.K. could reduce her visual magnification factor without blurring by exchanging her corneal contact lenses for spectacles of the same power. Some combinations (e.g. left eye +5 D, right eye –5 D) were also tried. In most cases the altered conditions were maintained continuously for 24 h, during which a subject moved about normally (with certain precautions for safety). After we realized that adaptive changes occur over a much shorter time span than 24 h, some short-term experiments were added.

The magnification factors were determined for every subject and refractive condition under static conditions. Subjects were fitted with eye coils and glasses and the head was supported by the bite-board. The subject fixated the target carefully while facing straight ahead and with the chair and head rotated 17° to the right and left. Without spectacles or with contact lenses, a subject under these circumstances (Fig. 1*A*) will counter-rotate the eye through an angle equal to that of the head rotation (possible sources of slight errors will be discussed later). With negative spectacles, perfect fixation requires a smaller eye than head rotation (Fig. 1*B*); positive spectacles have the opposite effect (Fig. 1*C*).

The nominal gain (G_{nom}) of the compensatory movement is the ratio of the rotation of the eye in the head (e) to the rotation of the head (h):

$$G_{\text{nom}} = -\frac{e}{h}. \quad (1)$$

The rotation of the eye in the head is not measured directly, but obtained by subtracting head position (h) from eye position in space or nominal gaze (g_{nom}):

$$e = g_{nom} - h. \tag{2}$$

We shall call the projection of the line of sight external to the spectacles, the effective gaze (g_{eff}). Assuming that under static conditions of fixation g_{eff} intersects the target the magnification factor (m) is defined as the corresponding nominal gain:

$$m = -\frac{e}{h}. \tag{3}$$

These magnification factors were determined for each eye separately (with the other eye covered) to avoid possible fixation with one eye due to ocular dominance. Under these conditions m was found to be reproducible for the same subject and same spectacles. Measurements in intermediate positions indicated constancy of m over the range of head excursions used (17° right and left). Determined in this way, m incorporates the effect of the lenses and some small other systematic deviations inherent to the experiment (see discussion of errors). A survey of m for all conditions used is given in Table 1.

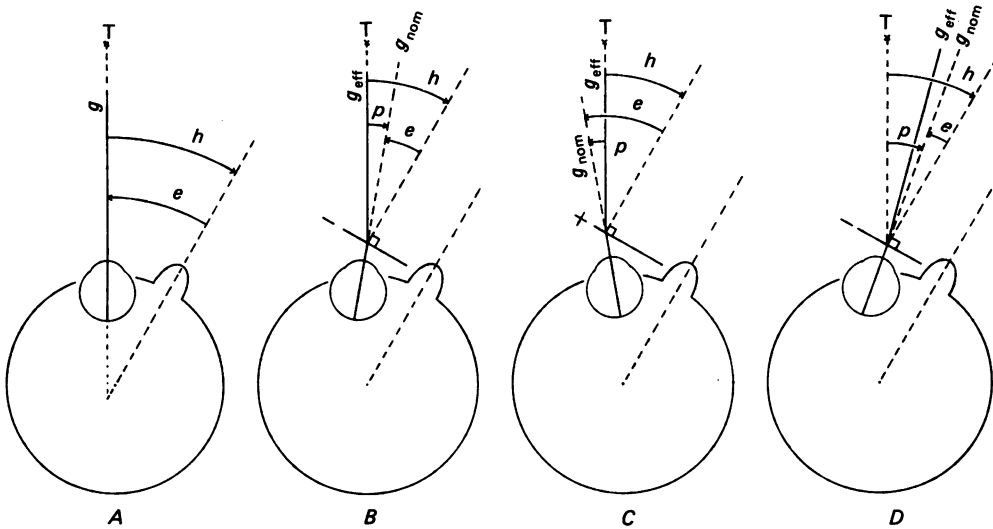


Fig. 1. Diagrams of the relation between head (h) and eye-in-head (e) rotation to maintain perfect fixation of a target (T) at infinite distance. In all cases head rotation equals 30° to the right as an example. A, no glasses; when e equals $-h$ the gaze (g) is aligned with the target. B, negative spectacles with magnification factor 0.66; e equals $-0.66 h$. Although the effective line of sight (g_{eff}) is aligned with the target, the angle of the eye in space (nominal gaze = g_{nom}) has rotated through an angle p ($= 10^\circ$) with the head. C, positive glasses with magnification factor 1.33; e equals $-1.33 h$. The nominal gaze direction has rotated through an angle p ($= 10^\circ$) opposite to the head. D, negative glasses as in B, but assuming an effective gain of only 0.5, i.e. a displacement of the effective gaze through 15° with the head. For $h = 30^\circ$, $e = -10^\circ$; $p = 20^\circ$. See eqns. (1)–(8) in text.

Collection of data

Each trial lasted 12.8 s and was started by the subject by pushing a button when he felt ready for the task. In this period digital position of head and eyes were sampled at 976 Hz. Four consecutive samples were averaged and stored on tape, with as a result a digital representation of the signals with an effective band width of 100 Hz. A session consisted of twenty to forty trials (two to three frequencies, active and passive, light and dark, sometimes different spectacles, each measurement made in duplicate).

TABLE 1. Changes introduced by experimental conditions. The habitual condition is shown for each subject on top. All required changes relative to this base-line condition

Subject	Conditions		Magnification factor		Required change (%)		Vision [§]	
	R eye	L eye	R eye	L eye	R eye	L eye	R eye	L eye
R.S.	0	0	0.980	1.026	0	0	c	c
	+5 D	+5 D	1.199	1.205	+22	+17	b	b
	-5 D	+5 D	0.850	1.272	-13	+24	b	b
	-5 D	-5 D	0.850	0.907	-13	-12	b	b
A.M.	own spectacles		0.861	0.945	0	0	c	c
	0	0	1.000*	1.000*	+16	+6	b	b
	-5 D [†]	+5 D [†]	0.733	1.153	-15	+22	c	b
	+5 D	+5 D	1.171	1.220*	+36	+29	b	b
H.C.	own spectacles		0.866	0.893	0	0	c	c
	+5 D	+5 D	1.182	1.169	+37	+31	b	b
W.C.	own spectacles		0.902	0.934	0	0	c	c
	+5 D	+5 D	1.170	1.169	+30	+25	b	b
E.K.	own contact lenses		0.976	0.994	0	0	c	c
	own spectacles		0.775	0.833	-21	-16	c	c
	0	0	1.000*	1.000*	0*	0*	b	b

* Values assumed, not measured.

† On top of own spectacles.

§ c: clear; b: blurred.

Analysis

The stored samples represent the positions of the eyes and head relative to earth-fixed co-ordinates. Due to the principle of the instrument the calibration of angular rotations is constant and independent of the subject. Only normalization to zero for straight ahead fixation of the target is necessary. For further calculations, head angle (h) is in the proper format but the eye angle or nominal gaze (g_{nom}) has to be converted to the effective gaze (g_{eff}). The effective gaze is equal to the sum of the position of the head and the position of the eye in the head, projected through the spectacles (Fig. 1D):

$$g_{eff} = h + \frac{e}{m}. \quad (4)$$

By substituting eqn. (2) it follows that

$$g_{eff} = \frac{g_{nom} - (1-m)h}{m}. \quad (5)$$

The effective angular gain can be expressed as:

$$G_{eff} = \frac{h - g_{eff}}{h}. \quad (6)$$

By substitution of eqn. (5) it follows that

$$G_{eff} = \frac{h - g_{nom}}{mh}. \quad (7)$$

Combination with eqns. (1) and (2) shows further that

$$G_{eff} = \frac{G_{nom}}{m}. \quad (8)$$

As we were interested in the smooth component, the data processing included calculation of eye and head velocities (using a sliding window technique) and deletion of the saccadic components. For details of this procedure see Collewiijn *et al.* 1981a. The cumulative smooth component was

constructed for the illustrations by lining up the remaining slow phases as if the smooth compensatory eye movement had continued during the deleted saccade at the velocity present just before the saccade. The saccadic gaps were not filled in and their position can, therefore, be seen in the reproduced eye movement records. Momentary gains were calculated for every window of 35 ms as the quotient of eye-in-head velocity and head velocity for the non-saccadic components only. Momentary gains were averaged over each trial which lasted 12.8 s. Negative gains (periods during which the eye went in the same direction as the head) occurred in fewer than 2% of the samples and were discarded. They occurred only near changes in the direction of head rotation due to small phase shifts of the oculomotor response with respect to the head movement. We have not pursued any detailed analysis of phase because phase differed only minimally from the value of 180° required for ideal compensation under all our experimental conditions.

The computation of gain as the moment-to-moment quotient of two derivatives determined over short time windows is likely to introduce much noise. The mean gain values calculated often showed standard deviations (s.d.) up to 0.40, which is much larger than the cycle-to-cycle variations in amplitude of the v.o.r. observed in the recordings. However, as we shall only discuss the mean gains over one or more periods of 12.8 s, the appropriate measure of variability is the standard error (s.e.) of the mean. As the number of (non-saccadic) gain samples collected in 12.8 s was typically larger than 2000, the s.e. of the mean gain was smaller than 0.01.

Sources of error

Although the accuracy of the instrument in determining the angles of eye(s) and head is virtually perfect, the conversion of these data into actual retinal position of the image of the target (or projection of the fovea on the plane of the target) is made slightly less accurate by some systematic and some random aberrations.

Finite distance of target. The target distance of 12.2 m means that the non-coincidence of the several real axes of rotation distorts the ideal angular relations to some degree. First, the principal nodal point of the optics of the eye lies anterior to the centre of rotation of the eye. This leads to retinal image rotation greater than the rotation of the eye relative to the target. As we have calculated in detail elsewhere (Steinman, Cushman & Martins, 1982) this error amounts in the present conditions to less than 0.05% and can thus be disregarded.

A much larger error is caused by the non-coincidence of the rotational axes of the head and the eye, the distance being of the order of 10 cm. (See also Blakemore & Donaghy, 1980 and Colleijn, Conijn & Tamminga, 1982). Also the relation between the rotational axes of the head and the chair was not exactly determined in our experiments and somewhat variable. A worst-case estimate of the compounded effects of these errors indicates an over-estimate of gain of at most 1%. Actually, this should show up as a systematic deviation of the magnification factors determined *without* spectacles to values slightly greater than unity. Such values were occasionally found (Table 1) and to obtain the best possible correction all data have been corrected by the magnification factors as behaviourally determined. Nevertheless, it is safe to assume an inaccuracy of 1% for gain and of 1% of the head movements for gaze.

Positioning of the annulus. Although the attachment of the annulus to the globe is extremely stable, a position of the annulus which is not concentric with the line of sight could lead to additional errors. If the coil were making a vertical angle θ with the visual axis, and the head (and eye) were tilted in the roll axis by an angle ϕ with maintained fixation, one would measure an apparent horizontal gaze shift (ψ) which can be expressed as

$$\psi = \theta \sin \phi. \quad (9)$$

For a roll of 90°, ψ would be equal to θ . This error was recently brought to our attention by J. Larsen and L. Stark and also considered in slightly different terms by Colleijn (1977). The error does not occur due to a misaligning of the coil alone, but in combination with head torsion, which may be generated by kinematic cross-coupling between yaw and roll during the head movements (Chouet & Young, 1974). To cause image instabilities as measured in our experiments misalignment of 10–17° (equivalent to a shift of 2–3.5 mm) of the coil and a coupling factor of 0.2 have to be assumed (J. Larsen & L. Stark, personal communication). We have not measured head roll, but the required misalignment seems very high. We estimate that the misaligning of the coil with respect to the limbus was less than 1 mm in virtually all sessions. Admittedly, the angle between the visual axis and the plane of the limbus is not known precisely. Obviously, this effect cannot occur during our

passive oscillations, during which the head was stabilized by a bite-board. The fact that the imperfections of gaze stability and its disjunctive components were not generally smaller during passive motion (when head rotation was purely horizontal) than during active motion argues against an artifactual origin of these phenomena of the kind suggested by Larsen and Stark.

RESULTS

We shall discuss our results mainly in terms of the mean velocity gain (nominal and effective, i.e. corrected for optics) of the smooth eye movements, which is shown in a number of diagrams. As the errors in the estimation of gain are smaller than 0.01 (see Methods) we shall specify this value to two decimal places and omit error bars in the diagrams of individual experiments. The illustrations of the eye movements show the head movements (scaled down by a factor 10) and the corrected, effective gaze movements after deletion of the saccades. In a number of cases the nominal gaze (position of the eye in space) is also shown.

Base-line performance

This was determined for the five subjects in their habitual optical conditions, i.e. wearing their own spectacles (A.M., H.C., W.C.), contact lenses (E.K.) or no correction (R.S.), to which their compensatory systems should be optimally adapted. Accordingly, the nominal gains were quite different among these subjects, and in particular it was relatively low in the myopes wearing spectacles. As averaging these nominal values would be meaningless, we show only the mean effective gains (incorporating the magnification factors) in Fig. 2, which demonstrates several important trends.

During active head movement in the light the mean gain is close to unity, but rarely precisely 1. The deviation from unity is expressed in appreciable instability of gaze during head movements, as is evident in recordings of gaze in base-line conditions (Figs. 5, 7 and 10). This phenomenon has already been discussed extensively elsewhere (Steinman & Collewijn, 1980; Collewijn, Martins & Steinman, 1981*a, b*; Steinman *et al.* 1982). Averaged over five subjects, three frequencies and two eyes, the effective gain in our sample was 1.01 ± 0.03 (s.d.) for active head movements in the light. However, this 'standard fixator' does not really exist as each subject deviated consistently by a few percent from the unity value. Similar consistent differences were present between the two eyes of each subject. A summary of gain for subject eyes (pooled for 0.33 and 0.66 Hz) during active and passive head motion in light and dark is given in Table 2. The apparent effect of frequency (Fig. 2) proved to be insignificant in an analysis of variance. For passive movement in the light, the average gain (for 0.33 and 0.66 Hz) was 0.99 ± 0.04 (s.d.) which is slightly lower than the value for the same frequencies during active movement (1.01 ± 0.03). This trend was present in all subjects. The difference proved to be significant ($P < 0.025$) in an analysis of variance (mixed model design without replications), taking into account the subject \times treatment interaction. Thus we conclude that in the light gain is slightly higher for active than for passive head motion.

For active head movements in the dark, the average gain (three frequencies, two eyes) was 0.96 ± 0.04 (s.d.), which is 0.05 lower than for similar motion in the light. This difference, although surprisingly small, was highly consistent (Table 2). Again,

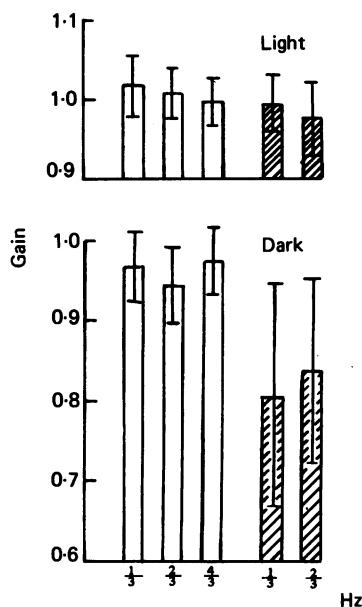


Fig. 2. Average effective velocity gains of compensatory eye movements for five subjects in the light (top) and in the dark (bottom) and for active (open columns) and passive (hatched columns) head movements. The error bars (± 1 s.d.) indicate the variability between subjects and eyes.

TABLE 2. Effective base-line gain for subject eyes during active and passive head movements in light and dark (values for 0.33 and 0.66 Hz pooled)

Subject	Eye	Light, active	Light, passive	Dark, active	Dark, passive
A.M.	R	1.05	1.05	1.02	1.00
A.M.	L	0.96	0.94	0.93	0.87
R.S.	R	1.03	0.99	1.03	0.73
R.S.	L	1.00	0.99	0.94	0.69
H.C.	R	1.03	0.99	0.95	0.77
H.C.	L	0.97	0.98	0.92	0.81
E.K.	R	0.99	0.96	0.90	0.69
E.K.	L	1.06	0.95	0.95	0.73
W.C.	R	1.01	0.96	0.98	0.94
W.C.	L	1.05	1.05	0.96	0.98
Mean		1.01	0.99	0.96	0.82
s.d.		0.03	0.04	0.04	0.12

no systematic effect of frequency was present. For passive motion in the dark at 0.33 and 0.66 Hz the average gain was 0.82 ± 0.12 (s.d.), which is much lower than the gain for the same frequencies of active motion (0.96 ± 0.04). Again this trend was found in all subjects; the larger s.d. was mainly due to increased intersubject variability. The mean difference of 0.14 was highly significant ($P < 0.005$) in a similar analysis of variance as applied to the data obtained in the light.

We conclude that for active head movements v.o.r. gain in the dark is only slightly lower than the gain of the v.o.r. working in synergy with visual control in the light, but that for passive motion in the dark (the usual condition used in testing the v.o.r.) gain is considerably lower and in addition shows a much larger variability.

*Adaptation to changes in magnification**Long-term experiments*

In four subjects, the magnification factor was increased (Table 1) for a period of 24 h by adding several dioptres to the normal correction. In all subjects this resulted in severely blurred vision. In view of the findings just discussed we shall emphasize the results for *active* head movements, with the three frequencies (0.33, 0.66 and 1.33 Hz) and replications (two recordings at each frequency) pooled. Therefore, each bar in Fig. 3 and similar diagrams is the mean of more than 12000 gain samples with a negligible standard error.

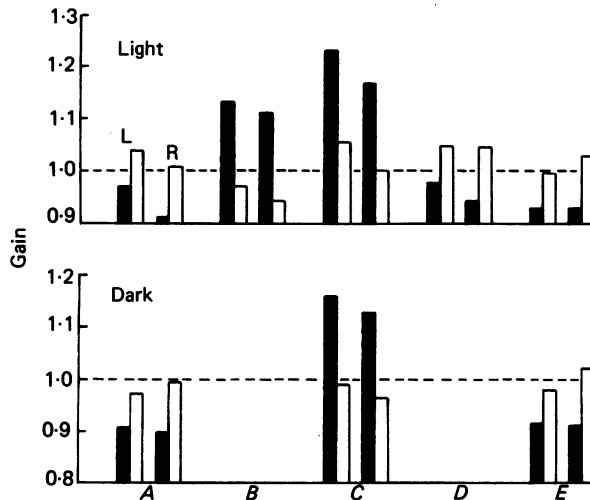


Fig. 3. Gain of compensatory eye movements for active head motion (frequencies pooled) at different stages of an adaptation experiment in which subject W.C. exchanged his normal (negative) spectacles for +5 D spectacles for a period of 24 h. *A*, base-line condition. *B*, just after changing spectacles. *C*, after wearing +5 D spectacles for 24 h. *D*, immediately after going back to own spectacles. *E*, 24 h after returning to own spectacles. Top: gain in the light; bottom: gain in the dark. Black columns: nominal gain; open columns: effective gain. Left two columns of each group of four (L): left eye; right two columns (R): right eye.

Fig. 3 shows the changes in gain (nominal and effective) for subject W.C., who replaced his negative spectacles by +5 D spectacles. The base-line effective gain was slightly above unity in the light and slightly below it in the dark (Fig. 3*A*).

During this experimental session, spectacles were exchanged and immediately after this the measurements were repeated in the light (Fig. 3*B*). Obviously, visual control effected an immediate increase in nominal gain, which was insufficient, however, to correct the added magnification completely. As a result, the effective gain was lower than in the base-line condition. In agreement with this undercompensation, the subject experienced some instability of the visual world during head movements in this early phase of the adaptation experiment. The next data were collected 24 h later (Fig. 3*C*). In the light compensatory eye movements were completely adapted for both eyes. The nominal gains had sufficiently increased to restore almost exactly the

base-line effective gains. Also, the gain of the v.o.r. tested in darkness had been increased similarly. Thus, even in the dark the effective gain was close to that before exposure to the new conditions. After these measurements, the positive spectacles were replaced by the subject's own glasses and compensatory eye movements in the light were recorded immediately (Fig. 3*D*). Effective and nominal gains adapted instantaneously to the changed requirements, but were still higher than the base-line conditions. Gain values close to the base-line levels were achieved 24 h after restoration of the normal visual conditions (Fig. 3*E*).

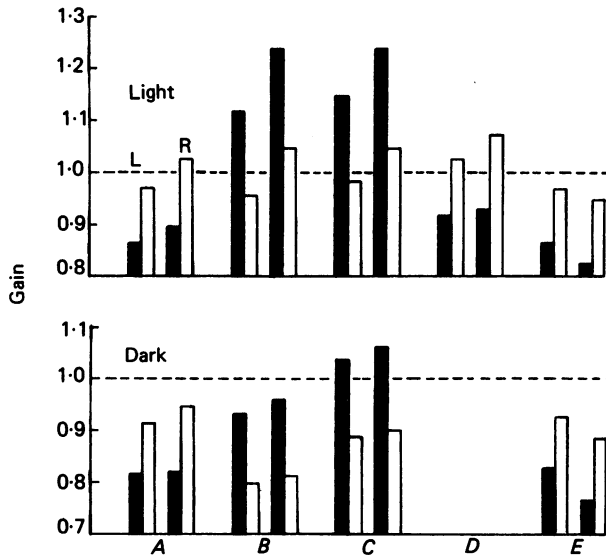


Fig. 4. Gain of compensatory eye movements during active head movements (frequencies pooled) at different stages of an adaptation experiment in subject H.C., who exchanged his normal (negative) spectacles for +5 D spectacles for a period of 24 h. *A*, base-line condition. *B*, just after changing to +5 D spectacles. *C*, after wearing +5 D spectacles for 24 h. *D*, immediately after going back to own spectacles. *E*, 24 h after returning to own spectacles. Conventions as in Fig. 3.

A similar experiment is shown in Fig. 4 for subject H.C., who also exchanged his normal (negative) glasses for +5 D spectacles. Although the required changes (37 and 31 % for right and left eye) were relatively large, adaptation in the light was almost as complete in the first minutes after the change (Fig. 4*B*) as after 24 h (Fig. 4*C*) with the effective gain of the two eyes distributed around unity.

Surprisingly, the nominal gains in darkness also proved to be already considerably augmented (Fig. 4*B*) in measurements made immediately after those in the light. Although the fast adaptation in the light probably left little retinal slip, adaptation of effective gain in the dark was more complete after 24 h although still below base-line level (Fig. 4*C*). The return to the normal condition (Fig. 4*D*) was followed by immediate, but incomplete adaptation in the light (effective gain remaining somewhat above normal). One day after returning to normal conditions gains had been lowered further and were even slightly below the initial values in light and dark (Fig. 4*E*). The effective gaze movements for three stages of adaptation in this experiment are shown in Fig. 5 for light and darkness and passive as well as active head movements.

Fig. 5 and other records of gaze show the computer-reconstructed cumulative slow component of gaze movements, after deletion of all saccadic components (indicated by gaps). Effective gaze was calculated with eqn. (5). In interpreting these records it should be realized that perfect stability would produce a flat line, undercompensation a motion of gaze in phase with the head and overcompensation a movement of gaze out of phase with the head.

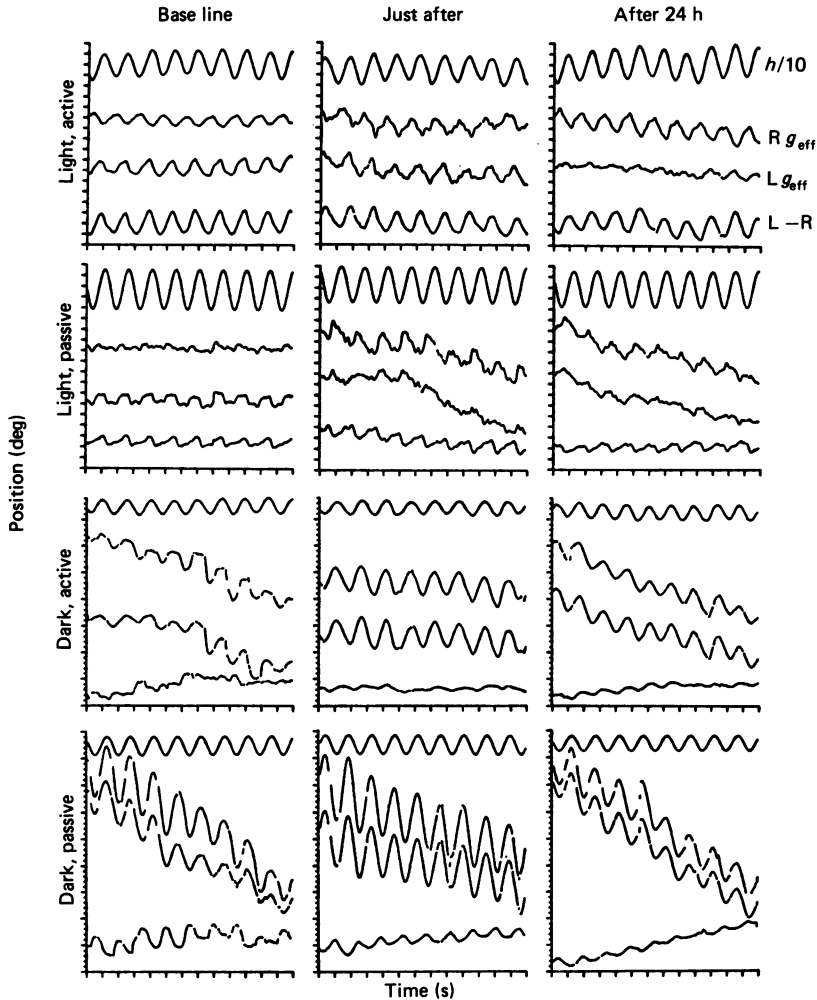


Fig. 5. Plots of head and gaze movements at several stages of the experiment in H.C. shown also in Fig. 4. $h/10$: head movements (frequency 0.66 Hz) divided by 10. $R g_{\text{eff}}$: computer-reconstructed effective smooth gaze movements of right eye with saccades deleted. $L g_{\text{eff}}$: same for left eye. $L-R$: difference between effective gaze of both eyes; disjunctive component of gaze. Passive and active head movements are shown in light and dark for the base-line condition, just after and 24 h after changing to +5 D spectacles.

In agreement with Fig. 4, Fig. 5 shows slight over-compensation of right eye gaze and as much undercompensation of left eye gaze for H.C. making active head movements in the light. As will be discussed later, this symmetrical distribution

around unity of the gain of both eyes is probably not coincidental but due to different magnification factors caused by the different optical power of the two spectacle glasses. The compensatory eye movement system seems to settle often for a compromise between unequal demands on the two eyes. Obviously, this introduces disjunctive movements of effective gaze; we have not tested whether these have a deleterious effect on binocular or stereoscopic vision. Overt diplopia was not noticed by our subjects except when very large discrepancies between the eyes were introduced.

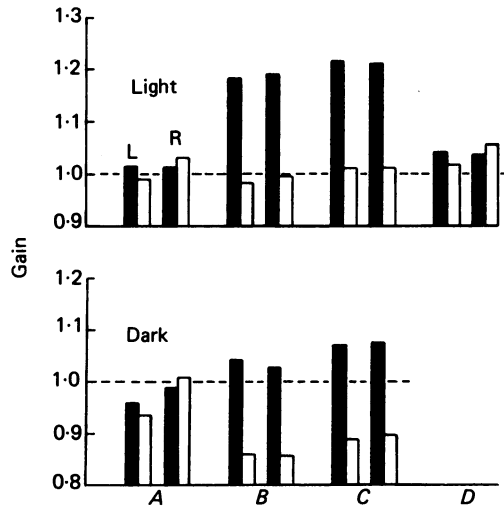


Fig. 6. Gain of compensatory eye movements during active head motion at different stages of an adaptation experiment in subject R.S., an emmetrope who put on +5 D spectacles for 24 h. *A*, base-line condition. *B*, just after putting on +5 D spectacles. *C*, after wearing +5 D spectacles for 24 h. *D*, immediately after removal of spectacles. Conventions as in Fig. 3.

The fast adaptation to the changed spectacles in the light is clear in Fig. 5. In the dark there was always some undercompensation, which was maximal just after the change of spectacles. Notice that the undercompensation in the dark was always considerably larger for passive than for active motion.

Figs. 6 and 7 show the results of a similar experiment in subject R.S., an emmetrope who wore the +5 D spectacles for 24 h. Also in this subject the compensatory eye movements for active head movements in the light showed only little undercompensation immediately after the spectacles were put on (Fig. 6*B*), further adaptation of the effective gain to approximate base-line level after 24 h (Fig. 6*C*) and a small over-compensation immediately after removal of the magnifying spectacles. In darkness a slower and less complete change in gain occurred. Even after 24 h the nominal gain had increased insufficiently to restore the effective gain of the v.o.r. to base-line level. Fig. 7 shows the reconstructed smooth component of gaze for subject R.S. The excellent adaptation in the light and partial adaptation in the dark can be clearly seen as well as the poor compensation during passive motion in the dark. Also subject R.S. made considerable disjunctive gaze movements. As was also the case for H.C. (Fig. 5), these seemed to be smallest during active head movement in darkness.

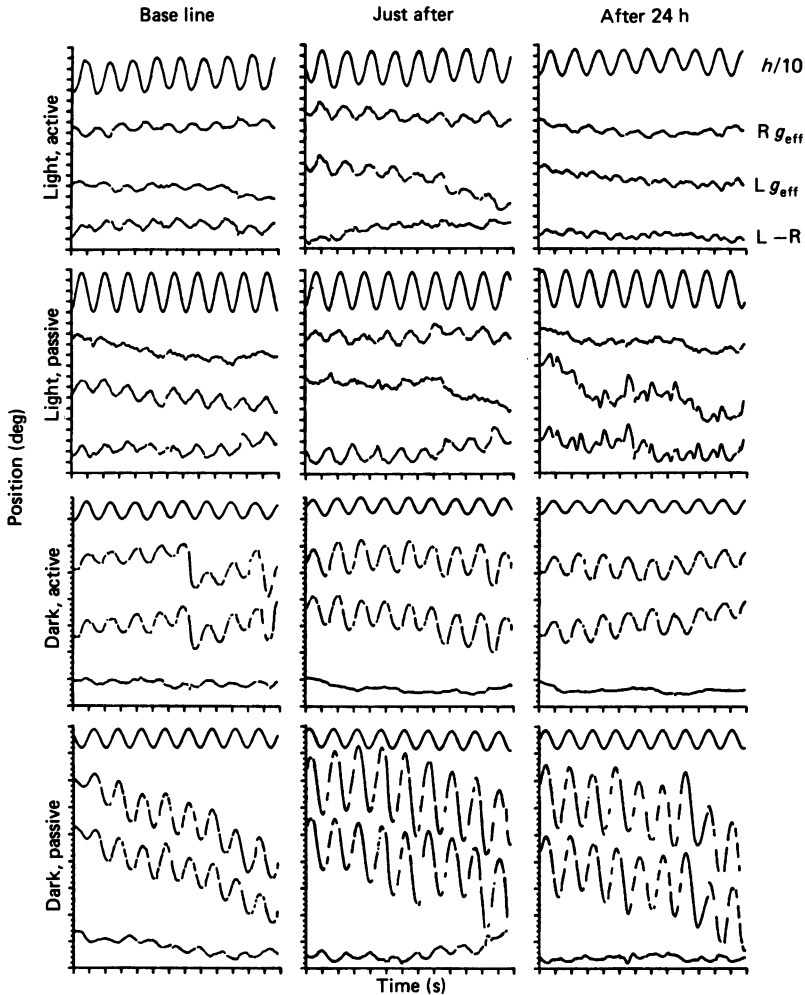


Fig. 7. Plots of head and gaze movements at several stages of the experiment illustrated in Fig. 6 for subject R.S. Conventions as in Fig. 5.

For subject A.M. essentially similar changes were found when he removed his negative spectacles for 24 h, a condition which required an extra magnification of 16% and 6% for the right and left eye.

The results of these four experiments are summarized in Fig. 8, for active and passive movements. The base-line conditions (Fig. 8A) show the trends discussed before (Fig. 2).

The changed optical conditions would, in the absence of changes in the nominal gain, reduce the effective gain to the theoretical values shown in Fig. 8B. The mean required magnification of gain was $1.22 \times$. Fig. 8C shows that immediately after the introduction of the magnifying conditions compensatory eye movements in the light reached almost the appropriate levels for passive as well as active movements. In the dark data at this stage were obtained for only two of the subjects (R.S. and H.C.). Both already showed some increase in gain at this stage (Figs. 4 and 6) compared

to their base-line values. These data show that gain for passive movement remained consistently lower than gain for active movement. After 24 h, adaptation in the light had been completed and was equivalent to base-line levels (Fig. 8D).

In the dark adaptation was very advanced (although incomplete) for active movements. It was complete (i.e. back to base-line level) for passive movements. Thus, adaptation affects the responses to passive as well as to active head movements, but the difference in response level for these two modes is roughly maintained.

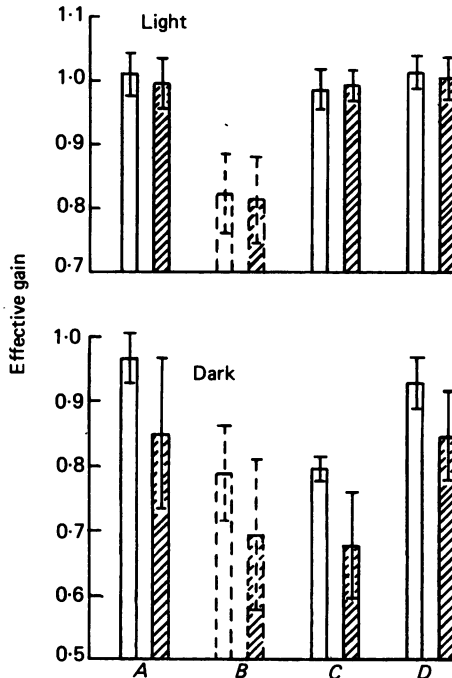


Fig. 8. Average effective gain of compensatory eye movements for four subjects (R.S., A.M., H.C., W.C.) in 24 h experiments involving adaptation to a magnifying condition (average required change +22%). Open columns: active head movements; hatched columns: passive head movements. Eyes and frequencies pooled. A, base-line condition. B, theoretical values to which the gain was reduced by the magnifying spectacles (pre-existing gain divided by change in magnification). C, real values obtained immediately after the change of spectacles. In the dark these values were obtained for two subjects (R.S. and H.C.) only. D, after 24 h adaptation to magnifying condition. The error bars (± 1 s.d.) indicate inter-subject variability.

The results just described were obtained while the subjects moved freely around during 24 h with blurred vision but unrestricted visual fields. As the recordings obtained in darkness within minutes after the change in visual magnification indicate a very rapid onset of adaptation, we complemented these data by some short-term experiments aimed specifically at this early phase of adaptation.

Short-term experiments

This type of experiment was done in a single session lasting up to 40 min. One eye was provided with a coil. Base-line performance in light and dark was recorded and

then new spectacles were put on the subject who, from then on, continuously watched the target while producing active head movements at 0.66 Hz. Samples of 12.8 s duration were recorded in light and in darkness at intervals of 2–5 min without interruption of this movement. These experiments revealed a very fast initial phase of adaptation.

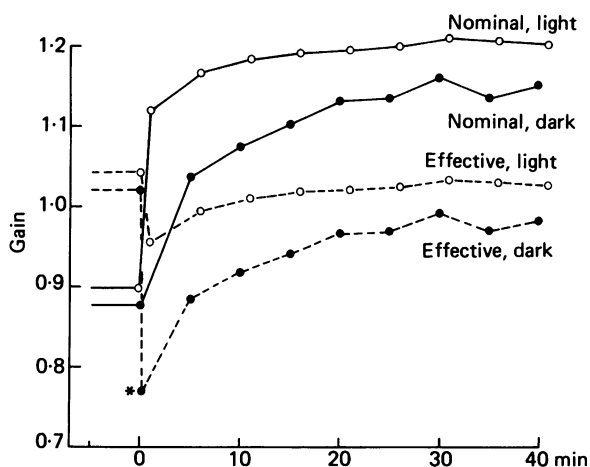


Fig. 9. Time course of nominal and effective gain in light and dark during a short-term adaptation experiment in which subject A.M. changed his normal, negative glasses for +5 D spectacles. Active head movements (at 0.66 Hz) were made continuously during a period of 40 min. * theoretical value to which effective v.o.r. gain in the dark was reduced from the pre-existing value by the magnifying lenses.

Fig. 9 shows the time course of nominal and effective gain in light and darkness for subject A.M., who exchanged his normal negative spectacles for +5 D spectacles at time zero. A.M.'s normal spectacles introduced different magnification factors for the two eyes (Table 1). Probably as a consequence, his effective base-line gains for the two eyes were distributed symmetrically around unity (Fig. 16), a situation also observed in subject H.C. (Fig. 4). Fig. 9 shows the gain of the right eye, which had a base-line value of 1.04 in this experiment.

The required change in gain for the measured right eye was +36%. The nominal gain in the light rose from the base-line value of 0.90 to 1.12 after only 1 min of exposure. However, the corresponding effective gain was lowered from 1.04 to 0.96. Thus, adaptation in the light was incomplete after 1 min. As can be seen in Fig. 9, most of the remaining deficit was corrected in the ensuing minutes and after about 30 min an early asymptotic level, close to the original effective gain value, was reached. A similar fast change was found for the v.o.r. recorded in the very brief intervals of darkness. The first point drawn for G_{eff} (dark) after $t = 0$ in Fig. 9 (asterisk) is the theoretical level to which G_{eff} was reduced by the spectacles. The first real measurement, made after 5 min of exposure, already showed considerable increase in gain of the v.o.r. in darkness. This rise continued and reached an asymptotic value of about 0.98 for G_{eff} , compared to the base-line value of 1.02, after about 30 min. Several moments of this experiment are illustrated in Fig. 10. In the base-line condition, there was some over-compensation (effective) for the right eye, which resulted in small displacements of effective gaze out of phase with the head. After

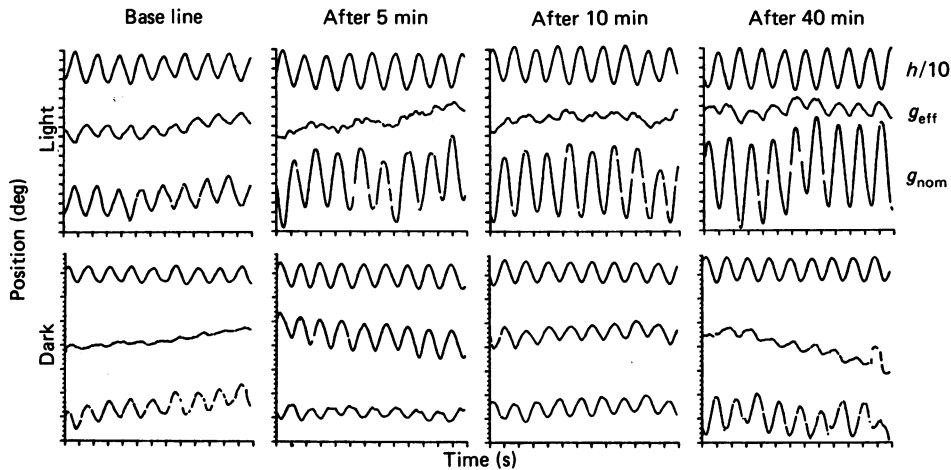


Fig. 10. Plots of active head movements (divided by 10) and effective and nominal gaze movements of right eye at different stages of short-term adaptation experiment in subject A.M., illustrated also in Fig. 9.

40 min, similar effective performance had been restored in the light, with transitional stages at 5 and 10 min. The nominal gaze movements were in phase with the head in the base-line condition (due to the negative spectacles) but out of phase as soon as the positive spectacles had been put on, with a progressive further increase in amplitude at later moments. Similar changes (shown at lower sensitivity) occurred in the dark. The gradual changes of the v.o.r. to achieve stability of effective gaze can be clearly followed in the lower half of Fig. 10.

A similar experiment for subject H.C. is shown in Figs. 11 and 12. For this subject, the adaptation in the light was faster than in A.M. Actually it was complete from the first minute, in agreement with the long-term experiment in H.C. (Fig. 4). In the dark, the effective gain was 0.97, which is more typical than the high value found in A.M. Adaptation in the dark was once again fast and reached asymptotic levels slightly above 0.9 within 10 min. These values are not significantly different from those found in the long-term experiment after 24 h with active motion at 0.66 Hz (plotted for comparison also in Fig. 11). A later repetition of the same short-term experiment in H.C. showed identical results. In a control experiment H.C. made continuous active head movements, watching the target and wearing his normal spectacles, for a period of 40 min. The gain of the compensatory eye movements in the light did not change at all during this period (measurements in the dark were not made).

Finally, an experiment which was similar but required a decrease in gain was done by providing subject R.S. with -5 D spectacles. Once again vision was blurred, as R.S. was unable to accommodate due to presbyopia. The target was fixated during active head movements at 0.66 Hz and the v.o.r. of the left eye was recorded at 2 min intervals during brief periods of darkness. As Fig. 13 shows, the effective gain in darkness was elevated in this case from 0.97 (base-line value) to 1.06 due to the negative glasses. Adaptation was extremely fast and in fact complete in the measurements taken in darkness only 4 and 6 min after putting on the spectacles.

These short-term experiments make it clear that adaptation of the v.o.r. to the

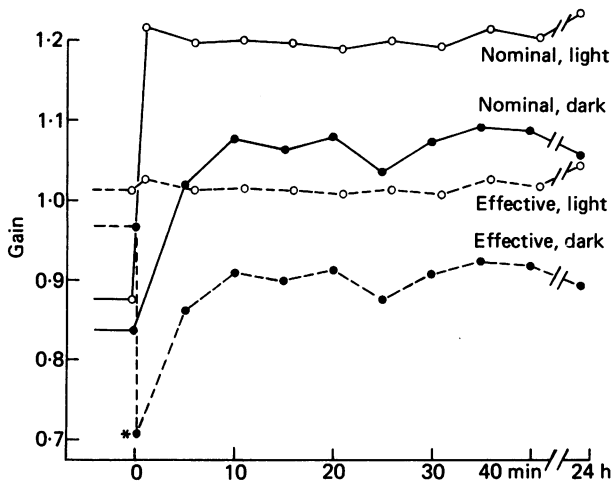


Fig. 11. Time course of nominal and effective gain for active head movements in light and dark during a short-term experiment in subject H.C. who exchanged his normal, negative glasses for +5 D spectacles. For comparison, values obtained in a similar experiment lasting for 24 h (Fig. 4) are also inserted. Further details as in Fig. 9.

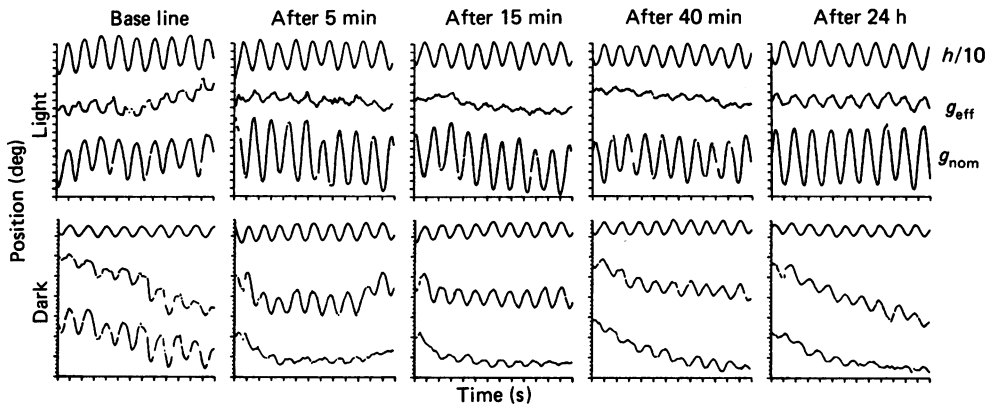


Fig. 12. Plots of active head movement (divided by 10) and effective and nominal gaze movements of right eye at different stages of short-term adaptation experiment in subject H.C., illustrated also in Fig. 11. Plots obtained in a similar experiment continued for 24 h are also shown for comparison.

modest changes required in our experiments is extremely fast and largely completed in 4–20 min, despite the fact that vision was blurred and the visual field restricted to a circular target area which had a diameter of only 4.7° .

This shows that stimulation of the peripheral retina is unnecessary for adequate, fast adaptation of the v.o.r.

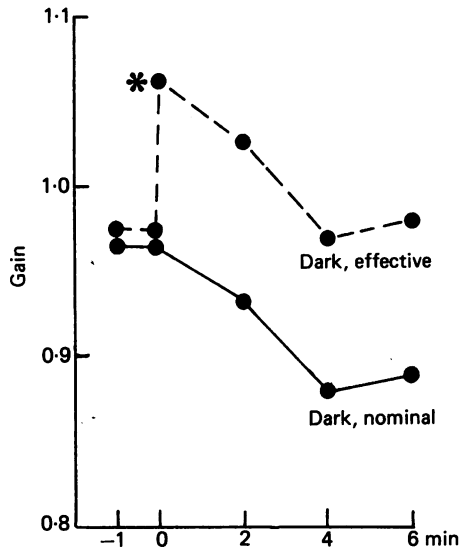


Fig. 13. Time course of nominal and effective gain for the left eye in the dark in a short-term experiment (lasting 6 min) in subject R.S., who normally wears no spectacles but put on -5 D spectacles. Conventions as in Fig. 9.

Exchange of contact lenses and spectacles

In subject E.K. we could dissociate changes in magnification factor from changes in visual acuity. With her usual contact lenses (worn in combination with the scleral annuli) E.K. had magnification factors close to unity, and in the light the effective gain for her right and left eye was distributed almost symmetrically around unity. In the dark gain was slightly lower for both eyes (Fig. 14 A). Leaving the annuli in place, we then removed the subject's corneal lenses and put on her negative spectacles, which allowed vision with good acuity but lower magnification.

Like most other subjects, immediate adaptation in the light was considerable but not complete which resulted in an elevated effective gain (Fig. 14 B). After wearing the spectacles for 24 h, effective gain was equal for both eyes and still slightly above unity. In the dark, effective gains were exactly adapted to the base-line values (Fig. 14 C). On another occasion, E.K. did not wear any refractive correction for 24 h which left her with blurred vision without essential changes in her magnification factor (which was not measured, but assumed to be unity in the last case). After this period, nominal gain in the light was not essentially different from gain in the baseline conditions (Fig. 14 D). In the dark it was also remarkably close to unity.

Unequal demands on both eyes

An important point in adaptation is whether the movement of the two eyes can be adjusted independently or only in parallel fashion. This problem is of practical interest, since in many cases unequal spectacle corrections for both eyes are required (Table 1). We explored this in a few experiments.

As a control experiment, R.S. was fitted with a -5 D lens for the right eye while the left eye was patched. In the first minutes after this change, the effective gains

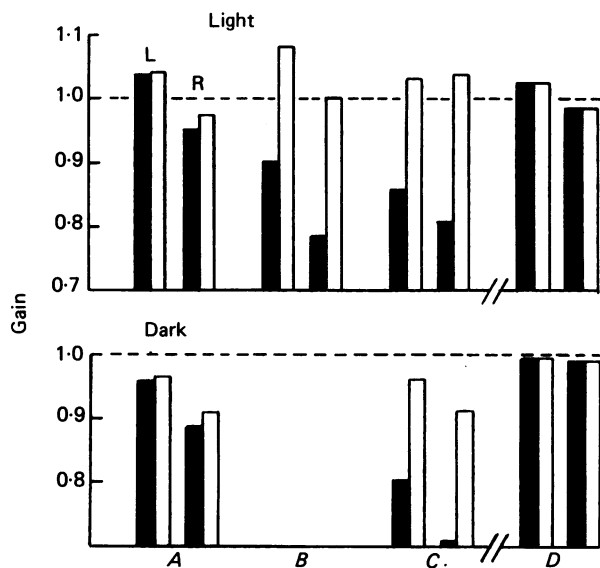


Fig. 14. Gain of compensatory eye movements during active head movements (frequencies pooled) at different stages of a 24 h adaptation experiment in subject E.K. *A*, base-line conditions, wearing own (negative) corneal contact lenses. *B*, immediately after exchanging contact lenses for own (negative) spectacles. *C*, after wearing spectacles for 24 h. *D*, after wearing no correction for 24 h (in a later experiment). Conventions as in Fig. 3.

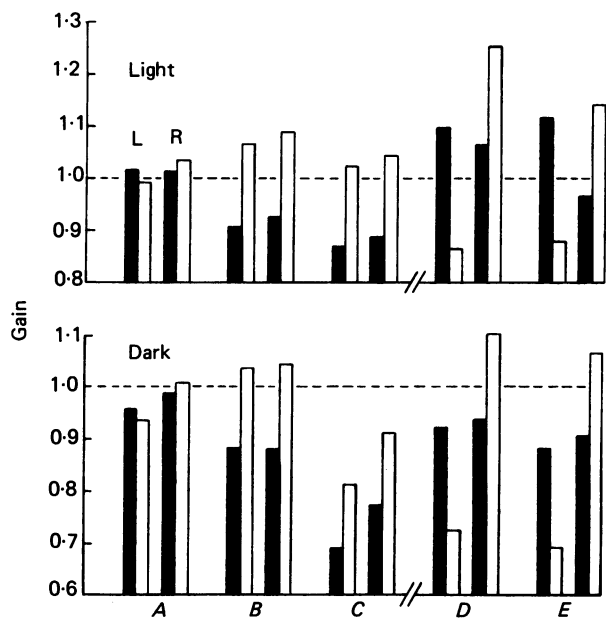


Fig. 15. Gain of compensatory eye movements during active head movements (frequencies pooled) during 24 h adaptation experiment in subject R.S. with different conditions for the two eyes. *A*, base-line condition. *B*, just after putting on -5 D glass for the right eye and patching the left eye. *C*, after 24 h adaptation to this condition. *D* and *E*, different experiment; gain just after (*D*) and 24 h after (*E*) putting on spectacles with a -5 D glass for the right eye and a $+5$ D glass for the left eye. Conventions as in Fig. 3.

were too high in the light and the dark. (For the calculation of effective gain, the same magnification factor, 0.907, was assumed for both eyes). Normal gains had started to decrease in the light as well as in the dark, as usual. This decrease was essentially conjugate (Fig. 15*A* and *B*).

After 24 h, the compensatory eye movements in the light were practically symmetrical for the two eyes and the effective gain was almost back to normal (Fig. 15*C*). In the dark, nominal gain had already decreased substantially shortly after the introduction of the new condition (Fig. 15*B*), although effective gain was still higher than normal. The changes were present in both eyes; the gain of the patched left eye decreased as much as the gain of the seeing right eye. After 24 h the gain of the left eye was even lower than the gain of the right eye, resulting in some disjunctive eye movements.

These findings demonstrate that information from one eye is able to control adaptation of the compensatory eye movements of both eyes in the correct direction.

In another experiment, R.S. put on spectacles with a -5 D lens for the right eye and a $+5$ D lens for the left eye. In addition to binocular blurring this caused appreciable aniseikonia. In the light, adaptation was very limited just after the change (Fig. 15*D*) although there was a slight difference in nominal gain between the two eyes. After 24 h (Fig. 15*E*) this difference was much enhanced. The nominal gains in the light were much lower for the right eye than for the left eye, which led to considerable disjunctive nominal as well as effective gaze displacements. However, the adaptation was insufficient to restore the stability of gaze of either eye to its base-line level. The effective gain was still too low for the left eye and too high for the right eye and, in fact, these errors were distributed symmetrically around unity. This shows that the system had great difficulties following the conflicting demands for both eyes even in the light, although the $+5$ D and -5 D lenses in a non-conflicting condition induced adaptation very efficiently in the same subject. In the dark, a slight decrease in nominal gain was seen which was about the same for both eyes (Fig. 15*E*).

Any difference between the eyes was similar to differences in the base-line condition and unrelated to the difference in spectacle magnification. The nominal gaze displacements in the dark remained essentially conjugate. As a whole this experiment suggests that differential adaptation of the compensatory eye movements of the two eyes is achieved with great difficulty and incompletely in the light, and not at all in the dark.

The same tendency was found in an experiment in subject A.M., in which the -5 D (right eye) and $+5$ D (left eye) lenses were mounted on top of his own negative spectacles. There is a difference between this experiment and the experiment with R.S. in that A.M. could attain sharp vision with the right eye by accommodation. R.S. could not. Accordingly, A.M.'s right eye dominated the adaptation process. In the light, adaptation was virtually complete for the right eye just after and also 24 h after the change in spectacles (Fig. 16) in that the effective gain for his right eye was at base-line levels.

The nominal gain of the left eye followed that for the right eye. The same happened in darkness during which adaptation of both eyes to the information provided by the right eye had begun just after the change and was complete after 24 h. No differential adaptation of the two eyes was seen in light or darkness and the conflict was

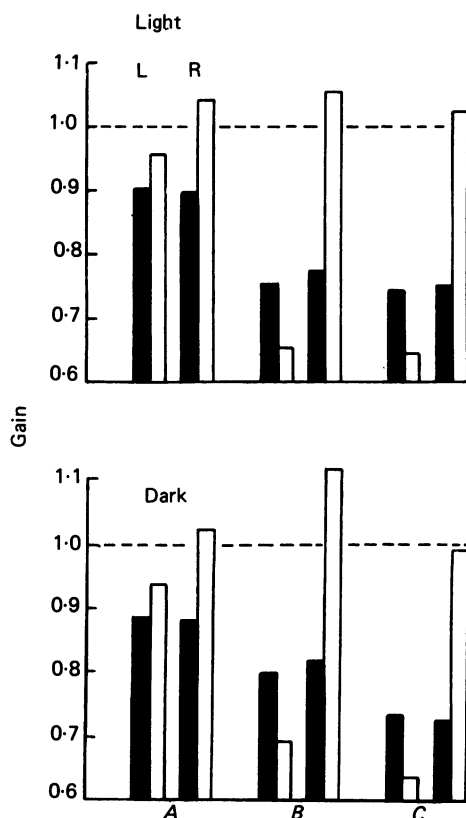


Fig. 16. Gain of compensatory eye movements for active head movements (frequencies pooled) during 24 h adaptation experiment in subject A.M., who put spectacles with a -5 D glass for the right eye and a $+5$ D glass for the left eye on top of his own (negative) glasses. A.M. could restore sharp vision for the right eye by accommodation. The right eye controlled adaptation, which was conjugate for the two eyes. *A*, base-line condition. *B*, just after; *C*, 24 h after putting on the extra lenses. Further conventions as in Fig. 3.

apparently resolved by using only the information provided by the eye with the better visual acuity. The maintenance of conjugacy of the nominal gaze displacements is illustrated in the gaze recordings of Fig. 17 which also show the excellent adaptation of the right eye in the light and in the dark.

DISCUSSION

Requirements for modest changes in the gain of compensatory eye movements, combined with active head movements, resulted in fast adaptation of the v.o.r. with a time constant of minutes rather than hours. This rate of adaptation is much faster than that observed in the closest related experiments in man (Gauthier & Robinson, 1975) and monkey (Miles & Eighmy, 1980). The difference with the rate of adaptation to visual inversion (see Introduction) is even larger.

This tendency suggests that the rapidity and efficacy of adaptation in our experiments was caused by the relatively small size of the required changes. This does

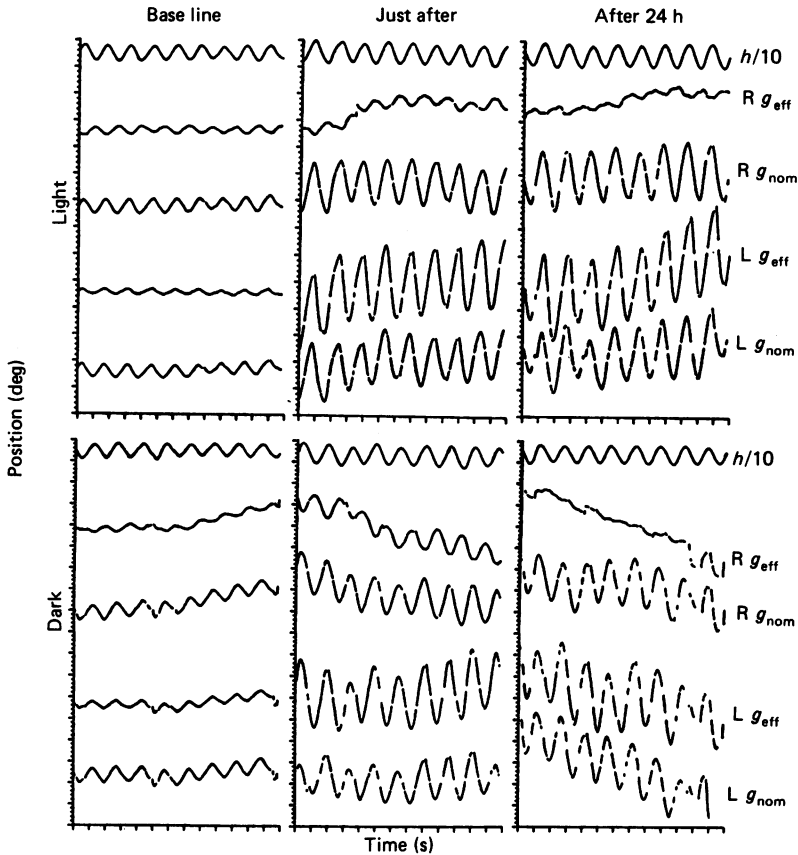


Fig. 17. Plots of active head movements (divided by 10) and effective and nominal gaze movements of right and left eye at several stages of adaptation experiment in subject A.M., illustrated also in Fig. 16. Spectacles with a -5 D glass for the right eye and a $+5$ D glass for the left eye were put on top of own (negative) spectacles.

not seem unreasonable in terms of naturally occurring demands. Most changes will be necessitated by processes of growth or degeneration, which are usually progressing slowly with time constants of months or years. As the adaptive system functions at a much faster rate, it will not be confronted with a large inadequacy, unless the damage is sudden and large or the limits of adaptability are exceeded. In this light we believe that sudden large changes in magnification, for example by a factor 2, 0.5 and especially -1 , as used in most previous experiments, may not reveal the most optimal range of adaptive performance.

A second important factor in the outcome of our experiments may be the use of active head movements during the acquisition and the testing of the adaptation. Active head motion by itself does not necessarily lead to fast adaptation, as shown by most previous adaptation experiments in which the subjects or animals were usually moving freely around between recording sessions. In fact, the natural motion behaviour had to be supplemented by passive oscillation in some experiments to speed up the adaptation process (Robinson, 1976). The only unnatural aspect of our stimuli

was the regular pacing. This could conceivably facilitate the adaptation process, especially in our short-term experiments in which continuous oscillation at a single frequency was used. However, similar early adaptation effects were noticed in the 24 h experiments during the tests run immediately after the change in optics (Figs. 3*B*, 4*B* and 6*B*). In this case, the v.o.r. measured in the dark had been significantly modified by the preceding brief series of trials in the light. A mixture of frequencies and active and passive motion had been used in the light for a total period of just over 2 min and yet the v.o.r. in the dark showed already consistently adaptation.

In the past the v.o.r. has been evaluated mainly by passive oscillation, which many contribute to the considerable spread in gain values reported, even for base-line conditions. For the monkey (*Macaca mulatta*) Keller (1978) reported a gain of about 0.85 at 0.5 Hz and about 0.90 at 1.0 Hz during passive oscillation in the dark. Miles & Eighmy (1980) reported a gain which was very close to unity and essentially flat between 0.1 and 1.0 Hz for the same species of monkey under similar conditions.

In general, lower values have been reported for man. To assure a certain level of general alertness subjects have often been required to perform mental arithmetic. Under such circumstances, for frequencies between 0.1 and 1.0 Hz human v.o.r. gain has been reported as about 0.70 (Benson, 1970); about 0.43 (Meiry, 1971, his Fig. 4); 0.70 (Gonshor & Melvill Jones, 1976*a*, their Table 1); 0.65 to 0.83, increasing with frequency (Barr, Schultheis & Robinson, 1976) and 0.54 to 0.90, increasing with frequency (Barnes & Forbat, 1979). Wall, O'Leary & Black (1978), using a pseudo-random binary sequence of accelerations, calculated a gain (velocity/velocity) of about 0.52.

Barr *et al.* (1976) have reported that specific instructions with regard to the subjective spatial frame of reference can effectively modulate the gain of the v.o.r. When subjects were asked to fixate in darkness an imagined target which was stationary in space, v.o.r. gain rose to 0.95. On the other hand, it fell to 0.35 when subjects imagined that the same target was fixed to the chair and rotating with them. We could confirm the general trend of these effects (Collewijn *et al.* 1981*a*), although we emphasized in our earlier report that gain rose to 0.83, not 1.00. This statement neglected the myopic status of subject A.M. which introduces normally a magnification factor of 0.86 for his right eye. Taking this into account, the effective gain of his v.o.r. actually rose to 0.97 while imagining a stationary target, in good agreement with Barr *et al.* (1976). Active head movements have been introduced only recently into investigations of the v.o.r. Takahashi, Uemura & Fujishiro (1980) made e.o.g. recordings during voluntary head rotations at 0.33, 0.66 and 1.0 Hz (similar to our stimuli). During mental arithmetic average v.o.r. gain in the dark for 0.66 Hz was 0.82 ± 0.13 (s.d.); fixation of an imagined target raised this to 0.97 ± 0.05 in the dark and 0.99 ± 0.02 in the light. Tomlinson, Saunders & Schwarz (1980) also analysed (using the e.o.g.) the human v.o.r. during active head motion. Without specific gaze instructions, they found a gradual increase in gain with frequency up to about 1 Hz where a value of unity was reached and maintained for higher frequencies up to 5 Hz. For frequencies of 0.33 and 0.66 Hz our data, obtained within single sessions, show clearly that the gain of the v.o.r. in darkness is much closer to unity during active than during passive head movements. These findings suggest that the gain of the v.o.r. in the dark has no fixed value and that the level is set by reference to vision, or to

an internal frame of reference which can be derived from imagined targets and even better from self-generated motion. One point of concern is whether the higher v.o.r. gain (apart from the lessened variability) with active motion might be simply explained by the synergistic action of proprioceptive input from the neck. However, the literature on the human cervico-ocular reflex does not support this possibility because its gain is low and its phase may be inappropriate for compensation.

Meiry (1971, Figs. 6 and 7) reported that this reflex caused eye movements in the compensatory direction (i.e. in phase with the body movement relative to the head) with a gain of about 0.08 for frequencies above 0.35 Hz. However, Takemori & Suzuki (1971), using sinusoidal oscillation of the body on the stabilized head at 0.25 Hz, found mostly eye movements *opposite* to the direction of body twist, with a gain of about 0.08. Barnes & Forbat (1979), in comparable experiments, found a mean gain of 0.05 with a phase lead of 21 to 80°, which is inappropriate for true compensation. Barlow & Freedman (1980) found a gain of about 0.03 for frequencies above 0.1 Hz using the instruction 'fixate in the dark' during passive neck torsion. Experiments in which subjects rotated their body and shoulders actively at roughly comparable frequencies and amplitudes did not indicate a higher gain during active motion. The recorded eye movements were mostly in counterphase with body motion and thus anticomensatory.

A meaningful contribution of neck reflexes to human ocular stability is thus far from established and the available data do not suggest that the improvement of compensatory eye movements during active instead of passive head movements is caused by addition of the cervico-ocular reflex to the v.o.r.

Although we have emphasized the results for active motion, responses to passive oscillation were recorded as a routine in the same sessions. The changes in gain for passive motion in the dark paralleled those for active motion (Fig. 8). The difference in gain between active and passive motion in the dark remained approximately constant during the adaptation process which shows that the adaptation was indeed localized in the v.o.r.

What is the mechanism controlling the adaptation process? There can be little doubt that retinal slip associated with head movements is the initial driving force. For the rabbit we have argued (Collewijn & Grootendorst, 1979) that the direction of adaptation (up or down) may be determined by a comparison of the direction of the retinal slip and the simultaneous eye movements. One of the arguments for this theory was our finding that visual stimulation alone (not accompanied by vestibular stimulation) was able to increase the gain of the v.o.r. Miles & Lisberger (1981) have argued that in the monkey retinal slip is compared to the ongoing head movements, not eye movements, to control the direction of adaptation. In agreement with this they found that optokinetic stimulation alone is ineffective in modulating the gain of the v.o.r. in the monkey. We confirm that also in man long term stimulation of the optokinetic system alone by a sinusoidal motion does not enhance the v.o.r., although the optokinetic response itself may slightly improve (R. M. Steinman & H. Collewijn, unpublished observations).

Miles & Lisberger (1981) have pointed out that retinal slip may not be the driving signal during much of the adaptation period because in many cases the visual pursuit system is capable of immediately supplementing the deficit of the v.o.r. to achieve

appropriate compensatory eye movements in the light. They have proposed that as a substitute the activity of the pursuit system, encoded in the activity of floccular Purkinje cells, would control the adaptation of the v.o.r. In agreement with this theory they could show that visual pursuit of a small target, the movements of which were linked to the head movements to simulate a change in visual magnification, was sufficient to induce adaptive changes in the v.o.r.

Our current data agree with this hypothesis of Miles & Lisberger (1981) in several respects. First, our visual targets subtended only a few degrees and yet were as effective in inducing adaptation as full view of the surroundings. Secondly, in many instances we saw that compensation in the light was almost perfect immediately after changing the optical magnification, but that nevertheless adaptation of the v.o.r. in the dark continued with a slower time course (Figs. 4, 8, 9 and 11). Although the net performance of the system in the light did not manifestly improve by this adaptation, the burden of the compensation was transferred in this time to the v.o.r., possibly to relieve the pursuit system from a routine stabilization task which would require constant effort and to keep it free to pursue targets moving independently of the head.

As we have discussed extensively before (Steinman & Collewijn, 1980; Collewijn *et al.* 1981*a, b*; Steinman *et al.* 1982), notwithstanding the adaptive systems, some remaining retinal slip was found in all our recordings of human compensatory eye movements, including the present ones. The present binocular recordings suggest one special mechanism which may in many cases prevent perfect compensation because this cannot be achieved for both eyes.

Our experiments introducing unequal demands on both eyes indicate that the adaptive system has great difficulty to adjust the nominal gain differently for the two eyes even in the light, but especially for the v.o.r. working alone in the dark. Although these experiments were few in number, they are supplemented by some observations in base-line conditions, to which our subjects had adapted for a very long time. Asymmetry between the eyes may be extrinsic or intrinsic in origin. Extrinsic asymmetry, due to unequal spectacle lenses was present in base-line conditions in subjects H.C. and A.M. (Table 1). Both subjects had adjusted their effective gain in the light to such a level that one eye overcompensated as much as the other eye undercompensated (Figs. 4*A* and 16*A*). In this way, retinal slip in both eyes was approximately equal but opposite. A similar symmetrical distribution of effective gain was achieved in the 24 h experiment with extremely different demands in subject R.S. (Fig. 15*E*).

Intrinsic asymmetries in the motor performance of the two eyes, caused for instance by different mechanical properties of the right and left orbital plant may also occur frequently, especially after surgery of the ocular muscles. It would be manifest as a consistently different nominal gain in the two eyes. This was found in subject E.K., who always made smaller compensatory movements with the right eye than with the left eye. In the base-line condition (Fig. 14*A*) she had adjusted the level of these gains such that the effective gains had an average level of unity in the light, which meant over-compensation for the left and undercompensation for the right eye.

These findings indicate that in most cases subjects will adapt the gain of both eyes to an intermediate level at which the sum of the slip signals obtained from the two

eyes is minimal. This implicates the summed retinal slip signals for both eyes as the primary driving force for adaptation. This signal seems to be used unless there is a distinct advantage in using the signal from one eye only, which was the case in the differential adaptation experiment in A.M. (Fig. 16), who under conditions allowing sharp vision in one eye only, adapted the nominal gain (of both eyes) to a level which minimized slip for the well focussed eye. The slip signals from the other eye, defocussed by 10 D, were apparently suppressed although in other cases (Figs. 4 and 11) slip of similarly defocussed images in both eyes were quite effective in producing adaptation.

However, even monocular adaptation in A.M. (Figs. 16 and 17) and R.S. (Fig. 15C) did not reduce slip to zero after 24 h adaptation, but to about the original amount of slip in the base-line condition.

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