

Asymmetrical Adaptation of Human Saccades to Anisometric Spectacles

Casper J. Erkelens,* Han Collewijn,* and Robert M. Steinman†

We report the extent to which effective asymmetrical saccadic adaptation was achieved by a myopic subject, who was exposed to "long-term" adaptation as he wore anisometric corrective spectacles for about 40 years and also the extent of "short-term" adaptation in this subject and two other subjects, who initially made conjugate saccades, when they wore newly fitted anisometric spectacles for about 8 hr. Two-dimensional binocular eye positions were measured with an accurate and precise revolving magnetic field-sensor coil technique. We found that long-term adaptation of vertical saccades was virtually perfect (almost 100% of the asymmetry introduced by the spectacles was corrected). Long-term adaptation of horizontal saccades was less complete and increased with target separation from about 40% for saccadic amplitudes of 5° to about 75% for amplitudes of 60°. Short-term adaptation of vertical saccades was virtually complete (100%) in one newly fitted subject and only partially complete (40%) in the other two subjects. The persistence of the adaptive asymmetry of saccades during monocular viewing showed that adaptation derived from plasticity in the programming of saccades and not from modification of vergence responses. Without the anisometric spectacles, 30 min of self-paced, one per second changes in binocular fixation between two targets, which required a version change of 45° in combination with a vergence change of 11°, did not induce any asymmetrical adaptation. This result shows that a specific repeated association of version and vergence eye movements was not sufficient to induce asymmetrical adaptation, leading us to suggest that the transient fixation disparities at saccade-offset might be the necessary stimulus for the asymmetrical saccadic adaptation we observed. Invest Ophthalmol Vis Sci 30:1132-1145, 1989

Saccades are used to change the direction of gaze quickly from one to another detail in the visual scene. Apart from minor differences in their dynamic properties,^{1,2} the saccades made by the two eyes are normally well yoked (conjugated) during either monocular or binocular viewing. This conjugacy at the motor level, often expressed as Hering's law of equal innervation, normally insures that saccades result in equal angular displacements of the retinal images in each of the eyes. There are, however, at least two conditions which make "equal innervation" unsuitable for maintaining optimal binocular viewing. The first condition is a neuromuscular asymmetry, such as a paresis of some of the muscles of one eye. The second

condition is an optical asymmetry, caused by the wearing of anisometric spectacles. Such spectacles introduce a different magnification factor for each of the two retinal images. In both types of conditions, continued effective binocular fixation would, ideally, require the development of asymmetrical motor commands. In the case of paresis, such adaptive processes would lead to the restoration of motor conjugacy, ie, equally large saccades in each eye. In the case of anisometric spectacles, adaptation would lead to saccades of unequal size in each of the two eyes. In this condition the ratio between the sizes of the saccades should, ideally, compensate for the different magnification factors of the spectacles. Both conditions would benefit from plastic changes.

Plasticity of commands to generate saccadic eye movements has been demonstrated in both humans and monkeys when the strength of the extraocular muscles of one eye was reduced. Kommerell et al³ reported that saccades made by a patient's paretic eye, which had good visual acuity, were orthometric, whereas saccades made by the nonparetic fellow eye, which had poor visual acuity, were hypermetric. These findings were confirmed by Abel et al,⁴ who also showed that the plasticity of saccades was reversible. They found, by forcing a patient to use his pa-

From the *Department of Physiology I, Erasmus University, Rotterdam, The Netherlands, and the †Department of Psychology, University of Maryland, College Park, Maryland.

Supported in part by the Foundation for Medical Research MEDIGON (The Netherlands) (grant no. 900-550-092), by NIH-NEI grant no. EY-04647 (USA), and by the Department of Psychology, University of Maryland.

Submitted for publication: June 16, 1988; accepted December 22, 1988.

Reprint requests: Dr. H. Collewijn, Department of Physiology I, Faculty of Medicine, Erasmus University Rotterdam, P.O. Box 1738, NL 3000 DR Rotterdam, The Netherlands.

retic eye while the good eye was patched, that the saccades of both eyes increased in size with a time constant of 0.85 days. Subsequently, by switching the visual input back from the paretic eye to the good eye, the saccades of both eyes decreased with a time constant of 1.54 days to the sizes they had before adaptation.

Plasticity has also been shown in monkeys by weakening both horizontal rectus muscles of one eye by severing a portion of their tendons. The hypometric saccades made by this eye became orthometric when the normal fellow eye was patched.⁵ These findings, as well as those of Kommerell et al³ and Abel et al,⁴ show that symmetrical increases in the size of paired, binocular saccades can be achieved. Viewing was functionally monocular in all these reports of plasticity, although it is possible that the patients had already accomplished some (incomplete) asymmetrical adaptations before they presented for treatment. Plasticity has also been demonstrated during binocular viewing. In the case of binocular viewing, paretic muscles of one eye demand asymmetrical adaptation to achieve an ideal oculomotor state. Snow et al⁶ showed for the first time in monkeys that saccadic adaptation was asymmetrical when both a tenectomized eye and its normal fellow eye remained unpatched. They showed that after about 30 days of binocular viewing, the ratio of horizontal saccadic magnitudes (tenectomized vs normal eye) had returned to values observed prior to tenectomy. This finding that the monkey's saccadic subsystem is capable of a certain amount of asymmetrical adaptation, raises the question of whether humans have a similar capability, whenever such an asymmetry is required for the maintenance of effective binocular fixation.

There is psychophysical work on phoria with implications for asymmetrical adaptation of saccadic size when each eye is confronted with a different demand. Unequal sizes of retinal images in each of the eyes create fixation disparities, whose size depends on the eccentricity of the binocularly fixated target. Ellerbrock, Fry and Allen⁷⁻⁹ have demonstrated that human subjects adapt to such induced vertical phorias. They measured the vertical phorias (by subjective methods) after the prolonged wearing of anisometric, corrective spectacles. In similar experiments, Hensen and North¹⁰ applied base-up prisms and found that the induced vertical phoria largely disappeared after only about 3 min of binocular visual experience. They hypothesized that such an adaptive process may be essential to enable compensation for changes in orbital mechanics, which normally occur with age.¹¹ Further evidence for a short-term adaptive mechanism acting differently in the two eyes was provided by Henson and Dharamshi.¹²

They magnified the visual image of one eye by a positive spectacle lens, maintaining optimal visual acuity by using it in combination with a negative contact lens of the same refractive power. They found (using a Maddox rod method) that the static horizontal, as well as vertical, eye positions were changed, largely compensating for the induced monocular image magnification after 2.5 hr of binocular visual experience.

These studies, in which phorias were measured subjectively, could not determine whether eye movements in general and saccades in particular, are subject to similar adaptive mechanisms as the eventually reached, static eye positions. It might be that saccades remain conjugated, leaving behind fixation disparities, which are subsequently removed by disjunctive, post-saccadic drift. The experiments of Snow et al⁶ suggest that the monkey can asymmetrically adapt the sizes of horizontal saccades.

However, horizontal eye movements are complicated by the common occurrence of vergence in combination with version. In contrast with traditional assumptions, they cannot always be distinguished easily by their dynamical properties. We recently found (Erkelens et al, in preparation) that vergence changes as large as 11° could be almost completely mediated by disjunctive saccades (with sizes of about 40° and 50° in each of the two eyes) when gaze was voluntarily shifted between targets that differed in direction, as well as in depth. Thus, horizontal saccades of different sizes, made during binocular viewing, do not necessarily reflect adaptation. Even when gaze is shifted between targets on an iso-vergence locus, all horizontal saccades show a disjunctive component in the form of a transient divergence of as much as a few degrees.¹ For horizontal saccades, the most convincing evidence for genuine asymmetrical adaptation would consist of a systematic size difference when gaze is shifted between monocularly viewed targets on an iso-vergence locus. Stronger evidence for adaptation would consist of the development of systematic and appropriate size differences in vertical saccades because vertical saccades have been found to be yoked even better than horizontal saccades.²

As was mentioned previously, there is a second condition in which asymmetrical saccadic adaptation is also demanded. Specifically, when refractive anomalies are corrected by anisometric spectacles. These spectacles make the retinal images in each eye unequal in size (contact lenses produce this problem only to a very minor extent¹³). Changes in binocular fixation from one to another target, viewed through anisometric spectacles, require saccades of unequal sizes. In the current study we investigated the extent to which saccades made by each of the eyes adapted

to its own magnification factor when anisometric spectacles were worn. Our study is novel because, until now, a major study of saccadic adaptation to unequal magnification factors has not been reported.

This study reports the extent to which effective asymmetrical saccadic adaptation was achieved by a myopic subject, who was exposed to "long-term" adaptation as he wore anisometric corrective spectacles for about 40 years, and also the extent of "short-term" adaptation in this subject and two other subjects, who initially made conjugate saccades, when they wore newly fitted anisometric spectacles for about 8 hr. We found that the human saccadic subsystem is indeed capable of asymmetrical adaptation. This adaptation was evident after short-term, as well as after long-term, exposure. It was more complete for vertical than for horizontal saccades.

Materials and Methods

Subjects

Three subjects (the authors) participated in the experiments. They had visual acuities of 20/20 or better, without ($n = 1$) or with ($n = 2$) correction. None of them showed any ocular or oculomotor pathologies, only some refractive errors. All subjects, an emmetropic and presbyopic male (R.S., age 60 years), a myopic and presbyopic male (H.C., age 51 years), and a myopic male (C.E., age 36 years), who wears negative contact lenses, were experienced in oculomotor research. The myopic subject H.C. has worn negative, anisometric spectacles for about 40 years (prescription: right lens: S-3.5, C-0.5, axis 175°; left lens: S-6.25, C-1.0, axis 175°). Thus, subject H.C. had an average anisometropia of 3 diopters. All subjects had good binocular vision and stereoacuity. H.C. was right-eye dominant; R.S. and C.E. showed virtually no dominance.

Eye Movement Recording Technique

The revolving magnetic field-sensor coil technique was used to record absolute horizontal and vertical eye positions of both eyes in space. The principle of this technique,¹⁴ as well as properties of the particular instrument used, have been described before.¹⁵ Briefly, sensor coils were attached to the eyes and homogeneous magnetic fields rotating in the horizontal and sagittal planes (field frequencies: 976 and 3904 Hz) were generated around the subject. The phase of the alternating electric potentials induced by the fields in a sensor coil is linearly related to the latter's angular orientation. In the instrument used in the present experiments, generation of the field and phase detection of the induced signals were digitally controlled; special filtering techniques allowed vir-

tually perfect separation between signals induced by horizontal and vertical fields. The noise level was <40" and linearity was better than 0.01% over 360°. Stability was better than 6" (for a fixed sensor coil) over periods from 1 sec to 24 hr. The maximum slewing speed of the digital output was 12,000°/sec. 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 Collewijn et al¹⁶ were used to measure the position of both eyes simultaneously. The stability of these coils on the eyes, when properly inserted, was documented by the inventors and confirmed for the current experimental apparatus.¹⁵ Head movements were minimized by using bite-boards with individually fitted dental impressions.

Stimuli

The visual targets consisted of 15 LEDs arranged on the horizontal and vertical meridians of an isovergence surface.¹ Specifically, targets were placed on a horizontal circle with a diameter of 91.4 cm (3 ft), which contained the targets as well as the centers of rotation of the eyes (assumed to be 13 mm posterior to the corneal plane). (The center of this circle was located about halfway between the eyes and the target.) Vertical targets were placed in the median plane on a circle with a radius of 91.4 cm, centered on the midpoint of the interocular baseline. Thus, all targets were located on one toroid surface, with different curvatures along the horizontal and vertical meridians, such that fixation of any point on this surface required the same vergence angle.¹ In the horizontal plane, angles between the central fixation LED in the straight-ahead position and target LEDs measured 2.5, 5, 10, 20 and 30° on either side of the central fixation point. In the median plane, angles measured 5 and 10° in the upward and downward direction.

Experimental Procedures

The experiment consisted of two similar sessions run on different days. In the first session, H.C. wore his normal, anisometric spectacles, R.S. wore no spectacles and C.E. wore his corrective contact lenses. The data from the first session served as a baseline for the saccadic adaptation to be measured in the second session. The data of H.C. also served as an estimate of his long-term saccadic adaptation to anisometric spectacles which had developed over a period of 40 years. In the second session, all subjects wore anisometric spectacles for about 8 hr. Subject H.C., who normally wore anisometric spectacles, wore additional spectacle lenses of -3 diopter in front of his

right eye and of +3 diopter in front of his left eye, thus reversing the habitual difference in magnification he had worn for 40 years. Subject R.S. wore a spectacle lens of +2 diopter in front of his left eye, while his emmetropic right eye continued viewing normally. The modification was just opposite for subject C.E., who wore his contact lenses with a +2 diopter spectacle lens in front of his right eye, while his left eye viewed normally. Despite some degradation of acuity, all subjects experienced binocular fusion most of the time and managed to proceed with their normal activities during the 8 hr period. This was considered an essential condition for the experiment, because conditions that would seriously compromise binocular vision might result in monocular suppression and, probably, elimination of the pressure for asymmetrical adaptation. Under the assumption that continued binocular viewing was essential for asymmetrical adaptation, it was immaterial whether the lens was applied, in the second session, to the dominant or nondominant eye. The degrading of acuity could have been prevented by using suitable combinations of spectacle glasses and contact lenses, but this was not attempted in this explorative experiment. One of the eyes was covered at all times when the spectacles had to be taken off during the insertion of the sensor coils, thus, avoiding inappropriate binocular stimulation at all times.

Each experimental session began with a calibration trial in which the horizontal and vertical position of each eye was recorded during binocular fixation of the central LED. These recordings formed the basis for eliminating offsets from the eye position recordings. No calibrations of magnitude were required, as the angular rotations, measured by the apparatus used, have absolute calibration. Subsequently, each session contained 23 trials during which the subject changed his fixation between two LEDs placed symmetrically about the central fixation point. The subject decided when to change fixation and ran each trial at a comfortable, self-paced rhythm of about 1 fixation change each second. Trials, which lasted 10 sec, were started on command of the subject. The horizontal and vertical positions of the two eyes were sampled at 488 Hz. Only the two LEDs serving as targets were lighted. Trials with binocular viewing were interleaved with trials with monocular viewing by either the left or right eye.

Data Analysis

Details of the storage and analyses of data have been described previously.¹⁴ Briefly, saccade-onset and saccade-offset were detected in off-line analysis by a velocity threshold of 15°/sec in combination

with a required minimum saccadic duration of 15 msec. By using these criteria all saccades, larger than 1°, were detected reliably. Velocities were calculated simply as the difference between two subsequent eye position samples divided by the sampling interval. No additional filtering, smoothing or window techniques were used. The effective bandwidth of both position and velocity was 244 Hz. The quotients of the magnitudes of paired saccades, made by the left and right eye during binocular and monocular viewing, were computed. The adaptation required by the wearing of anisometric spectacles was computed as the quotient of the movement angles covered by the viewing left or right eye during monocular fixation changes between pairs of targets along the horizontal or vertical meridian. This procedure measured the overall magnifying effect of the spectacles on the eye movements; it included effects of positioning of the lens, shape of the lens, viewing outside the optical center of the lens, and possible misalignment of the lens. The amount of saccadic adaptation achieved was computed as the percentage of the required adaptation present in the ratios of paired saccades during monocular viewing. Ocular vergence was calculated by subtracting the right eye position from the left eye position.

Results

Long-Term Saccadic Adaptation

Subject H.C. made unequal horizontal and vertical saccades with both eyes when he wore his normal, anisometric, corrective spectacles. Representative records of his horizontal saccades are shown in Figure 1 and representative records of his vertical saccades are shown in Figure 2. Saccades made by his left eye were smaller than saccades made by his right eye, as would be expected by the differences in retinal image size induced by his spectacles. The mean difference in target separation induced by the spectacles was 8.2% \pm 0.8 for the vertical dimension and 7.8% \pm 1.4 for the horizontal dimension.

Another striking feature of these records, which is typical for all horizontal saccades in all subjects,¹ can also be seen in Figure 1: H.C.'s eyes diverged at the onset of his horizontal saccades. Specific only for H.C. was that this initial divergence was followed by a second change in vergence starting just prior to saccade-offset. The eyes diverged once more during rightward saccades, but converged during leftward saccades. H.C.'s transient divergence coincident with saccade-onset helped him correct the asymmetry in the required magnitude of his rightward saccades that had been introduced by his anisometric spectacles, but counteracted the same asymmetry required for

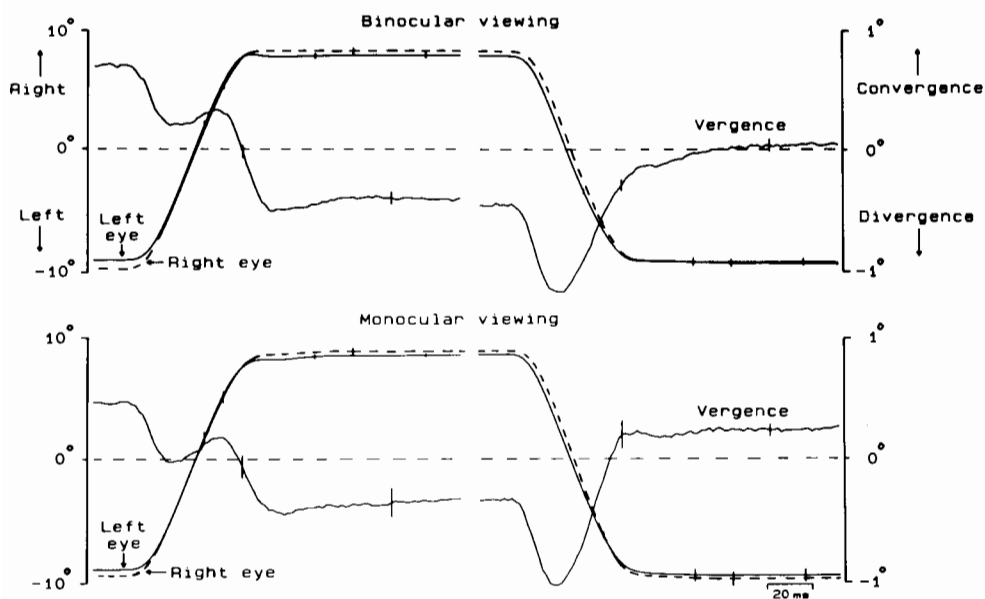


Fig. 1. Position profiles (means of four successive saccades) of 20° horizontal saccades made by subject H.C. when he wore his normal, anisometric spectacles. Monocular viewing was with the right eye. The computed traces of horizontal vergence have been amplified by a factor of 10 (right-hand scales) for reasons of clarity. The dashed, horizontal lines indicate zero vergence, i.e., the vergence angle during binocular fixation of the straight-ahead fixation point. Vertical bars in the traces indicate ± 1 SD.

his leftward saccades. As a result, the required asymmetries in saccadic magnitude of the left and right eye were larger for rightward than for leftward saccades. In other words, the amount of long-term adaptation to anisometric spectacles depended on the direction of the saccades. Rightward saccades were more adapted than leftward saccades. Residual fixation disparities after the insufficient vergence changes were gradually reduced by post-saccadic drift, and had been largely eliminated by the time the next change in fixation was made. The time-courses of the

vergence responses were very similar during binocular and monocular viewing, although variability of the vergence responses was larger during monocular viewing.

Changes in vertical vergence during vertical saccades (Fig. 2) were less complicated than changes in horizontal vergence during horizontal saccades (Fig. 1). Vertical vergence changed in the appropriate direction immediately after the onset of upward, as well as downward, saccades. Vergence changed smoothly throughout all vertical saccades and vergence had

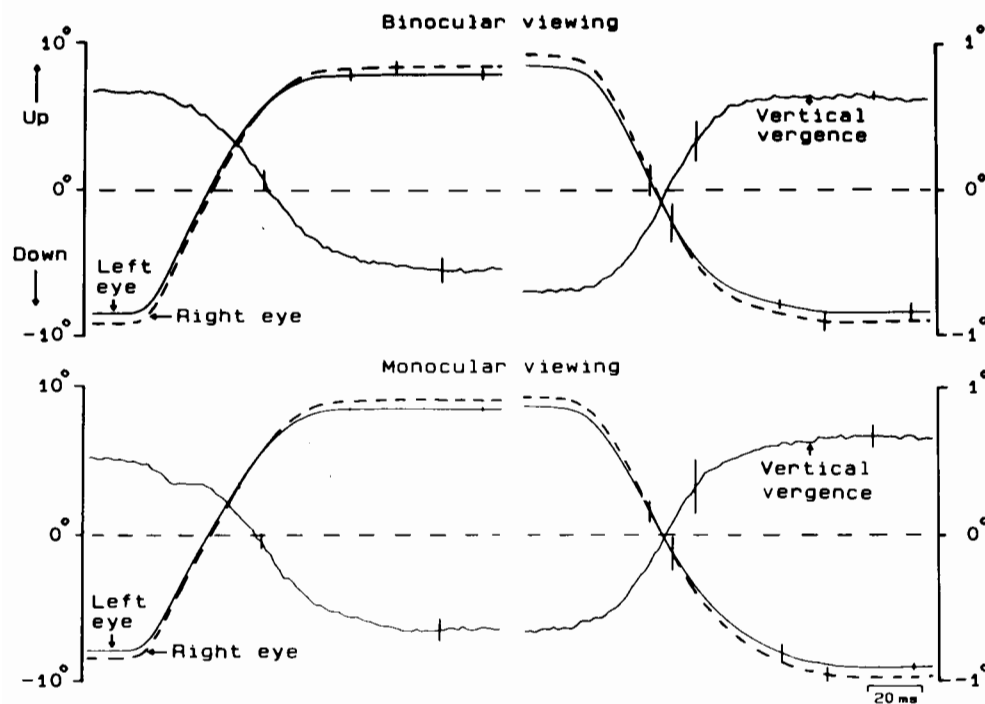


Fig. 2. Position profiles (means of four successive saccades) of 20° vertical saccades made by subject H.C. when he wore his normal, anisometric spectacles. Monocular viewing was with the right eye. See Figure 1 legend for other details.

stabilized within about 100 msec after saccade-offset. The changes in vertical vergence during binocular and monocular viewing were very similar. Net adaptive changes in vertical vergence during vertical saccades were larger than net adaptive changes of horizontal vergence during horizontal saccades of similar amplitude. Long-term vertical adaptation was much better than horizontal long-term adaptation.

Figure 3 shows that binocular differences in the amplitudes of vertical saccades closely matched the asymmetry of image magnification induced by the anisometric spectacles. This was not the case for horizontal saccades. Saccadic adaptation achieved was, on average, only 40% of what was required when target separation was 5°. The percentage of adaptation achieved increased with target separation, up to about 75% for target separations of 60°. Thus, the amount of adaptation differed considerably in the vertical and horizontal directions and, moreover, adaptation was not uniform over the horizontal range. The superiority of H.C.'s long-term adaptation on the vertical meridian is actually greater than suggested by Figure 3 because his astigmatic correction of the two eyes was different (see *Methods*). This difference made the magnification factor slightly larger in the vertical than in the horizontal direction. Despite these higher requirements, saccadic adaptation was complete in the vertical direction, whereas it was far from complete in the less demanding horizontal direction.

The relative effectiveness of long-term saccadic adaptation along the horizontal and vertical meridians are summarized in Table 1, where fixation disparity at saccade-offset is given. Fixation disparity was computed as follows: first, the difference between eye position at saccade-offset and the eye position during steady, monocular fixation (assumed to represent target position) was computed for each eye. Then, fixation disparity was computed as the difference between the fixation errors of each of the eyes.

Table 1 shows that the vertical fixation disparities at the offset of vertical saccades were extremely small (generally below 5'). Horizontal fixation disparities at the offset of horizontal saccades were considerably larger, ranging from 0.3° up to about 2°. Despite the presence of these large, fixation disparities, the subject did not experience loss of fusion after any saccade as would be expected from prior work on natural retinal image motion.^{17,18}

Short-Term Saccadic Adaptation

Representative horizontal and vertical saccades made by subject R.S. before and after a period of about 8 hr of adaptation to anisometric spectacles

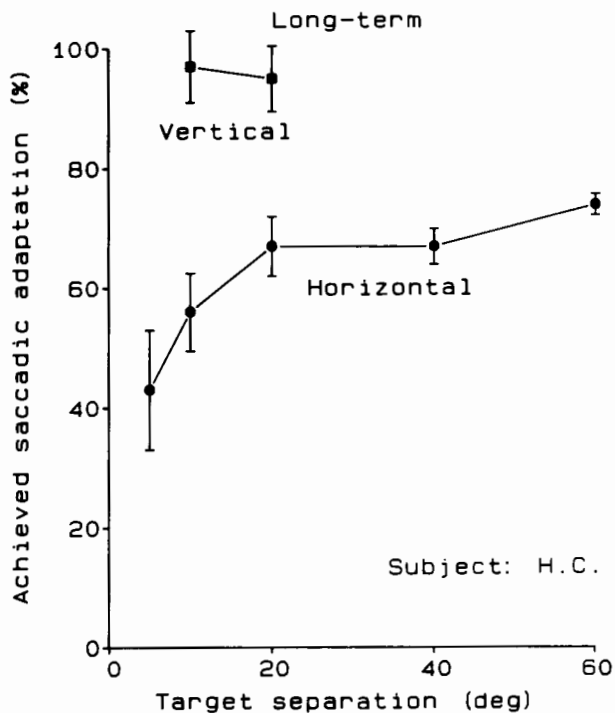


Fig. 3. Long-term, saccadic adaptation to anisometric spectacles computed as the percentage of adaptation required by the spectacles. Means \pm 1 SD are shown for horizontal (dots) and for vertical (squares) saccades.

are shown in Figures 4 and 5. His binocular saccades, made before adaptation, were similar to those described previously^{1,2} in that transient divergence was a characteristic feature of his horizontal saccades which were relatively well yoked. After adapting to the new spectacles for 8 hr, the horizontal saccades made by each of his eyes clearly showed unequal amplitudes. The second, newly fitted subject, C.E., also adapted the size of his saccades. In subject R.S. the left eye made larger saccades than the right eye, while subject C.E. made larger saccades with his right eye after adaptation. The directions in which the saccades had adapted corresponded with the different magnifications of the spectacle lenses worn by each subject. The mean difference in target separation for the left

Table 1. Fixation disparity present at saccade-offset

Target separation (deg)	Horizontal (min arc)	Vertical (min arc)
5	26 \pm 15	
10	21 \pm 18	4 \pm 11
20	45 \pm 31	5 \pm 17
40	87 \pm 43	
60	116 \pm 77	

Mean horizontal fixation disparity at the offset of horizontal saccades and mean vertical fixation disparity at the offset of vertical saccades for subject H.C., wearing his normal, anisometric corrective spectacles (N = 8).

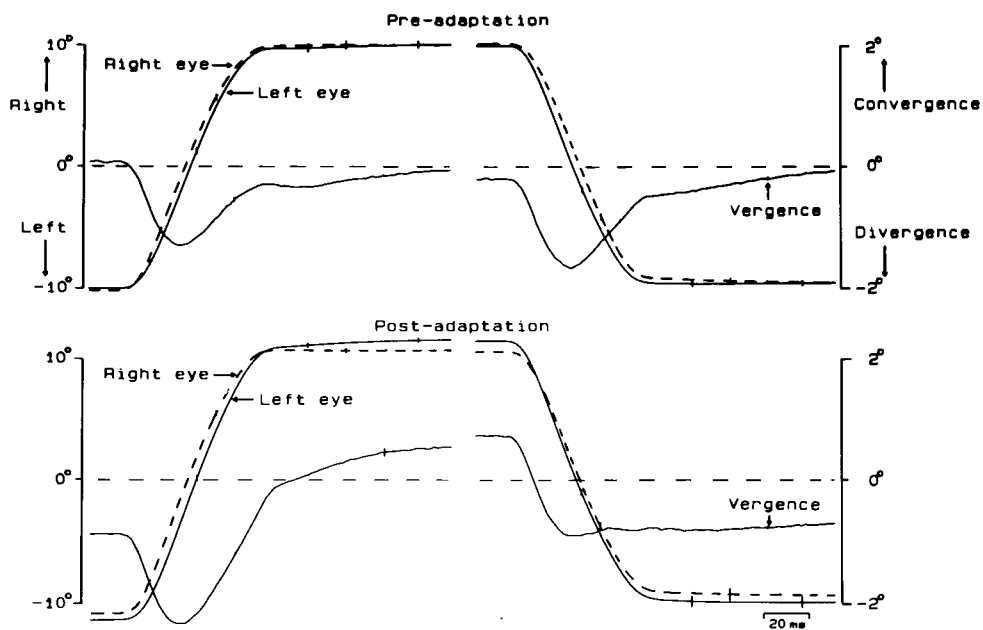


Fig. 4. Position profiles (means of four successive saccades) of 20° horizontal saccades made by subject R.S. during binocular viewing. The saccades reproduced were made with normal vision before adaptation (upper traces) and after anisometric spectacles had been worn for 8 hr (bottom traces). The computed traces of horizontal vergence have been amplified by a factor of 5 (right-hand scales) for reasons of clarity. The dashed, horizontal lines indicate the vergence angle during binocular fixation of the straight-ahead fixation point. Vertical bars in the traces indicate ± 1 SD.

and right eyes, derived from the eye positions of the monocularly viewing eye, was $8.2\% \pm 1.2$ for subject R.S. and of $6.8\% \pm 0.9$ for subject C.E. The transient divergence, occurring just after the onset of all horizontal saccades, favored the required adaptation during rightward saccades in subject C.E., and during leftward saccades in subject R.S. Thus, when the spectacles required a change in the divergent direction, the required change was achieved easily. Consequently, these saccades were followed by only a small

disjunctive, post-saccadic drift. However, when the spectacles demanded a change in the convergent direction, the initial inappropriate divergent movement was made and the necessary convergence could only be achieved partially during the saccade. The necessary convergence was completed after the saccade by disjunctive, post-saccadic drift. Subject C.E. with his newly fitted spectacles and subject H.C. with his normal anisometric spectacles made larger saccades with the right eye. The vergence traces were very sim-

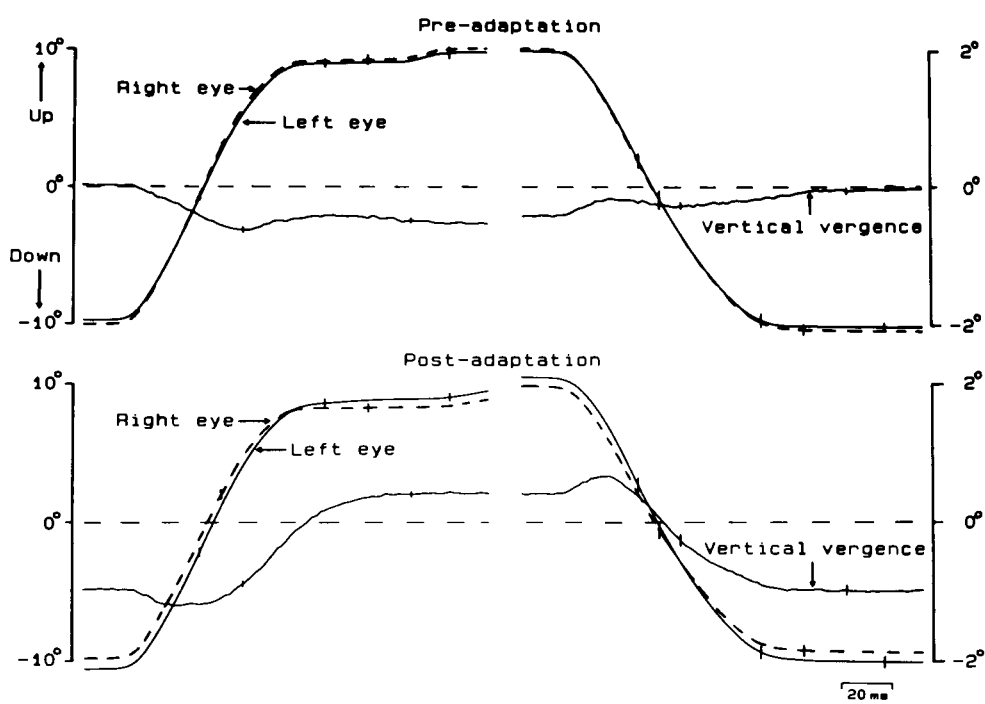
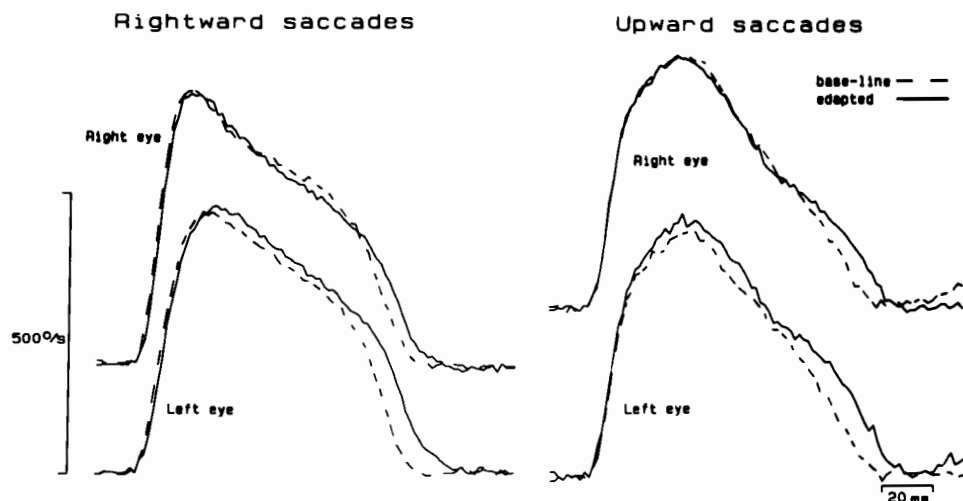


Fig. 5. Position profiles (means of four successive saccades) of 20° vertical saccades made by subject R.S. during binocular viewing. The saccades reproduced were made with normal vision before adaptation (upper traces) and after anisometric spectacles had been worn for 8 hr (bottom traces). See Figure 4 legend for other details.

Fig. 6. Velocity profiles (means of four successive saccades) of 20° saccades made by subject R.S. during binocular viewing. The saccades were made with normal vision before adaptation (dashed traces) and after anisometric spectacles had been worn for 8 hr (line traces).



ilar in these two subjects. Subject R.S. with his newly fitted spectacles made larger saccades with his left eye. As a result, his vergence traces were very different from those of the other two subjects.

Vertical saccades made before adaptation were well yoked in subject C.E. A vertical fixation disparity was observed in subject R.S. when he fixated vertically eccentric targets (Fig. 5). All vertical movements of R.S.'s right eye were slightly larger than those of the left eye. After 8 hr of adaptation to the spectacles, the relative sizes of the vertical saccades made by the two eyes had changed in both subjects. In subject C.E., the change in vertical vergence which resulted from the unequal, vertical saccades started immediately after the onset of these saccades, and was not completed at their offset. A substantial further change in vergence was made after saccade-offset. In subject R.S., vertical vergence initially changed in the wrong direction (Fig. 5). This change in vergence corresponded to the habitual changes in vertical vergence that had accompanied his vertical saccades before adaptation. About halfway through the saccade, the incorrect change in the direction of vertical vergence was corrected. About 100 msec after a saccade, vergence stabilized and hardly changed until another vertical saccade was made.

A detailed examination of the time-course of vergence showed that saccadic adaptation did not occur uniformly throughout the trajectory of the saccades in both subjects. This can be seen by comparing velocity profiles of saccades before and after adaptation. Such comparisons can be made in Figure 6. Differences in the velocity of all saccades were very small during their acceleration phase. The effects of adaptation became clear only when the saccades had reached their maximum velocity. From there on, the interocular velocity differences accumulated

throughout the deceleration phase. Adaptation affected the duration, as well as the velocity, of horizontal saccades. Here, saccades were prolonged when they increased convergence, and they were curtailed when they decreased convergence.

The relative effectiveness of short-term adaptation was evaluated in the same way as was employed in the long-term experiment already described, namely, by computing the ratios of sizes of binocular saccades during monocular viewing as a percentage of the size required by the anisometric spectacles. The results of this analysis are shown in Figure 7. Short-term adaptation of horizontal saccades in subjects R.S. and C.E. showed the same features found for long-term adaptation in subject H.C. (Fig. 3). Namely, the amount of adaptation achieved did not meet the re-

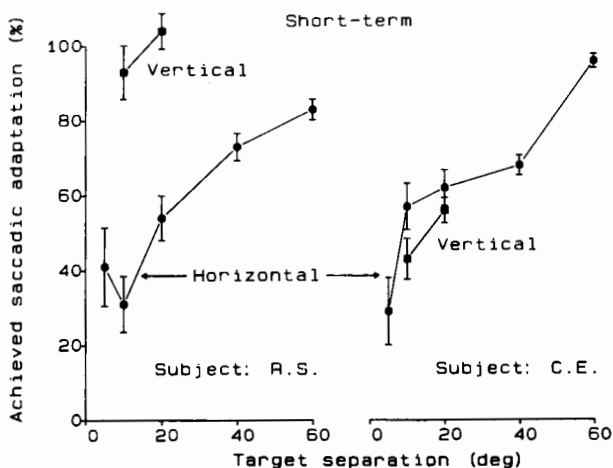


Fig. 7. Short-term, saccadic adaptation to anisometric spectacles computed as the percentage of adaptation required by the spectacles. Means ± 1 SD are shown for horizontal (dots) and for vertical (squares) saccades.

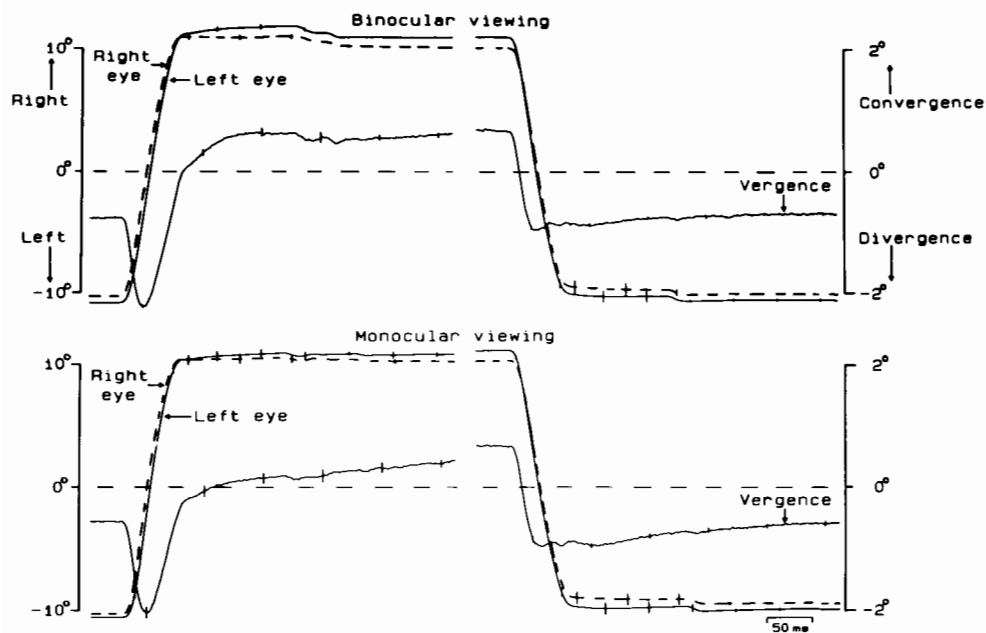


Fig. 8. Position profiles (means of four successive saccades) of 20° horizontal saccades made by subject R.S. The saccades were made after anisometric spectacles had been worn for 8 hr. Monocular viewing was with the right eye. See Figure 4 for other details.

quirements set by the anisometric spectacles along the horizontal meridian. It was only about 40% for the smallest horizontal saccades tested (5°), but increased with target separation up to about 80 to 90% for 60° saccades. Along the vertical meridian, there was a conspicuous difference between the adaptations achieved by the two newly fitted subjects who served in the short-term experiment. In subject R.S., vertical adaptation was close to 100%, the long-term adaptation value shown by subject H.C. (Fig. 3). Short-term vertical adaptation was far from perfect in subject C.E.—only about 40%. This value was similar to that found for short-term adaptation of horizontal saccades and not very different from the long-term value found for subject H.C. when the horizontal target separations were the same size.

An important question remains now that we have seen that short- as well as long-term adaptation was possible. Namely, had the programming of leftward and rightward saccades changed in such a way, that it was no longer dependent on immediate visual feedback appearing at saccade-offset? This was tested by comparing the vergence traces under monocular and binocular viewing conditions. Vergence changes were very similar under monocular and binocular viewing during horizontal, as well as during vertical, saccades. Moreover, the vergence traces in both viewing conditions showed the same post-saccadic drifts. All subjects showed slightly larger asymmetries in their adapted saccades during binocular viewing but these differences amounted to less than 5% and we, therefore, conclude that post-saccadic visual feedback was only of marginal importance. These results are illustrated in Figures 8 and 9.

Clearly, the asymmetry of binocular saccades, which developed during only 8 hr of binocular visual practice, were not responses to the momentary fixation disparity of the target during binocular viewing. The observed asymmetries in the binocular fixation pattern represented plasticity of the mechanisms that program the sizes of saccades.

Conditions Sufficient to Induce Saccadic Adaptation

Anisometric spectacles change the absolute disparities of all nonfixated targets. For targets lying on the horizontal meridian, their apparent positions are rotated around the vertical axis through the binocular fixation point. This implies that, during the wearing of anisometric spectacles, leftward saccades are generally associated with changes in vergence in one direction, while rightward saccades are associated with changes in vergence in the opposite direction. We hypothesized that this bias of vergence, which is associated with saccades in specific directions, might be sufficient to induce the asymmetrical, saccadic adaptation. We tested this idea by having the three subjects alternate fixation between two LEDs, requiring a change in version of 45° and a change in vergence of 11° . Both LEDs were placed on the horizontal plane through the eyes. One LED was positioned on the iso-vergence surface with a diameter of 91.4 cm (target vergence about 4°), 20° rightwards from the straight-ahead position. The other LED was lying on the iso-vergence surface with a diameter of 24 cm (target vergence about 15°), 25° to the left of the straight-ahead position. The subjects, who wore their normal refractive corrections, alternated binocular

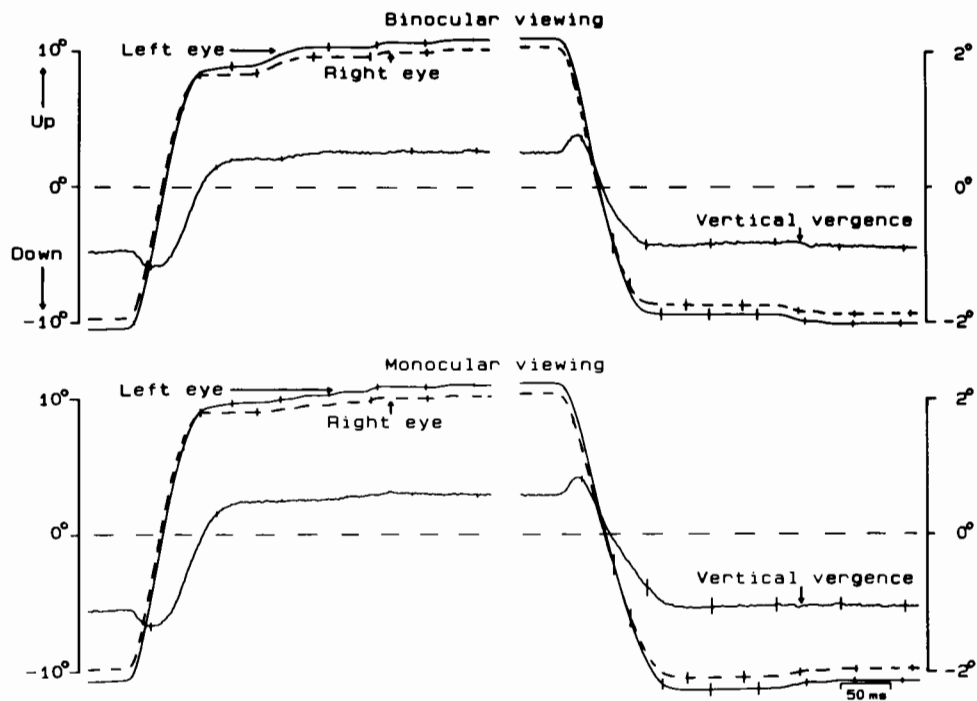


Fig. 9. Position profiles (means of four successive saccades) of 20° vertical saccades made by subject R.S. The saccades were made after anisometric spectacles had been worn for 8 hr. Monocular viewing was with the right eye. See Figure 4 for other details.

fixation between the two LEDs for 30 min, employing a comfortable rhythm. All leftward saccades were accompanied by an increase in convergence and all rightward saccades by a decrease in convergence during the 30 min of specific version-vergence pairing. One eye was covered after this period of vergence-training. Next, the subject alternated monocular fixation between two LEDs lying symmetrically about the straight-ahead position in the horizontal plane on the iso-vergence surface with target vergence of about 4°. These saccades were compared with horizontal preadaptation saccades to see whether the saccades had developed an asymmetry as a result of the specific version-vergence training. The result was negative in all subjects. The horizontal saccades were as conjugated as ever after the period of training, showing that asymmetrical saccadic adaptation, in our experiment, was not induced by a prolonged association between specific directions of changes in version and vergence. Some other process must operate to induce relatively rapid asymmetrical saccadic adaptation.

Short-Term Readaptation of Long-Term Adapted Saccades

Subject H.C. is exposed to asymmetrical changes in retinal image sizes very frequently, namely each time he puts on or takes off his normal spectacles. H.C. was tested to determine whether he could adapt more rapidly to a new condition of anisometropia than the other two subjects who made such a change for the

first time in the present experiment. In other words, we sought to find out whether a subject can learn to adapt his saccades more rapidly by adapting them frequently over many years. Subject H.C. made saccades which differed from the saccades he normally made (Figs. 1, 2) by adding additional, anisometric lenses on top of his normal, corrective spectacles. Representative horizontal and vertical saccades, made by H.C. during binocular and monocular viewing after 8 hours of adaptation to additional anisometric lenses, are shown in Figures 10 and 11.

When he wore his normal spectacles, H.C.'s rightward saccades were associated with vergence changes in the divergent direction, whereas leftward saccades were associated with changes in the convergent direction (Fig. 1). The additional, anisometric lenses required a reversal of this relationship: rightward saccades in association with changes in the convergent direction, and leftward saccades with changes in the divergent direction. Inspection of vergence traces showed that this goal was not achieved after 8 hr of binocular visual practice, but significant progress had been made. These partial saccadic adaptations after 8 hr of binocular visual experience with the altered spectacles are shown in Figure 12. As can be seen in this figure, adaptation of vertical saccades was still far short of the level of nearly perfect adaptation we had obtained in our other experiments. On the horizontal meridian, adaptation had also not reached the level achieved by this subject over a long period of time (Fig. 3). This was particularly true for the larger target separations. Overall, vertical and horizontal saccades

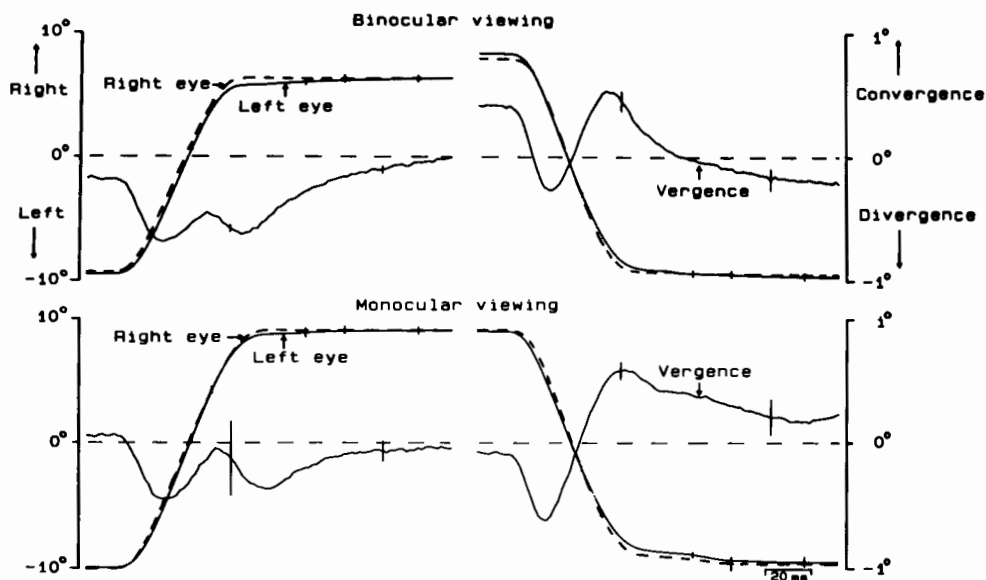


Fig. 10. Position profiles (means of four successive saccades) of 20° horizontal saccades made by subject H.C. The saccades were made after newly fitted, anisometric spectacles had been worn for 8 hr. Monocular viewing was with the right eye. See Figure 1 for other details.

showed similar percentages of achieved adaptation, both were relatively incomplete after 8 hr.

Discussion

Are There Multiple Levels of Asymmetrical Saccadic Adaptation?

The present results confirm the observation made by Snow et al⁶ that saccades can adapt to conditions which are different for the two eyes. The differences were mechanical in nature in the experiments of Snow et al⁶ and visual in the present experiments. Mechanical and visual inequalities between the two

eyes would seem to require similar changes in the generation of binocular saccades. However, there may be some subtle differences. When the muscles of one eye are weakened, retinal target separations remain unchanged in both eyes, but gaze-shifts between targets having identical separations in the two eyes require different motor commands. During the wearing of anisometric spectacles, retinal target separations are changed differently in the two eyes, but gaze-shifts between targets that have identical angular separations in the two eyes still require identical motor commands. This may imply that, during the wearing of anisometric spectacles, asymmetrical

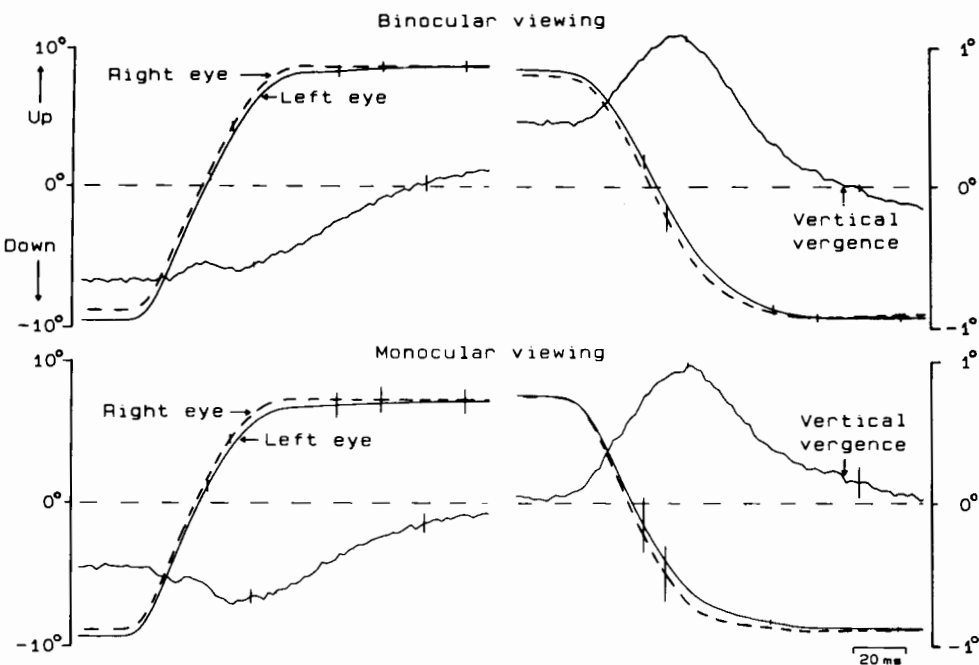


Fig. 11. Position profiles (means of four successive saccades) of 20° vertical saccades made by subject H.C. The saccades were made after newly fitted, anisometric spectacles had been worn for 8 hr. Monocular viewing was with the right eye. See Figure 1 for other details.

adaptation is mainly concerned with the reinterpretation of visual information, while after weakening of extraocular muscles, asymmetrical adaptation relates to the adjustment of only the motor commands controlling the muscles of the affected eye. Therefore, the weakening of extraocular muscles and the wearing of anisometric spectacles may stimulate adaptive mechanisms which address different stages in the programming of binocular saccades. The fact that horizontal saccades made by a tenectomized eye recovered fully to their original size after 30 days of adaptation,⁶ whereas adaptation of horizontal saccades to anisometric spectacles was still far from complete after 40 years of adaptation, provides some evidence for the existence of more than one level in the asymmetrical, adaptive mechanism, one visual, the other motor.

The Effective Stimulus for Asymmetrical Saccadic Adaptation

The nonconjugate, saccadic component, which is manifest after a period of adaptation to anisometric spectacles, was maintained during monocular viewing. This shows that asymmetrical saccadic adaptation reflects plasticity of the central mechanism involved in the programming of saccades, rather than a response of this mechanism to immediate visual feedback. The negative outcome of our experiments in which a subject consistently paired a change in the direction of gaze with a change in vergence in a fixed relation shows that the mere prolonged systematic association of vergence and version is not an effective stimulus for the asymmetrical adaptation of saccadic size. It seems more likely that systematic absolute disparities, occurring at the end of saccades, that are large enough to compromise fused binocular viewing, are the effective stimuli. It is well known that the tolerance for vertical absolute disparities is much smaller than for horizontal disparities.¹⁹ In this respect, our finding that the asymmetrical adaptation of saccadic size was much more complete along the vertical than along the horizontal meridian, suggests that adaptation in each direction is only as good as necessary for maintained fusion.

Degrees of Freedom of Saccadic Adaptation

Spatial aspects: The current findings extend the known number of degrees of freedom of saccadic adaptation. Most importantly, they show that the eyes can be treated independently in the adaptive process. Furthermore, they show that the adaptive changes can be different on the horizontal and vertical meridians, and that the percentage of change can vary also with the size of the required saccades. Taken together,

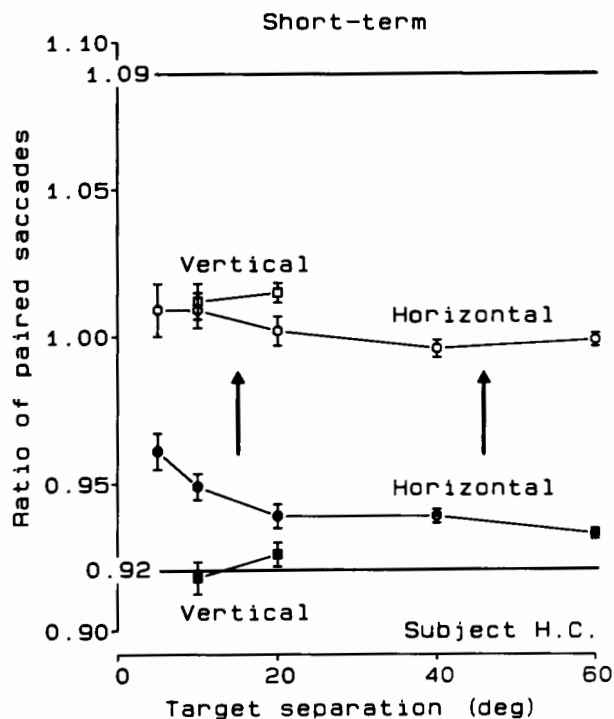


Fig. 12. Short-term, saccadic readaptation to newly fitted, anisometric spectacles computed as the percentage of adaptation required by the new spectacles. Means \pm 1 SD are shown for horizontal (dots) and for vertical (squares) saccades.

these findings suggest that saccadic adaptation may involve a point-by-point adjustment of sensory-motor maps, rather than a resetting of a few global parameters that control saccade size. This concept is in line with some other findings in the literature as well as with our present results. Kommerell et al³ and Abel et al⁴ showed that, in patients suffering from a unilateral paresis of extraocular muscles in one eye, modification of the saccadic gain for one horizontal direction did not affect the size of saccades in the opposite direction. Our experiments were only suitable to show directional effects in the sense of meridional selectivity because anisometric spectacles do not differentiate between opposite directions. However, a curious amplitude dependency was found for horizontal saccades, which adapted to reach a maximally tolerated, absolute disparity, rather than a fixed overall percentage. This result contrasts with that of Deubel et al,²⁰ who showed that an intra-saccadic target displacement, following a primary target displacement of a specific amplitude, induced adaptive changes in saccades of all amplitudes. Consequently, these authors suggested that a single gain element determined the saccadic size for all target eccentricities. The crucial difference between our experiments and those of Deubel et al²⁰ is that the latter authors trained the eye only for one specific amplitude; the

subsequent generalization of adaptation to other amplitudes observed by them may be due to the lack of a pressure for asymmetrical adaptation to different amplitudes. In our conditions, subjects proceeded with their normal behavior, which provided pressure for asymmetrical changes in saccade sizes for saccades of very different sizes. We believe there is probably a general rule for adaptive processes: namely, adaptive processes will not differentiate further than the level specified by the stimulus. For instance, if only one eye is stimulated, both eyes will adapt in parallel³⁻⁵; if only one meridian is stimulated, all meridians may adapt similarly. Asymmetrical adaptation will evolve only when asymmetrical adaptation is specifically required in order to obtain optimal vision. Very recently, Viire et al²¹ observed an even higher degree of asymmetrical saccadic adaptation than the level of asymmetry that was required by the wearing of anisometric spectacles. They found that the saccades made by monkeys adapted asymmetrally after surgical weakening of only one of the horizontal recti of one eye.

Asymmetrical recalibration of sensory-motor processes is well suited for coping with changes inherent to development, aging and disease. Such processes will often affect muscles, neurons or orbital tissues in a local, nonuniform way, so that global adjustments, such as an overall change in saccadic size, would be of little help in alleviating oculomotor errors. However, differentiation may have its price: we do not know over what range asymmetrical adaptation is feasible, but it may be a smaller range than is possible for adaptation to a uniform, global change in oculomotor requirements. The common occurrence of persistent problems of binocular motor coordination in the clinic suggests that the range of asymmetrical adaptation is rather limited. A lower limit for adaptation to interocular differences, suggested by our experiments on the adaptation of *vertical* saccades, is about 8%.

Temporal aspects: Saccades are produced by a pulse-step change in the activation of the eye muscles, with the pulse magnitude determining peak velocity and the step amplitude determining the final position of the eye. Saccadic adaptation to changed external conditions is thought to be established by the adjustment of the gains of the pulse- and step-generating mechanisms.⁵ Deubel et al²⁰ suggested that saccades are adapted to changed visual conditions in a simple, parametric manner, namely by changing a single gain element which determines the saccadic sizes for all target eccentricities. However, symmetrical, as well as asymmetrical, saccadic adaptation shows features that are at odds with such a simple, single gain element, control. Asymmetrical saccadic adaptation to changes in mechanical⁶ and visual conditions (this

report) show the need for several gain elements, namely one for each eye and one for each meridian. Miller et al²² found that symmetrical, adaptive modification of saccades of specific direction and amplitude does not completely transfer to saccades with different spatial parameters. They suggested that saccadic adjustment is specific for the direction and, to some extent, specific for the amplitudes of saccades. This suggestion implies highly complex adaptive controllers. Our speculations on the control of saccadic adaptation, made on the basis of different asymmetrical adaptive changes on the horizontal and vertical meridians, also imply highly complex adaptive controllers.

The preceding arguments against saccadic adaptation being produced by simple parametric adjustment of saccadic controllers were based on the observed spatial characteristics of saccadic adaptation. However, there are temporal aspects of saccades associated with asymmetrical saccadic adaptation which also oppose the idea that saccadic adaptation is established by a resetting of the gain parameters of the pulse- and step-generating mechanisms for saccades of a specific amplitude and direction. These temporal aspects of asymmetrical saccadic adaptation are most easily studied by comparing the time-courses of vergence, associated with saccades in their normal and adaptive states. We compared *horizontal vergence*, associated with yoked horizontal saccades (Fig. 4, upper figure), with: (1) horizontal saccades after long-term adaptation (Fig. 1); (2) horizontal saccades after short-term adaptation (Fig. 4, lower figure); and (3) horizontal saccades after short-term readaptation (Fig. 10). This comparison showed that the transient divergence, present in unadapted, horizontal saccades, was not affected by asymmetrical saccadic adaptation. Comparison of horizontal vergence, associated with horizontal saccades, before and after short-term adaptation (Fig. 4) showed that asymmetrical adaptation started after the saccade had gone about *halfway*. The timing on the vertical meridian was different. *Vertical vergence* during vertical saccades showed that asymmetrical adaptation started at the *onset* of vertical saccades after long-term adaptation (Fig. 2). Normally, vertical saccades are well yoked and not accompanied by a systematic change in vertical vergence.² This suggests that asymmetrical saccadic adaptation is confined to the final part of horizontal saccades because of an intrinsic asymmetry which is present in all horizontal binocular saccades. Short-term asymmetrical saccadic adaptation occurred even at a later stage of horizontal saccades in the subject who had been exposed to long-term asymmetrical saccadic adaptation. Comparison of horizontal vergence after long-term adaptation

(Fig. 1) with horizontal vergence after short-term re-adaptation (Fig. 10) shows that after readaptation, saccadic asymmetry, which started about halfway through the saccades, developed initially in the direction opposite to the direction required by the magnification factors of the new anisometric spectacles. The changes in vergence during this period, however, were rather similar to those made during the wearing of the habitual anisometric spectacles (Fig. 1). Thus, the horizontal saccades initially still showed the features characteristic of saccades established by wearing a particular pair of spectacles for a long time. Vergence turned to the direction appropriate to demands imposed by the new spectacles only shortly after saccade-offset. The late occurrence of asymmetrical saccadic adaptation was also observed in the vertical saccades of subject R.S. (Fig. 5), who showed, alone among the three subjects, habitual, small changes in vertical vergence before adaptation. This habitual asymmetry persisted in the early stages of his adapted saccades, to be followed only later by the establishment of an asymmetry in the adaptive direction. From the time-courses of adapted, vertical and horizontal saccades, we conclude that asymmetrical adaptation starts from the onset of saccades, unless the adaptation has been preceded by saccadic adaptation with a different asymmetry or by an intrinsic inequality of the individual's binocular saccades. In the case of an already existing asymmetry of binocular saccades, the new adaptive process leaves the old asymmetry unchanged, and implements the saccadic adjustments required by the external conditions only at a later stage of the saccadic time-course. Thus, a clear difference between short-term and long-term adaptation is, that long-term adaptation cannot be easily overridden by a different, new, short-term adaptation. Whether this reflects different long- and short-term processes, or merely a difference in degree of imprinting, cannot be decided from our present evidence.

The characteristics of asymmetrical saccadic adaptation make it very difficult to believe that adaptation is achieved by resetting of gain parameters of the pulse- and step-generating mechanisms. It seems more likely that the adaptive mechanisms change the temporal form of the pulse and step signal into a signal with a pulse- and step-like time function, a time function which seems to become more complicated when subjects have a more tangled history with regard to intrinsic or learned saccadic asymmetries.

Key words: eye movements, binocular saccades, saccadic adaptation, asymmetrical adaptation, anisometropia

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