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# SHORT-TERM NONCONJUGATE ADAPTATION OF HUMAN SACCADES TO ANISOMETROPIC SPECTACLES

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**Abstract**—It has been demonstrated before that the long-term wearing of anisometropic spectacles may induce nonconjugate adaptations of saccades. Saccades then become different in size in the two eyes. We examined the time-course and the limits of such adaptations of horizontal and vertical saccades during the short-term (1–6 hr) wearing of anisometropic spectacles. After only 1 hr of conditioning to 2 D of anisometropia, the nonconjugate size-adaptations were almost complete along the horizontal meridian. For progressively larger anisometropias (up to 8 D) the adaptative nonconjugacies after 1 hr became also systematically larger. An anisometropia larger than 6 D did not further increase the rate of adaptation during the first 6 hr of conditioning, which suggests that about 6 D of difference in spectacle correction, causing size differences of about 12%, may be the upper limit of the nonconjugate adaptive range of the saccadic subsystem. Post-saccadic drift of horizontal saccades was also adequately changed. In addition, nonconjugate adaptations had developed in smooth-pursuit eye movements. All of these plastic changes persisted during monocular viewing, indicating that the basic programming of these eye movements was changed.

Hering's law Saccades Adaptation Aniseikonia Anisometropic spectacles Post-saccadic drift Smooth-pursuit

## INTRODUCTION

In the preceding paper (Lemij & Collewijn, 1991) we demonstrated nonconjugate adaptations of saccades, and also of smooth-pursuit eye movements, in habitual, long-term, wearers of anisometropic spectacles. These are spectacles with lenses that have different refractive powers, resulting in visual images that are differently sized for the two eyes. Nonconjugate adaptation was expressed as differences in magnitude between the movements of the two eyes, which adequately matched the differences in image-size. Movements of the eye provided with the larger image were larger than those of its fellow eye. Our results confirmed and extended an earlier report on such long-term adaptation by Erkelens, Collewijn and Steinman (1989).

Such adaptive nonconjugacies apparently violate Hering's law of equal innervation, if this law is interpreted, as usually, in the sense that movements are equally large for the two eyes. However, as we pointed out, the tenet of Hering's observation was that eye movements are so well coordinated that the two eyes are always aimed at the same object (Hering, 1868). Nonconjugate adaptation actually contributes to this coordination, instead of violating it. It restores the *functional* yoking of the eyes, thereby disrupting their *physical* yoking. We even postulated (Lemij & Collewijn, 1991) that the excellent yoking of the eyes, found under most normal circumstances, is also the result of adaptive pressure, calling for conjugacy as the most desirable baseline performance. In this view, Hering's law would represent the, flexible, endpoint of an adaptive process, rather than a rigid, inborn coupling.

In the present paper we shall examine the early stages of adaptation that take place within hours after the first-time wearing of anisometropic spectacles by normal, naive subjects. Erkelens *et al.* (1989) showed that nonconjugate adaptations of saccadic eye movements to 2 D of anisometropia already occur within about 8 hr. Results on short-term nonconjugate adaptations have been also communicated by Zee and Levi (1989) and, very recently, by Schor, Gleason and Horner (1990). We shall extend the previous study of our group (Erkelens *et al.*, 1989) by exploring the rate, as well as the limits, of such short-term adaptations. To that end, we systematically varied both the time of wearing of the spectacles (range: 1–6 hr) and their degree of anisometropia. Because an anisometropia of about 5 D is, as a clinical rule of thumb, considered as the upper limit of what may be tolerated, we adopted some anisometropias that were smaller, and also some that were larger than 5 D. To allow for a comparison between horizontal and vertical adaptations, we used spherical lenses, providing equal magnification factors in all meridians. As long-term nonconjugate adaptation has also been demonstrated in post-saccadic drift (Lemij & Collewijn, 1991), we studied, in addition, the effects of the short-term wearing of such lenses on the movements of the eyes shortly after saccadic offset. In addition, we examined short-term nonconjugate adaptations of smooth-pursuit eye movements. The present results have been reported before as part of a doctoral thesis (Lemij, 1990).

## METHODS

### *Subjects*

Three subjects took part in these experiments. They were between 25 and 28 yr old. None of them had any history of ocular or oculomotor pathology. These three subjects had refractive anomalies in both eyes that were, normally, corrected by rigid contact-lenses. With their own corrections, all subjects had visual acuities of 5/5 or better in either eye. Because functional binocular vision was regarded as essential for nonconjugate adaptation, all three subjects were tested on stereopsis (test charts: TNO tests for stereoscopic vision), which proved to be good in every one (stereoacuity: 60 sec arc or better).

### *Adaptation stimuli*

Subjects were fitted with spectacle-frames containing only one lens, in front of the right eye. This lens was spherical and its refractive power was $-2$, $-4$, $-6$ or $-8$ D. Different lenses caused a reduction in image size along any meridian of approx. 4, 8, 12 and 16%, respectively. Slight variations in magnification ($<1\%$) were present between subjects, probably due to differences in the distance between the spectacle lens and the nodal points of the eyes, as a result of differences in the shape of the face. In order to maintain the same, good visual acuity with every pair of spectacles, subjects replaced their own right-sided contact-lens by one that neutralized the refractive power of the spectacle-lens, and, in addition, corrected the subject's own refractive anomaly. The power of the contact lens was thus equal to the subjects habitual correction, summed with the opposite (positive) power of the (negative) spectacle lens. The overall effect of this spectacle-lens/contact-lens combination was as follows: the spectacle-lens reduced the size of the visual image for the right eye, whereas the contact-lens compensated for the blurring the spectacle-lens induced. A contact-lens causes only minimal image magnification (see Bennett & Francis, 1962), and does not call for any changes in the size of eye movements, because it moves along with the eye, and therefore does not affect the angular separation between visual targets subtended at the centre of rotation of the eye. The use of the spectacle-lens/contact-lens combination required that our subjects were already well habituated to the wearing of rigid contact-lenses. Therefore, the number of subjects was rather small. Soft contact-lenses could not be used, because they cannot be worn together with the sensor coils used to record the eye movements (see below). The actual magnification induced by each contact-lens/spectacle-lens combination was determined from monocular fixations of targets at known separations, executed with and without the spectacles.

Before the subjects ever wore the spectacles, baseline recordings were made, to document the initial state of conjugacy. On a later day, they started their first adaptation experiment by wearing the anisometropic spectacles with the smallest anisometropia (2 D) for 1 hr continuously. On separate days, the wearing-time of the same spectacles was gradually increased to 2, 4 or 6 hr at a stretch. To reduce any possible carrying over of long-lasting nonconjugate adaptations between successive sessions, the experimental days were interleaved by two or more resting days during which no adaptation was required. The same procedure was, thereafter, followed with other spectacles, increasing in anisometropia (4, 6 or 8 D). The complete set of adaptation experiments, consisting of 16 sessions on which spectacles were worn for a variable amount of time, was spread, for each subject, over a period of more than 2 months. The subjects went on with their normal daily activities while wearing the spectacles. To allow a direct comparison with the results of Erkelens *et al.* (1989), the three subjects were finally also fitted with one positive lens ($+2$ D) in front of the right eye for 6 hr continuously. This lens magnified the visual image along all meridians by approx. 4%.

### *Experimental procedures*

The same materials and methods were employed as described in detail in our preceding paper on long-term nonconjugate adaptation to anisometropic spectacles (Lemij & Collewijn, 1991). In short, the movements of both eyes were simultaneously recorded by means of magnetic sensor coils, developed by Collewijn, Van der Mark and Jansen (1975) in a Robinson's type magnetic field configuration (Robinson, 1963). The accuracy of the recordings was better than 1% and the noise level was less than 1.5 min arc.

After the completion of each adaptation-period, sensor coils were applied onto each of the eyes of the subject. To that end, the spectacles had to be taken off briefly. During this period one eye was kept covered at all times, to prevent any symmetrical visual input, that might interfere with the effects of the spectacle-wearing. Thereafter, the actual experiments were run. During the trials, the subjects wore the spectacles. The subjects were seated facing a white, toroid screen that provided no stimulus for disjunctive eye movements (see Lemij & Collewijn, 1991). Subjects made repetitive gaze-shifts between two, continuously present, bright-red He–Ne laser spots at a comfortable pace, indicated by a sound that beat steadily at a rate of 45/min. The subjects were asked to carry out the gaze-shifts as accurately as possible. The targets were positioned symmetrically about the straight-ahead position, 10 or 30 deg apart, either horizontally or vertically. At the beginning of each trial, the targets were displayed in their new position, and the subjects were allowed to practise if they wanted to. Actual data-collection lasted for 12 sec in each trial and was started by the subjects themselves when they felt ready for the task. Subjects were asked not to blink during data collection, to avoid the occurrence of associated eye movements (Collewijn, van der Steen & Steinman, 1985). Viewing was binocular, or monocular with either eye. The order of the trials was randomized for every subject. After completing the saccade trials, the subjects tracked a single target that followed a circular trajectory (dia: 30 deg) at constant velocity (11 deg/sec), both during binocular viewing and during monocular viewing with either eye.

All recordings were stored on disk. The equipment was pre-calibrated for an average sensor-coil. Recordings made of steady fixations of targets with known positions during monocular viewing with either eye, made without the spectacles, served to fine-tune the calibrations off-line, necessitated by possible off-center-positioning of the sensor coils on the eyes, as well as variations in sensitivity between coils. Target-positions and eye-positions were transformed off-line, by a special computer program, into Helmholtz's coordinates, as these coordinates could not be obtained directly. The equations we used to transform Fick's eye coordinates into Helmholtz's coordinates have been presented elsewhere (Collewijn & Erkelens, 1990).

### *Data analysis*

All recordings were analyzed by computer software, which computed saccade-size and mean post-saccadic drift-velocity of every saccade, according to standard criteria, as described before (Lemij & Collewijn, 1991). These results were then analyzed with a statistical software package (SPSS-X). The numbers of data were balanced for the four conditioning-periods, the four degrees of anisometropia, the two meridians, the two target amplitudes and the direction of the saccades. We then calculated the size-differences between paired saccades of the two eyes, as well as the vergence-deficits at saccadic offset. Vergence-deficit was defined as the difference between the required difference in saccade-size between the two eyes, as measured from monocular fixations, and the actual difference in size of binocular saccades. Mean values were calculated and the same data were also submitted to a multivariate analysis of variance (MANOVA). To meet the requirements of normal distributions and homogeneous variances, all parameters were logarithmically transformed.

## RESULTS

### *Saccadic size*

Nonconjugacy of saccades in the two eyes developed in all 3 subjects. It was already manifest after 1 hr of continuous wearing of any of the 4 different anisometropic spectacles, which varied in anisometropia between 2 and 8 D. The size-differences always developed in the direction required by the anisometropic spectacles. Therefore, we shall henceforth describe the nonconjugate changes as *adaptive*.

Differences in nonconjugate adaptations between subjects were very small. Therefore, only main trends will be discussed. The short-term adaptive nonconjugacies were manifest during binocular viewing, and also during monocular viewing. Figure 1 presents some typical recordings of horizontal saccades, before and after adaptation to 2 D of anisometropia during 1 hr, obtained with the right eye covered (i.e. the eye that was required to make the smaller eye movements). The right, covered eye, made, after conditioning, saccades that were about 1.5 deg smaller than those of the left, viewing eye. This shows that the adaptive change had become hard-programmed in as little as 1 hr of adaptation.

Both the duration of the wearing of the anisometropic spectacles and the degree of anisometropia affected the magnitude of the short-term nonconjugate adaptation of saccades. This magnitude varied, however, also with the target amplitude (10 or 30 deg), the viewing condition (binocular or monocular viewing) and the meridian (horizontal or vertical). In Fig. 2 we present mean values of the differences in saccadic size between the two eyes as a function of the wearing-time of the spectacles for every anisometropia tested. As mean values, averaged for the two target amplitudes, the three viewing conditions and the two meridians would not be very meaningful, the data of Fig. 2 relate only to horizontal saccades, made between targets that were positioned 30 deg apart, while viewing was binocular. During monocular viewing, and also at the smaller target amplitude (10 deg), the nonconjugate size-changes of horizontal saccades differed only quantitatively, but not qualitatively from these results. Figure 2 shows that the saccadic size-differences between the two eyes increased with the anisometropia of the spectacles ($F_{3,6} = 8.90$; $P < 0.05$). Above 6 D of anisometropia, however, the rise was not significant ($P > 0.9$), which suggests that a ceiling in the sensitivity to aniseikonia or in the rate of nonconjugate adaptation had been reached. The lack of statistical significance between 6 and 8 D of anisometropia may also be due to the larger variability in interocular size-differences of horizontal

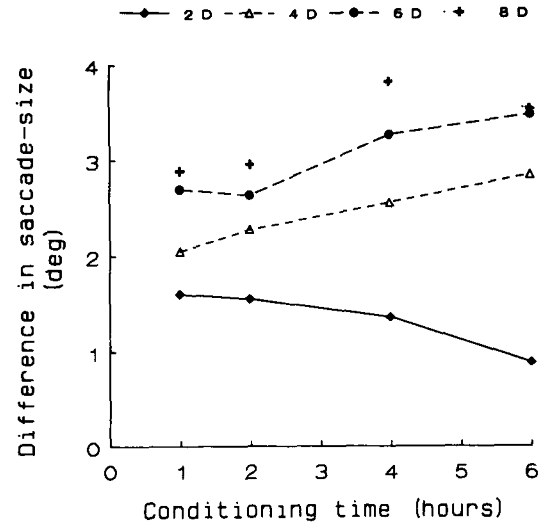

Fig. 2. Mean differences in saccadic size between the two eyes, plotted as a function of the conditioning-time, for the four degrees of anisometropia. These data relate to horizontal saccades made during binocular viewing at a target amplitude of 30 deg. Before conditioning, the mean difference in saccadic size between the two eyes (binocular viewing; target amplitude: 30 deg) was 0.06 deg (SD: 0.45 deg). For clarity, the standard deviations have been left out of the graph; standard deviations varied, for 2 and 4 D anisometropias between 0.44 and 0.70 deg, and for 6 and 8 D anisometropias between 0.80 and 1.22 deg.

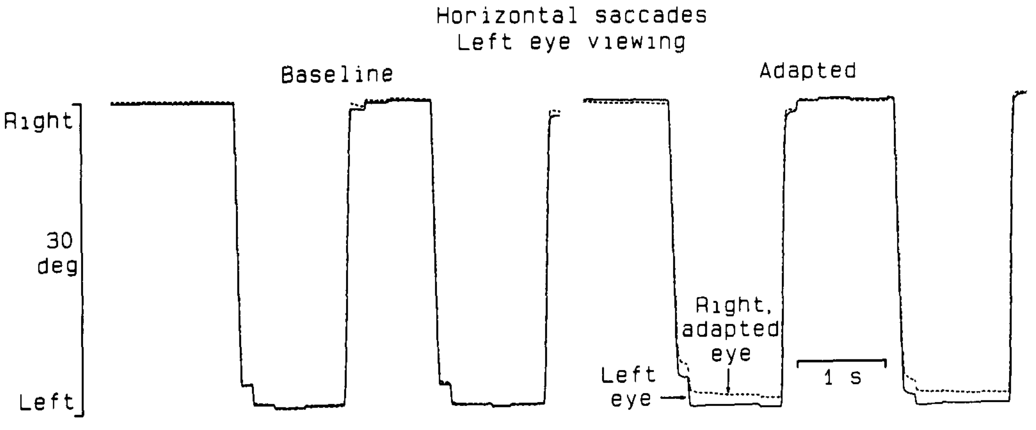

Fig. 1. Typical recordings of horizontal saccades of each eye made with the left eye viewing. The left panel shows baseline recordings, and the right panel shows recordings made after 1 hr of adaptation to 2 D of anisometropia. Target amplitude: 30 deg.

saccades at these anisometropias (SD between 0.8 and 1.22 deg; binocular viewing, nominal target amplitude: 30 deg) than at anisometropias of 2 and 4 D (SD between 0.44 and 0.70 deg; binocular viewing, same target amplitude). After only 1 hr of adaptation, saccades of the two eyes differed in size by about 1.6 deg for the smallest anisometropia (2 D) and by about 2.8 deg for the two largest anisometropias (6 and 8 D). With prolonged wearing of the spectacles, the differences in saccadic size between the two eyes generally increased. This increase occurred, in comparison to the first hour of adaptation, rather slowly. It averaged about 0.7 deg over 5 hr ($F_{3,6} = 7.56$; $P < 0.05$). However, with the smallest anisometropia (2 D), the difference in magnitude between saccades of the two eyes, did not increase as a function of wearing-time. On the contrary, this difference was gradually reduced by about 0.7 deg, to become approx. 0.9 deg after 6 hr of adaptation ($F_{9,18} = 4.37$; $P < 0.005$).

To examine the efficacy of these short-term adaptations, we have plotted the mean vergence-deficits at saccadic offset as a function of the conditioning-time for the various anisometropias in Fig. 3. These data relate to the same, horizontal saccades as shown in Fig. 2 (30 deg saccades, binocular viewing). Vergence-deficits went up with larger anisometropias ($F_{3,6} = 97.2$; $P < 0.0005$). At the smallest anisometropia (2 D), they were, on average, only about 0.1 deg. With the largest anisometropia (8 D) vergence-deficits were much larger: about 2.5 deg after 1 hr of adaptation (for horizontal, 30 deg saccades during binocular viewing). By comparing Figs 2 and 3, one can conclude that, in spite of the fact that the difference in saccadic size between the two eyes generally increased with the anisometropia, these nonconjugate adaptations also fell increasingly short at larger anisometropias. As a consequence, the average degree of nonconjugate adaptation of horizontal saccades made during binocular viewing decreased from about 90% of the amount required by the spectacles for 2 D anisometropia to about 60% for 8 D anisometropia.

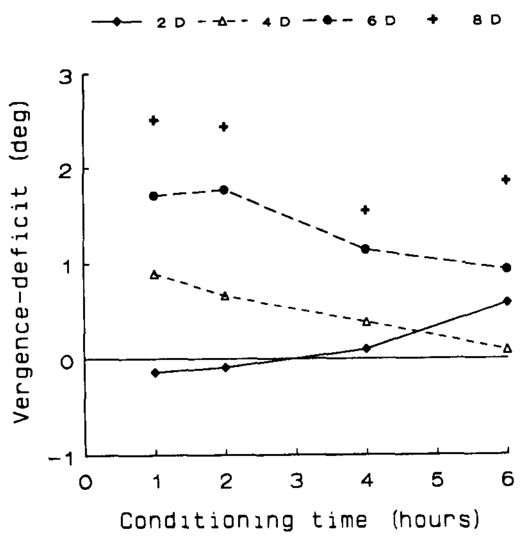

Fig. 3. Mean vergence-deficits plotted as a function of the conditioning time. These data relate to the same saccades as in Fig. 2. Standard deviations were identical to those in Fig. 2.

With 4 D of anisometropia, adaptation of horizontal saccades (binocular viewing) was almost completed to the ideal amount as required by the spectacles after only 6 hr of adaptation (Fig. 3). With 6 D of anisometropia, the nonconjugate adaptation occurred at about the same rate as with 4 D of anisometropia, but it was still not complete after 6 hr. As this duration of adaptation is fairly short, the nonconjugate adaptation to 6 D of anisometropia would presumably have improved with prolonged wearing of the glasses. It is not clear what the time-course of adaptation beyond 6 hr of conditioning to 8 D of anisometropia would be like, because all 3 subjects were better adapted after 4 hr than after 6 hr of adaptation. As was already pointed out in relation to Fig. 2, the magnitude of nonconjugate adaptation, surprisingly, went down with prolonged wearing of 2 D anisometropic spectacles. This decline in adaptational nonconjugacy of horizontal saccades occurred in all 3 subjects.

For vertical saccades, differential changes in size were two- to four-fold smaller than for horizontal saccades ($F_{1,2} = 46.7$; $P < 0.05$). To quantify the vertical adaptations, we have plotted in Fig. 4 the mean differences in saccadic size between the two eyes for vertical saccades, as a function of the spectacle wearing-time for the four various anisometropias. Like Fig. 2, Fig. 4 relates to binocular viewing and a 30 deg target amplitude. Changes in the yoking of vertical saccades averaged only about 0.5 deg after 1 hr of adaptation. Unlike with horizontal saccades, these changes did not increase with the anisometropia. With continued conditioning, however, the differences in size between saccades of the two eyes became slightly larger and amounted to about 1.0 deg in 5 additional hours. This increase by about 0.5 deg was about as large as with horizontal adaptations. This

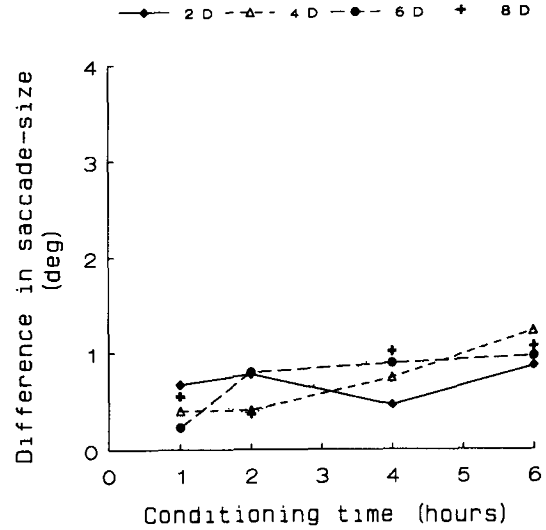

Fig. 4. Mean differences in size between vertical saccades of the two eyes, plotted as in Fig. 2. Viewing was binocular and the target amplitude equalled 30 deg. Before adaptation, the difference in saccadic size between the two eyes averaged 0.09 deg (SD: 0.28 deg). Standard deviations have, again, been left out of the graph for clarity. Standard deviations varied, for all anisometropias, between 0.25 and 0.47 deg.

adaptive increase in nonconjugacy occurred also with the 2 D anisometropia, in contrast to the decline in nonconjugacy that was observed in horizontal saccades. As a result of the poorer adaptation of vertical saccades, compared to that of horizontal saccades, the vergence-deficits at saccadic offset of vertical saccades were relatively large. On average, they were about 2.5 deg larger than with horizontal saccades, and sometimes as large as 5 deg. Another contrast with horizontal, nonconjugately adapted saccades, was that, along the vertical meridian, the adaptational differences in saccadic size between the two eyes were similarly variable across all four anisometropias (SD approx. 0.3 deg; binocular viewing, nominal target amplitude: 30 deg).

Although we did not systematically examine fusion, all 3 subjects frequently experienced vertical diplopia, which increased as a function of the degree of anisometropia, notably in the upper oculomotor field. With anisometropias of 4 D and less, fusion was usually complete after 6 hr of conditioning in all eye-positions.

Virtually the same trends as described above existed, for each meridian and for each subject, during monocular viewing, and also for the smaller target amplitude of 10 deg. However, the magnitudes of these adaptational changes were significantly different. Figure 5 presents mean differences in saccadic size between the two eyes for the two various target amplitudes after 6 hr of conditioning. We have

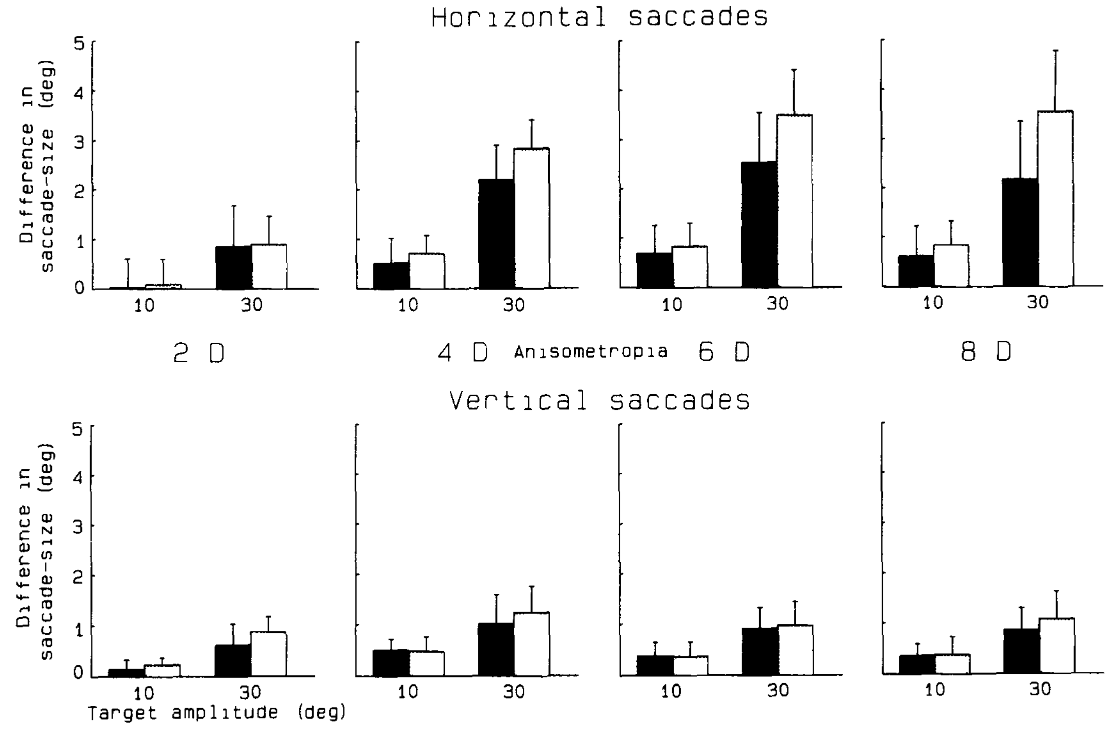

Fig. 5. Mean differences in saccadic size between the two eyes (+SD) for horizontal and vertical saccades after 6 hr of conditioning. Distinctions are made for the two target amplitudes, the two viewing conditions (left eye viewing and right eye viewing pooled) and the four degrees of anisometropia. Solid bars relate to monocular viewing, open bars to binocular viewing.

also distinguished between the four degrees of anisometropia, the two meridians and the viewing conditions (i.e. binocular viewing or monocular viewing viewing with either eye). Figure 5 shows that, during binocular viewing, the differences in saccadic size between the two eyes were generally larger than during monocular viewing ($F_{2,4} = 14.8$; $P < 0.05$). Furthermore, this effect of the viewing condition was larger for horizontal saccades than for vertical saccades ($F_{2,4} = 7.18$; $P < 0.05$). For horizontal saccades, made at a target amplitude of 30 deg, the viewing condition affected the yoking of saccades by as much as about 0.8 deg, as opposed to about 0.2 deg for vertical saccades. However, with 2 D of anisometropia the difference in size between horizontal saccades of the two eyes was, after 6 hr of adaptation, equally large in either viewing condition. In fact, the gradual decrease in saccadic nonconjugacy with prolonged adaptation to 2 D of anisometropia, following an initially large nonconjugacy after 1 hr of conditioning (Figs 2 and 3) was also present in monocular viewing. It is also clear from Fig. 5 that the difference in saccadic size between the two eyes was, not surprisingly, larger at the larger target amplitude than at the smaller target amplitude ($F_{1,2} = 126.1$; $P < 0.01$). This increase was four- to five-fold for horizontal saccades and about two-fold for vertical saccades. Compared with the exactly three-fold increase that was required by the spectacles, it is clear that the degree of adaptation was not a fixed percentage of these requirements.

The present results showed that short-term nonconjugate adaptation of vertical saccades was less complete than for horizontal saccades, which contrasted with the results of Erkelens *et al.* (1989), who found that such adaptation was either equally complete in the two meridians or more complete for vertical saccades than for horizontal saccades. One difference between that study and the present one was that Erkelens *et al.* (1989) used a positive (+2 D) spectacle-lens, instead of the negative lenses we used. Therefore, we repeated the experiment by Erkelens *et al.* by having our subjects also wear, for 6 continuous hours, a positive, spherical (+2 D) lens in front of the right eye. With the exception that eye movements of the right eye were now larger than those of the left eye, there was no significant difference in nonconjugate adaptation, compared to when the subjects had worn −2 D for 6 continuous hours.

### *Post-saccadic drift*

Post-saccadic drift was also differentially adapted for either eye ($P < 0.05$). When the right eye, i.e. the eye provided with the negative spectacle lenses, made abducting, rightward saccades, backward post-saccadic drift ensued which increased in velocity with the degree of anisometropia (Fig. 6). As an example, baseline mean velocities of this backward drift were about 0.1 deg/sec, whereas they became as high as about 2 deg/sec with 8 D of anisometropia. The concomitant, adducting saccades of the fellow eye also showed increasingly higher post-saccadic drift-velocities at larger anisometropias. These velocities could become as high as about 2.1 deg/sec (baseline: 0.6 deg/sec). However, this drift was directed onward, as opposed to the backward post-saccadic drift of the right eye. Therefore,

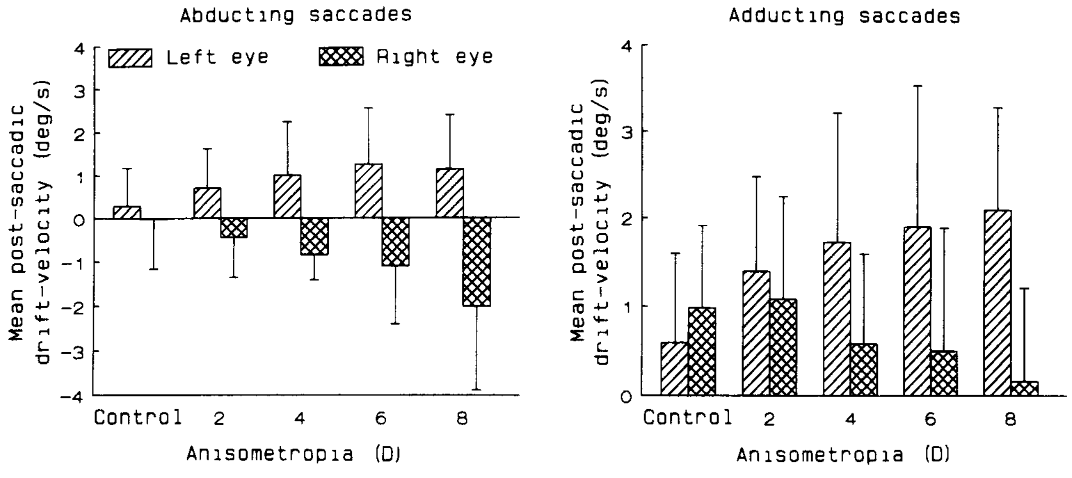

Fig. 6. Mean post-saccadic drift-velocities (+SD) of abducting saccades (left panel) and adducting saccades (right panel) for the various degrees of anisometropia. Positive drift-values onward drift; negative drift-values indicate backward drift.

the asymmetrically adapted post-saccadic drift for these, rightward, saccades, reduced the vergence-deficits existing at saccadic offset. Likewise, post-saccadic drift of leftward saccades was also asymmetrically adapted, with the same effect of reducing the vergence-deficits (Fig. 6). These results confirm similar findings by Erkelens *et al.* (1989). The reduction of the vergence-deficit by post-saccadic drift might suggest that the drift was merely a fusional vergence eye movement. Importantly, however, post-saccadic drift velocity during binocular viewing was not significantly different from when viewing was monocular. This argues strongly against a mere vergence-movement, because the strongest stimulus for vergence, disparity (Erkelens & Regan, 1986) is evidently absent during monocular viewing. There was no significant effect whatsoever of the conditioning-time on post-saccadic drift-velocities. The post-saccadic drift-velocities were slightly higher at the larger target amplitude, than at the smaller one, which confirms similar findings by Kapoula, Robinson and Hain (1986). More importantly in the present context, the target amplitude did not significantly affect the asymmetrical adaptation of the post saccadic drift-velocities. Post-saccadic drift of vertical saccades was not affected by the short-term wearing of anisometropic spectacles.

### *Smooth-pursuit*

Similarly to the saccades, smooth-pursuit eye movements became unequally large in the two eyes after adaptation to the anisometropic spectacles. These differences persisted during monocular viewing, but they were larger during binocular viewing. As with saccades, the adaptations were more complete along the horizontal meridian than along the vertical one. All these effects are illustrated in Fig. 7, which displays typical recordings under various conditions. Nonconjugacy generally became larger with increasing anisometropia, although this increase appeared to have reached its maximum at an anisometropia of 6 D. Prolonged wearing of the spectacles only slightly affected the difference in size between the movements of the two eyes. Along the horizontal meridian, the largest increase in adaptive nonconjugacy was achieved within 1 hr of adaptation, just as for saccades.

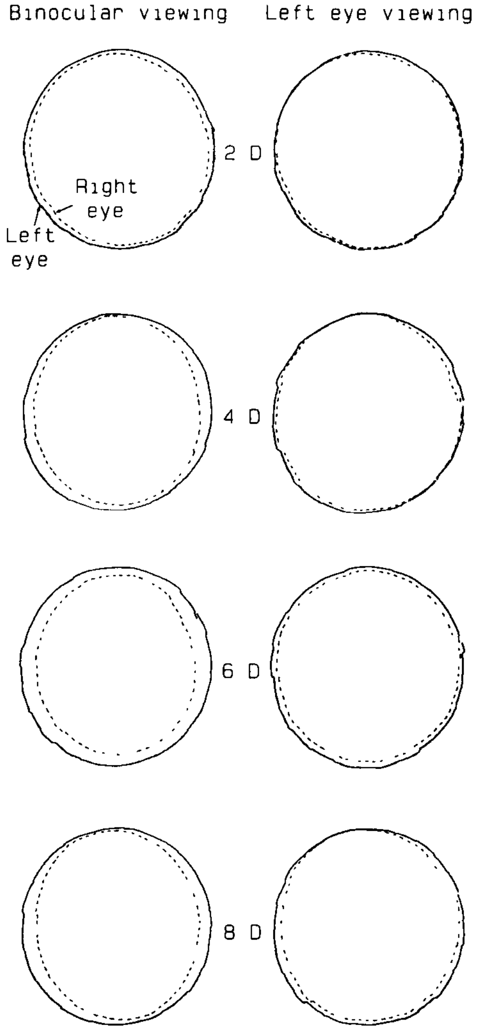

Fig. 7. Typical recordings of both eyes made during the smooth-pursuit task after 6 hr of adaptation to the four various degrees of anisometropia. The recordings displayed in the left panels were made during binocular viewing; the right panels relate to monocular viewing with the left eye.

### *Perception*

A remarkable subjective phenomenon occurred in every subject. After wearing the anisometropic glasses for several hours, all subjects reported that the visual world became distorted in such a way that all objects on the right side of the visual field appeared smaller, and at the same time, closer by. We did not quantify this illusion in any sense, because it was beyond the scope of our oculomotor experiments. The same illusion, associated with anisometropic spectacles, was also described and partly explained by Ogle (1962).

When the subjects took off their spectacles, after completion of the measurements, they occasionally observed double-images, notably during downward or upward gaze. These effects were transient and usually disappeared within about 3 min of normal binocular viewing. All subjects were under the impression that it took more time to adapt to the spectacles, than to readapt back to normal. No recordings of eye movements were made during readaptation to sustain this subjective impression with objective recordings.

## DISCUSSION

The present experiments demonstrate that saccades, and also smooth-pursuit eye movements, may undergo nonconjugate adaptation to anisometropic spectacles in a very short period of time. Large nonconjugacies occurred in as little as 1 hr. The remarkable speed and magnitude of these very short-term adaptations suggest that the oculomotor system may normally also adapt rapidly and to an adequate extent to changes that take place as a result of growth, ageing, disease or fatigue. This flexibility of the oculomotor system, which presumably applies somewhat similarly to other sensori-motor control systems, suggests that many such changes remain concealed.

A remarkable feature of horizontal short-term adaptations was, that the largest change in adaptive nonconjugacies had developed within only 1 hr of conditioning. Thereafter, adaptations continued relatively slowly. Time-courses of adaptational changes of the saccadic subsystem have been reported earlier. Abel, Schmidt, Dell'Osso and Daroff (1978) closely followed the adaptational changes in saccade-size in a patient who had suddenly developed a unilateral medial rectus paresis. By covering the normal eye for about 1 week, they observed that the saccades of the paretic eye gradually became larger in the appropriate direction. The largest change occurred during the first day. On the days that followed, adaptive changes were considerably smaller. They fitted an exponential curve to the time-course of these adaptive changes, with a time constant of 0.85 days. Deubel, Wolf and Hauske (1986), and Deubel (1987) let subjects, and also monkeys, track a target that jumped. During the execution of the saccade, the target made a smaller, second jump, either consistently in the same direction, or, on different occasions, consistently in the opposite direction as the first step. They observed that the size of the primary saccades adapted adequately (i.e. became larger or smaller, depending on whether intra-saccadic target-displacements had been onward or backward, respectively) in as little as a few hundred trials. Again, the rate of these adaptations roughly followed an exponential time-course, being fastest at the beginning of the experiments. Similar results were obtained by Albano and King (1989).

Although the experiments of Abel *et al.* (1978), Deubel *et al.* (1986), Deubel (1987) and Albano and King (1989) related only to symmetrical adaptations of saccades, our present results suggest that somewhat similar time-courses apply to nonconjugate adaptations, in the sense that they also appear to occur most rapidly at the beginning of the adaptive stimulus, and more gradually after prolonged stimulation. The rate of nonconjugate adaptation during the first hour of conditioning remains unclear. To elucidate this point, saccades would have to be recorded from the moment that nonconjugate adaptive changes were called for. Viirre, Cadera and Vilis (1988) also demonstrated that large, nonconjugate adaptations may occur very rapidly. They surgically weakened one horizontal rectus muscle of one eye in monkeys, and left the operated eye patched for one week. Thereafter, the patch was removed, so that vision was restored. The surgically induced unilateral saccadic dysmetria then largely disappeared within a few hours.

The present experiments show that the rate and the degree of these short-term adaptations are not necessarily uniform for every meridian. In our subjects, the most predominant adaptive changes occurred along the horizontal meridian. In contrast with the horizontal nonconjugate adaptations, which reached a substantial magnitude in only 1 hr of conditioning, thereby displaying the somewhat exponential time-course mentioned above, vertical nonconjugate adaptations were comparatively small, despite equally large pressures for such adaptation along either meridian. Due to the variability of our data it remains inconclusive whether the vertical adaptations also followed pseudo-exponential time-courses. Insight into the various time-courses could possibly provide helpful information in solving the question whether adaptations along either meridian were fundamentally different or not. The investigations of short-term nonconjugate adaptations by Erkelens *et al.* (1989) showed larger changes along the vertical meridian than along the horizontal one. We ruled out the possibility that this discrepancy could be due to the different kind of spectacle-lens they used. Therefore, it is most likely that idiosyncrasies underly the different outcomes of these two studies. The nonconjugate short-term adaptability of vertical saccades is further strongly supported by the recent study by Schor *et al.* (1990), who used a regimen in which subjects had to make almost exclusively vertical saccades for a period of 2 hr. Significant nonconjugate adaptation of vertical saccades (persisting during monocular viewing) was obtained under those conditions. It is conceivable that our subjects made more horizontal than vertical saccades in their free behaviour, with better adaptation of horizontal saccades as a result.

Both the present study and that by Erkelens *et al.* (1989) also suggest that the adaptations along either meridian may take place independently from each other. If such independence were indeed present, then it might be possible to achieve nonconjugate adaptation along one meridian only, without any change along the orthogonal meridian, provided an adequate stimulus were present. Experiments which demonstrate such meridian-specific adaptations will be reported on in detail in a next paper (Lemij & Collewijn, in preparation; for a preliminary communication, see Lemij & Collewijn, 1989, and Lemij, 1990).

We found that the amount of short-term nonconjugate adaptation of saccades, along either the horizontal or the vertical meridian, was not a fixed percentage of what was called for by the spectacles at the various target amplitudes. This result agrees closely with our previous results on long-term nonconjugate adaptations to anisometropic spectacles, although such a fixed, parametric adjustment has been put forward as a general control-strategy for adaptive changes within the saccadic subsystem (Deubel *et al.*, 1986). Our present results strengthen our previous contention that nonconjugate adaptation presumably takes place on a point-to-point basis of sensori-motor coordinates, rather than through a simple resetting of a few gain parameters, as suggested by Deubel *et al.* (1986). For a more detailed discussion on this issue, see Lemij and Collewijn (1991).

Our study also provides some evidence on the limits of short-term nonconjugate adaptation of the saccadic subsystem. In our experiments, the adaptations to 8 D of anisometropia were not significantly different from the adaptations to 6 D of anisometropia. We do not know if prolonged wearing of the 8 D anisometropic spectacles would eventually have yielded larger nonconjugates in saccadic size between the two eyes than with equally long adaptation to 6 D of anisometropia. Our results comply, however, with the clinical rule of thumb that anisometropias larger than about 5 D are poorly tolerated. However, this poor tolerance does not necessarily have to be caused by limitations of the oculomotor system, but may also be due to limitations in sensory fusion, which may be exceeded by the aniseikonia. Other examples of limited adaptations of the oculomotor system, frequently secondary to disease, are well-known in clinical practice (Leigh & Zee, 1983).

In the present study, we examined the adaptive behaviour of eye movements to a visual stimulus. We confined our study to the eye movements themselves, i.e. to the output-level of adaptation, without regard to other, earlier levels. However, during conditioning, adaptive changes also appear to take place at an input-level. We observed that, with 2 D of anisometropia, differences in saccadic size between the two eyes, after an initial rise following 1 hr of spectacle-wearing, went down with prolonged wearing in all subjects (for horizontal saccades). This suggests that the sensitivity for the stimulus that drives nonconjugate adaptation decreased gradually with time. With larger anisometropias, we did not observe any reduction of the nonconjugacy that had first developed. Because nonconjugate adaptations were, however, far from complete with these larger anisometropias, as opposed to the almost perfect adaptation that had been achieved in 1 hr with the 2 D anisometropia, it appears that such reduction in sensitivity may only occur when a critical, high degree of nonconjugate motor-adaptation has been reached. Possibly, this fall in the sensitivity to the stimulus that drives nonconjugate adaptation, is parallelled by adaptive changes at a sensory level, i.e. at a level where the two foveal images are fused. Although such adaptive changes at a sensory level are somewhat speculative, they would explain why many habitual spectacle-wearers in our previous experiments (Lemij & Collewijn, 1991) were also only partly adapted.

We also observed short-term nonconjugate adaptations of post-saccadic drift, which confirm and extend somewhat similar findings by Erkelens *et al.* (1989). Asymmetrical adaptations of post-saccadic drift, secondary to unilateral tenectomies of external eye-muscles have also been reported in monkey (Snow, Hore & Vilis, 1985). Post-saccadic drift of smaller saccades usually has a slightly lower mean-velocity than the drift that follows larger saccades (Kapoula *et al.*, 1986). Therefore, nonconjugate post-saccadic drift could, in principle, merely be an epiphenomenon of the smaller saccades, that are made unilaterally after nonconjugate adaptation to anisometropic spectacles. In that case, the change in yoking would be characterized by a small reduction in mean drift-velocities only in the eye that made the smaller saccades. Because we observed that post-saccadic drift had not simply become slower in the eye that made the smaller saccades, but, instead had changed in the direction appropriate for further reduction of residual vergence-deficits after saccadic offset, we conclude that the change in yoking of the two eyes during post-saccadic drift was truly adaptive, and not just an epiphenomenon. It is known that, in monkey, post-saccadic drift may adapt independently of saccades (Optican & Miles, 1985). These results suggest that adaptive motor-changes occur at various levels.

Smooth-pursuit eye movements also developed nonconjugacy in a short period of time. In fact, they closely followed the nonconjugate adaptations of saccades. This brings up the question whether these two very different kinds of versional eye movements, and possibly also other eye movements, are controlled, as far as the yoking of the eyes is concerned, by the same pre-motor circuits. The present results provide no evidence on this question, because our subjects carried out their normal daily activities during the conditioning periods, and therefore received plenty of adaptational stimuli for either type of eye movement. Only by stimulating selectively one of the two kinds of eye-movements during the adaptation-period can it be found out whether these two oculomotor subsystems share a set of pre-motor circuits that control the yoking of the two eyes. The recently published experiments by Schor *et al.* (1990) addressed this problem specifically by using dichoptic, disjunctive training stimuli that elicited preferentially either saccades or smooth pursuit. Their results show that selective nonconjugate adaptation of either saccades or pursuit can indeed be obtained.

The present results confirm those of Horner, Gleason and Schor (1988) and Schor *et al.* (1990), who found nonconjugate vertical smooth-pursuit eye movements after 2 hr of adaptation to aniseikonia. Optician, Zee and Chu (1985) studied smooth-pursuit eye movements in patients with unilateral eye-muscle palsies. However, they confined their observations to the adaptive processes that occurred after the patching of one eye. As far as other eye movements are concerned, nonconjugate adaptations of the vestibulo-ocular reflex have been reported in monkey after external eye-muscles had been unilaterally severed (Snow *et al.*, 1985; Viirre *et al.*, 1988). There is some evidence that, in man, nonconjugate adaptation of the vestibulo-ocular reflex may develop to aniseikonia within 24 hr (Collewijn, Martins & Steinman, 1983; Schor, Gleason & Horner, 1988). However, Collewijn *et al.* (1983) concluded that this nonconjugate adaptation was very hard or sometimes even impossible. In their experiments, they supplied their subjects' eyes with a negative, spherical (−5 D) lens on one side and a spherical lens of opposite power (+5 D) on the other side. If subjects already had any refractive anomalies, these corrections were added to their own spectacle-corrections. Importantly, no contact-lens was provided to compensate for the induced blurring. This blurring may possibly explain why nonconjugate adaptation of the vestibulo-ocular reflex was so difficult to bring about. Another possible explanation for a poor nonconjugate adaptation of the vestibulo-ocular reflex in their experiments might be that the aniseikonia was too large, and beyond the adaptive range of vestibulo-oculomotor system.

In conclusion, the oculomotor system appears to be highly capable of adapting its metrics adequately to various stimulus arrangements requiring nonconjugacy for coordinated binocular scanning or pursuit in a very short period of time. This may help maintain is proper functioning throughout a lifetime, in spite of the wear and tear imposed by growth, ageing, disease or injury. There are certain limits to these adaptations; in case of anisometropic spectacles nonconjugate adaptation of saccades and smooth-pursuit eye movements may still take place rapidly to anisometropias of about 8 D, but these adaptations are, after 6 hr of conditioning, far from complete.

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