Unequal Amplitude Saccades Produced by Aniseikonic Patterns: Effects of Viewing Distance

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This study describes differences in horizontal and vertical disconjugate saccades under far and close viewing conditions of two dichoptically presented aniseikonic random checkerboard patterns. At far viewing, disconjugacy of horizontal saccades requiring divergence was accomplished intrasaccadically after several minutes; for convergence the intrasaccadic disconjugacy was limited. Size differences partially persisted in open-loop trials. At close viewing intrasaccadic divergent changes in conjugacy were instantaneous, but motor storage during open-loop was absent. It is concluded that disconjugate saccades to targets at far distance lead to an adaptation process, whereas at close viewing distance horizontal disparity is a visual compensation process used directly to scale the relative amplitudes of both eyes, not leading to adaptation. The time–course of disconjugate vertical saccades was much slower, with mostly postsaccadic vergence. Nearby viewing enhanced the disconjugacy of vertical saccades.

Saccades   Adaptation   Aniseikonia   Vergence   Human

INTRODUCTION

Humans and other foveate species use saccades to bring the line of sight from one object of interest to another. With the development of a fovea parallelled by frontal eyed vision enabling stereoscopic depth perception, it is imperative that the amplitudes of the saccadic movements of both eyes are precisely matched in order to bring the retinal projections of an object of interest upon the foveas of both eyes. When the objects of interest are at optical infinity, saccades are essentially conjugate, with the exception of a small transient divergence during the saccade (Collewijn, Erkelens & Steinman, 1988a; Zee, Fitzgibbon & Optican, 1992). However, when we change fixation between objects at different directions and distances, as we frequently do under natural circumstances, saccades become disconjugate which allows to accomplish most of the required vergence during the saccade (Erkelens, Steinman & Collewijn, 1989b; Maxwell & King, 1992).

There are a number of other, albeit less common, situations where disjunctive saccades have to be made. Subjects with anisometropia, provided with different

spectacle correction for the two eyes, see two images of differing size (aniseikonia). A number of investigators (Erkelens, Collewijn & Steinman, 1989a; Oohira, Zee & Guyton, 1991; Lemij & Collewijn, 1991a,b) have found that subjects fitted with anisometropic spectacle lenses make saccades that differ in size corresponding to the demand of the different magnification of the spectacle lenses [2–3% per dioptre (Rubin, 1974)]. Under these circumstances a process of motor learning or adaptation takes place, which can be demonstrated by the fact that under monocular viewing the saccades in the two eyes are still disconjugate (Lemij & Collewijn, 1991a,b, 1992). Presumably because this motor learning has implicitly been attributed to a long-term adaptative process, most studies have been concerned with changes in the conjugacy of saccades measured after wearing anisometropic spectacles for at least 1 hr.

Recently, we studied the earliest stages of induced aniseikonia. In a series of experiments (van der Steen, 1992, 1993) we used dichoptically presented, aniseikonic checkerboard patterns backprojected on a translucent screen 122 cm in front of the subject. The images were separated by red–green filters. The images were identical except that one was compressed by 8% (corresponding to approx. 3 D difference in spectacle correction). Subjects were instructed to make saccades symmetrically across the midline paced by a metronome (one saccade every 2 sec). With this stimulus arrangement, horizontal saccades of the two eyes became disconjugate within

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5–7 min. The differences in saccadic metrics persisted during open-loop testing immediately after the adaptation period, suggesting that a very fast motor learning process had taken place. Similar results were obtained by Eggert and Kapoula (1992) using polarizing filters. In another series of experiments (Bush, van der Steen & Miles, 1994), the same paradigm was used in both monkeys and humans. In this experiment the patterns were dichoptically presented with a stimulus arrangement of orthogonal polarizing filters back-projecting the overlapping images on a screen placed in front of the subjects at a distance of 33 cm. With these experimental conditions, both humans and monkeys immediately made saccades of unequal amplitude without any prior period of adaptation. In addition, when the subjects were tested during monocular viewing the disconjugacy was lost immediately, disclaiming any form of motor learning. Because viewing distance was one of the differences between the two experimental arrangements, we investigated the effects of this factor on the ability to make disconjugate saccades. In this paper we will show that tonic vergence angle, which is inversily related to viewing distance, influences the dynamics and motor learning of binocular disconjugate saccades.

We also studied the disconjugacy of vertical saccades and the effects of viewing distance. Vertical saccades are known to be well yoked, with little transient vergence during the saccade (Collewijn, Erkelens & Steinman, 1988b). Several groups studied disconjugate vertical adaptations. Such adaptations can be completed only after several hours of stimulation (Henson & Dharamshi, 1982; Erkelens *et al.*, 1989a; Schor, Gleason & Horner, 1990; Lemij & Collewijn, 1991a). During short-term adaptation, Lemij and Collewijn (1991b) reported a slower and less complete adaptation for vertical saccades than for horizontal saccades after 1 hr of adaptation. In this paper we present the earliest effects of exposure to vertical aniseikonia on the yoking of vertical saccades.

METHODS

Subjects

Six subjects participated in the experiments. None of them had a history of ocular or oculomotor pathology. Visual acuities were 6/6 for either eye and all subjects had good stereopsis (60 sec arc or better tested with the TNO test for stereoscopic vision).

Stimulus presentation

The subjects faced a tangent screen placed at one of three possible distances (144, 55 and 37 cm). Because mostly we compared the results at 144 cm with the results at 37 cm, these two distances are referred to as far distance and close distance respectively. Two superimposed images (horizontal and vertical dimensions 65 deg) generated by a graphical workstation with stereoscopic capabilities (Silicon Graphics, Iris 4D/210GTXB) were backprojected on this screen via a video projection system

(Sony, Tokyo) connected to the workstation. The left and right eye views were alternatingly displayed in rapid succession (each view with half of the refresh rate of the monitor, which was 120 Hz). The resolution of the monitor when operating in stereoscopic mode was 1024 pixels horizontally × 492 pixels in vertical direction (effectively this was half of the vertical resolution in the normal mode). With an eyewear consisting of liquid crystal shutters for each eye that were switched in exact synchronization with the images as they were displayed on the screen, each eye saw only the image intended for it.

Three different kind of stimuli were provided with this arrangement [see Fig. 1(A)]. The first was used for the calibration of the coil signals (top), the second was a random checkerboard pattern (elements on average 1 deg, bottom), and the third consisted of two single horizontally-oriented overlapping lines, one presented to each eye (centre). Only one of the lines had vertical crossmarks (2 deg) located at 10 deg symmetrically from the centre. Thus, along the orientation of the line, vergence operated in open-loop mode because the eye seeing the line with the crossmarks was driving the other eye.

Eye movement recordings and calibration

Binocular saccadic eye movements were recorded using scleral search coils (Skalar, Delft). Horizontal and vertical eye movements were sampled at a rate of 500 samples/sec with 12-bit precision by an external intelligent data-acquisition system (CED 1402, Cambridge Electronic Design, Cambridge) connected to a PC. Prior to digitization, the signals were fed through a low-pass analogue filter with a cut-off frequency of 100 Hz. The overall noise level was less than 1.5 min arc.

Calibration procedure

Calibration procedure consisted of an approximate calibration of the coils before the experiment, whereas during the experiment calibration trials were included before and after the adaptation paradigm. In these trials, subjects had to fixate targets located at 0, 5, 10 and 15 deg along the horizontal and vertical meridian [see Fig. 1(A)]. These calibration trials were used to correct the coil signals off-line with the following procedure. First, the exact position of the fixation points with regard to each eye were calculated based upon their positions on the screen, the centre position of the screen relative to the subject's head and the interocular distance. A computed set of theoretical fixations for each eye was compared with the actual eye movement readings during fixation of each of the points. Then, taking into account the non-linear relation between eye rotations and output voltage of the coils we corrected the offsets and gain for each eye channel.

Experimental procedures and data analysis

The subjects were seated in the experimental setup with the head restrained by a chin rest and a head support. After insertion of the coils and fitting of the stereoscopic
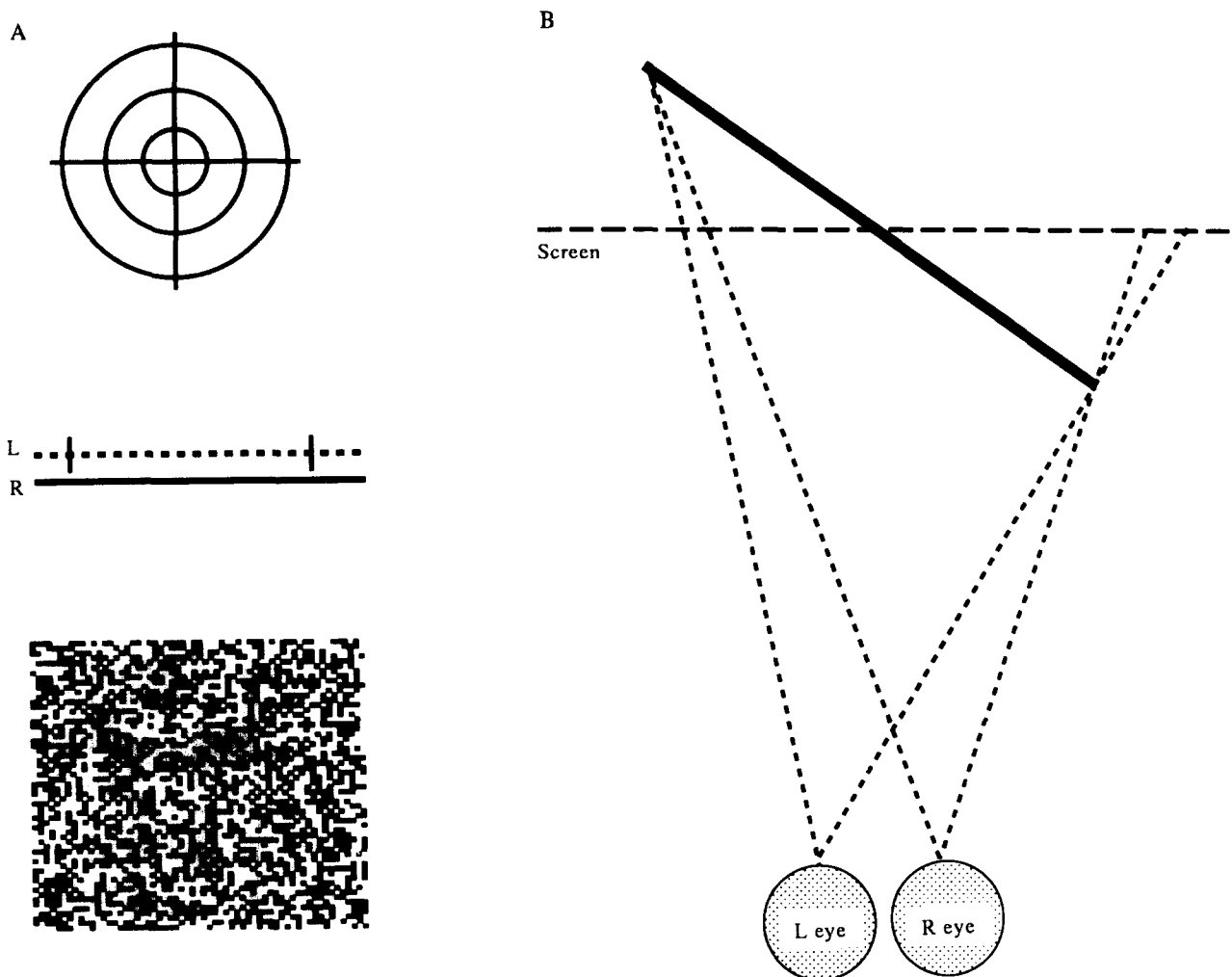
A

B

FIGURE 1. (A) Examples of the three types of stimulus presentations. Top: the calibration. The intersections of the horizontal and vertical line with the three concentric circles were at 5, 10 and 15 deg. Centre: the open-loop stimulus. In reality the two lines were overlapping during the stimulus presentation. Bottom: the pattern used during the control and aniseikonia trials. (B) Top view of the dichoptic viewing arrangement. The image seen by the right eye was smaller than that seen by the left eye. This aniseikonia produces a binocular single image slanting away from the observer, such that for leftward saccades the eyes diverged, and for rightward saccades the eyes converged (drawing not to scale).

eyewear, the subjects ran through the calibration procedure (see above) followed by presentation of two dichoptically presented checkerboard patterns of equal size ("control"). During presentation of the checkerboard pattern, subjects were instructed to make saccades between two self-selected points ± 10 deg symmetrically about the centre of the screen. The advantage of this procedure was that there were no attentional conflicts between background pattern and a target; the disadvantage was that it would likely lead to a variability in saccade amplitude. By encouraging the subjects to use the same selected targets throughout the experiment, the variability in saccade amplitude was limited to 1.5 deg ($n = 6$) on average. During presentation of each stimulus, the subjects made voluntary saccades paced by a metronome (0.5 Hz). Then, we presented the open-loop stimulus (open-loop "pre") to the subjects, in which subjects made saccades back-and-forth along the horizontal line to the cross-hair targets that were visible to one eye only. Next, the subjects viewed the aniseikonic checkerboard patterns. The image presented to the right eye was

reduced by 8% either along the horizontal or the vertical meridian. This created a disparity gradient that for horizontal saccades required the subjects to converge for rightward saccades and to diverge for leftward saccades, as when viewing a slanted wall [see Fig. 1(B)]. During the presentation of the aniseikonic patterns, a series of 24 trials was collected. Each trial in which 4–6 saccades in either direction were collected, lasted 30 sec including the preparation time needed to setup the next trial. Subjects performed one trial with horizontal (or in the case of vertical aniseikonia, vertical) saccades, alternated by a trial in which the subjects made diagonal saccades. The total period to which the subjects viewed the aniseikonic images lasted 12 min. The data presented in this paper only discuss the effects of aniseikonia on the pure horizontal or vertical saccades. After the trials with aniseikonia we repeated the open-loop ("post") and control tests.

The recordings were analysed off-line by computer programs. Saccades were detected after the offset and gain correction procedure. First, the saccades were

identified with the following criteria: (i) a velocity threshold of 15 deg/sec; (ii) a minimum amplitude of 10 deg; (iii) an acceleration threshold of 2500 deg/sec^2. Second, the precise moments of saccade on-and offset were determined by computing the mean and SD of the presaccadic acceleration from 50 to 10 msec before the initially detected start of the saccade. The point where acceleration first exceeded the mean pre-saccadic acceleration ± 2 SD was taken as saccade onset. With the same acceleration based criterion precise saccade offset was detected starting from the moment of saccade peak velocity. The moment where the acceleration fell within the presaccadic mean acceleration ± 2 SD was taken as saccade offset. For each saccade of each eye we computed its amplitude, peak velocity and duration. Vergence signals were obtained by subtraction of the left eye from the right eye. Note that in our experimental arrangement rightward saccades were associated with convergence (positive), leftward saccades with divergence (negative).

To quantify the disconjugacy of the saccades we computed the following vergence parameters: (i) the total vergence obtained during the saccade (V_{a1}); (ii) the total vergence from the start of the saccade until 200 msec after the saccade (V_{a2}); (iii) the divergence and convergence peak velocities; (iv) the required theoretical vergence (V_t), defined as 8% (equal to the actual size difference) of the amplitude of the largest saccade, which in our experiments always was the left eye. From these values we calculated the average relative vergence (ARV), and the average vergence error (AVE). The ARV is defined by the actual vergence (V_{a1}) as a fraction of the required vergence (V_t). Positive values indicate convergence, negative values divergence. The AVEs immediately after (AVE$_1$) and 200 msec after the end of the saccade (AVE$_2$) were computed from the difference between the required vergence (V_t) and the actual vergence (V_a) and then expressed as a proportion of the required vergence:

$$ARV = V_{a1}/V_t,$$

$$AVE_1 = (V_t - V_{a1})/V_t$$

$$AVE_2 = (V_t - V_{a2})/V_t.$$

Differences between the experimental conditions were tested for statistical significance with the Student's t-test for paired means.

RESULTS

General effects

The dichoptically presented patterns were immediately fused by all six subjects. None of the subjects reported diplopia when he or she viewed the aniseikonic images and made horizontal saccades. In contrast with this, when vertical compression of one image was used and subjects were instructed to make vertical saccades, three out of six subjects reported some initial diplopia in the upper or lower field that gradually disappeared. The other observation was that although the two aniseikonic patterns introduced a disparity gradient, similar to the

situation that occurs when viewing a slanted wall, subjects usually did not perceive a slant, or if they did, the perceived slant angle was much less than the theoretical slant angle. In the following section, the effects of aniseikonia on saccadic eye movements will be shown for horizontal and vertical saccades in relation to the viewing distance. It should be noted that although all subjects had their idiosyncracies in relation to velocity, duration and profile of the saccadic and vergence movements, even during conjugate saccades, the main effects that will be described apply to all subjects.

Horizontal saccades

Even when the patterns seen by the two eyes were identical (control stimulus), saccades were associated with transient changes in vergence. Sometimes small net vergence changes were observed after each saccade. The intrasaccadic and postsaccadic vergence errors were idiosyncratic. In general, the subjects showed a transient divergence [see Fig. 2(A, B)], although one of the subjects (G2) had a small initial convergence followed by
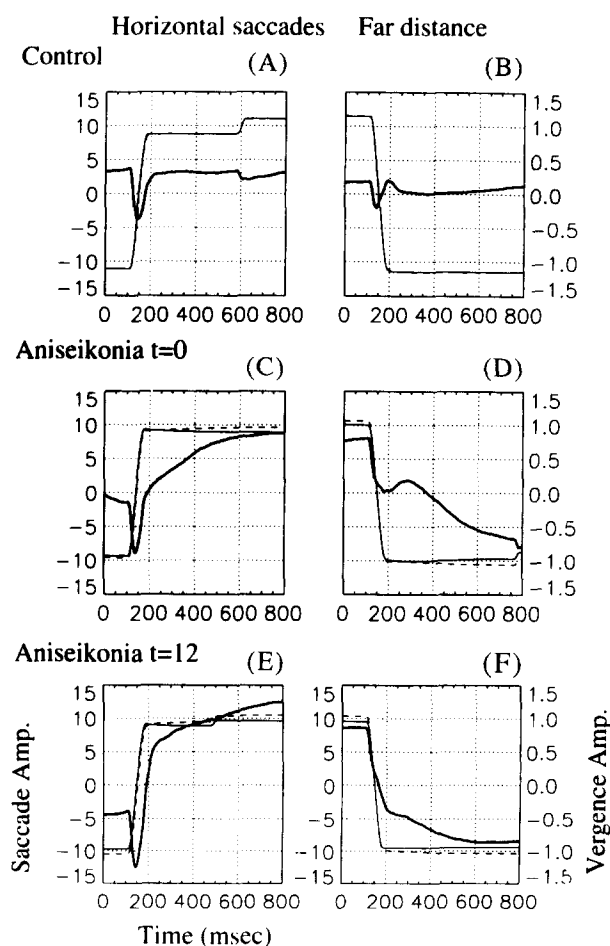

FIGURE 2. Individual rightward (positive) and leftward (negative) saccades of subject G1 viewing the dichoptic patterns at a distance of 144 cm. In this and all other similar figures the following conventions are applicable. The saccadic movement of the right and left eye are indicated by the solid and dashed lines respectively (scaling on left). The bold trace is the vergence signal (left − right eye), amplified by a factor of 10 (scaling on right); divergence = downward, convergence = upward. (A, B) Control situation; (C, D) $t=0$, the first aniseikonia trial; (E, F) after 12 min of aniseikonia.

TABLE 1. Mean values of the ARV for six subjects at far distance

	Open-loop pre	$t = 0$	$t = 12$	Open-loop post	Post − Pre
Divergence					
G1	−0.31	−0.37	−0.71	−0.47	−0.16
G2	−0.34	−0.40	−0.45	−0.45	−0.11
PB	−0.22	−0.67	−0.74	−0.37	−0.15
ST	0.05	−0.16	−0.48	−0.05	−0.10
HL	−0.09	−0.59	−0.92	−0.19	−0.10
HV	0.03	−0.35	−0.75	−0.23	−0.26
Convergence					
G1	−0.18	0.12	0.33	−0.11	0.07
G2	−0.12	0.16	0.52	−0.06	0.06
PB	−0.30	0.33	0.32	−0.29	0.01
ST	−0.30	0.42	0.43	−0.22	0.08
HL	−0.23	0.27	0.44	0.05	0.28
HV	− 0.45	0.37	0.11	−0.44	0.01

a transient divergence. Introduction of the aniseikonic patterns had the effect that the saccades became disconjugate. Despite the demand for convergence during rightward saccades, the transient divergence persisted. However, as will be shown, the time–course and amount of disconjugacy was dependent on viewing distance.

Disconjugate saccades at far distance

The immediate effects of presenting the aniseikonia at a viewing distance of 144 cm are shown in Fig. 2(C, D). Figure 2(C) shows a binocular rightward saccade in combination with a transient fast divergence, followed by a slow convergence with a slope of 3.5 deg/sec. The vergence necessary to get a fused image in this initial phase of the aniseikonia, was achieved almost exclusively after the saccade. Figure 2(E) shows the version and vergence trace for the same subject after 12 min of making horizontal rightward saccades across the aniseikonic patterns. The transient divergence is still present, but the rising flank of the transient has increased. As a result approx. 50% of the required vergence is made within the saccade, whereas the remaining part is accomplished after the saccade with a slow vergence movement (slope 1.6 deg/sec).

For leftward saccades (associated with divergence), the changes in disconjugacy are more pronounced. The profile of the transient divergence changed as a function of exposure time to the aniseikonic stimulus. At the onset of the aniseikonia trials [$t = 0$, Fig. 2(D)], the rising flank of the transient was partially suppressed, but the intrasaccadic ARV was still far from complete (mean 0.44, $n = 6$). After 12 min the mean ARV for divergence associated with horizontal leftward disconjugate saccades had increased to 0.67 ($n = 6$), and only a small fraction of the required vergence was accomplished with a slow postsaccadic vergence movement [Fig. 2(F)]. The ARV values for all subjects are summarized in Table 1. Figure 3 illustrates the changes in ARV; those for divergence are shown Fig. 3(A), those for convergence in Fig. 3(B). For each subject a cluster of five bars is plotted (for a detailed explanation see the figure caption). At this point of data presentation, note the changes that have occurred in the ARV during the aniseikonia trials at $t = 0$ and at $t = 12$

(second and third bar of each cluster respectively). Despite individual differences (see Table 1), both for leftward saccades (with divergence) and for rightward saccades (with convergence) the changes in ARV between $t = 0$ and $t = 12$ averaged over all subjects were significant ($P < 0.001$ and $P < 0.05$ respectively).

The increase of the ARV over time when viewing the aniseikonic patterns, is parallelled by a gradual reduction of the vergence error immediately after the saccade
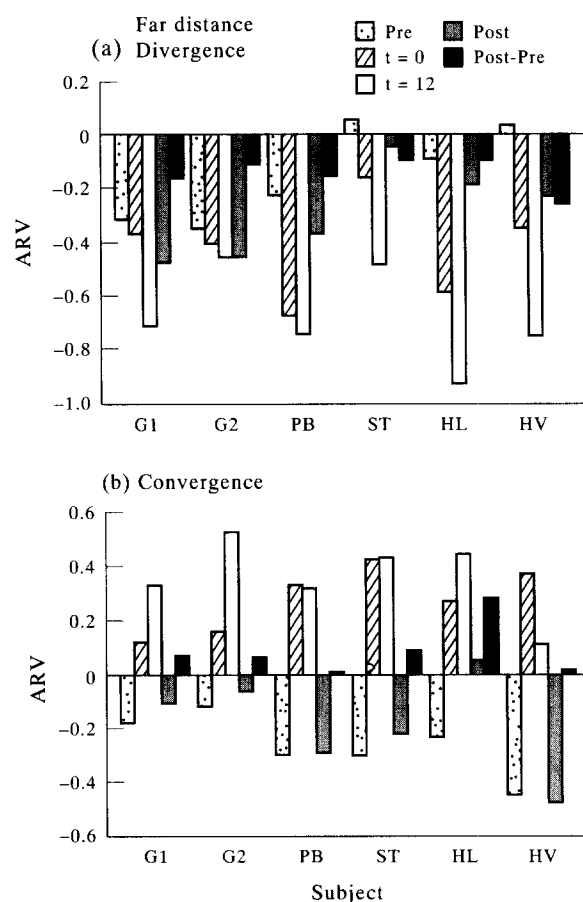

FIGURE 3. Average relative vergence for all six subjects during open-loop pre, at the start of the aniseikonia ($t = 0$), at the end ($t = 12$) and during open-loop post. The fifth bar (■) of each cluster represents the difference between pre and post open loop. Negative values indicate divergence, positive values convergence.
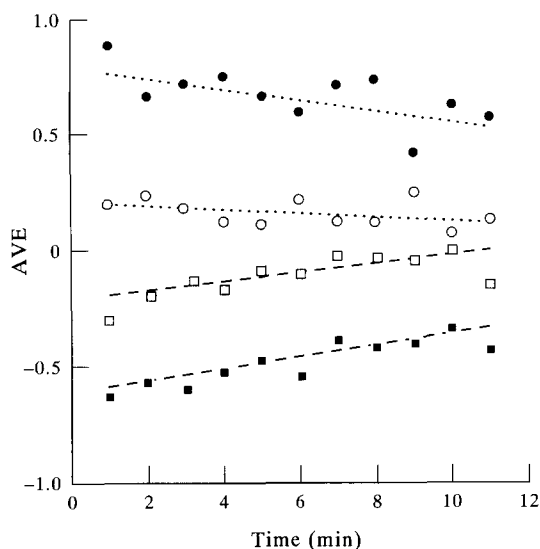
FIGURE 4. Averaged relative vergence errors for horizontal disconjugate saccades as a function of time in subject G1. To facilitate the distinction between convergence (circles) and divergence (squares) errors, the latter are plotted as downward going. Solid symbols, error immediately after the saccade; open symbols, errors 200 msec after the saccade. Each symbol represents the mean error, averaged over 4–6 saccades in each direction for a particular trial. For further explanation see text.

(AVE_1). Figure 4 shows the AVE immediately (solid symbols) and 200 msec (open symbols) after the saccade for one subject. The errors for leftward (divergent) saccades are plotted as negative values, those for rightward saccades (convergent) as positive. Differences exist in the time–course of the reduction of the vergence error between convergent and divergent saccades. In all subjects the intrasaccadic vergence error (AVE_1) reduced faster and was more complete for divergent saccades than for convergent saccades. For subject G1 whose data are plotted in Fig. 4, the slope of the linear regression line fitted through the AVE data points was 0.02 deg/min, both for divergence and convergent saccades. The values, however, varied considerably from subject to subject [overall means ($n = 6$) for divergence and convergence were 0.02 and 0.004 deg/min respectively]. The postsaccadic vergence error 200 msec after (AVE_2) was small in all subjects (mean values 0.09 and 0.11 deg for divergence and convergence respectively).

In conclusion, for disconjugate saccades associated with convergence, most of the required vergence is accomplished after the saccade, whereas for divergent saccades a larger fraction of the required vergence is accomplished during the saccade.

Saccade disconjugacy in open-loop trials

To test if motor learning had taken place, we compared the disconjugacy of saccades in the open-loop condition before and after 12 min of exposure to aniseikonic checkerboard patterns. To facilitate comparison, in Fig. 5 we show the open-loop responses of the same subject as in Fig. 2. The open-loop responses before the aniseikonia trials ("pre") are presented in Fig. 5(A), those immediately after the aniseikonia trials ("post") in

Fig. 5(B). Note that this subject had a small tonic divergence of 0.2 deg for right-and leftward saccades in the open-loop condition.

In the post open-loop test, the subject had a small but consistent convergence during rightward saccades. Athough the differences between the immediate pre and post open-loop postsaccadic vergence were small (0.1 deg), the differences in pre and post vergence angle 200 msec after the saccade were considerably larger (0.5 deg).

For leftward saccades associated with divergence, the difference in vergence amounted only 0.2 deg, but the profile of the slow postsaccadic vergence was different. The changes in vergence in the pre and post open-loop tests, expressed as the ARV, are given in Table 1 and Fig. 4 (fifth bar of each cluster). The overall differences between pre and post open-loop ARV were statistically significant both for divergent and for convergent saccades ($P < 0.01$ and $P < 0.5$ respectively).

In conclusion, under far distance viewing conditions, saccades made after a period of aniseikonia remain partially disconjugate even under open-loop conditions, indicating that to some extent the motor system has adapted. On the other hand, the motor learning is only partial, because the intrasaccadic disconjugacy amounted on average only 22% ($n = 6$) of the required vergence.

Disconjugate saccades at close distance

With four out of the six subjects we repeated the experiment with the stimuli presented at a viewing distance of 37 cm. An example of the effects of changing the viewing distance are shown in Fig. 6. Figure 6(A, B)
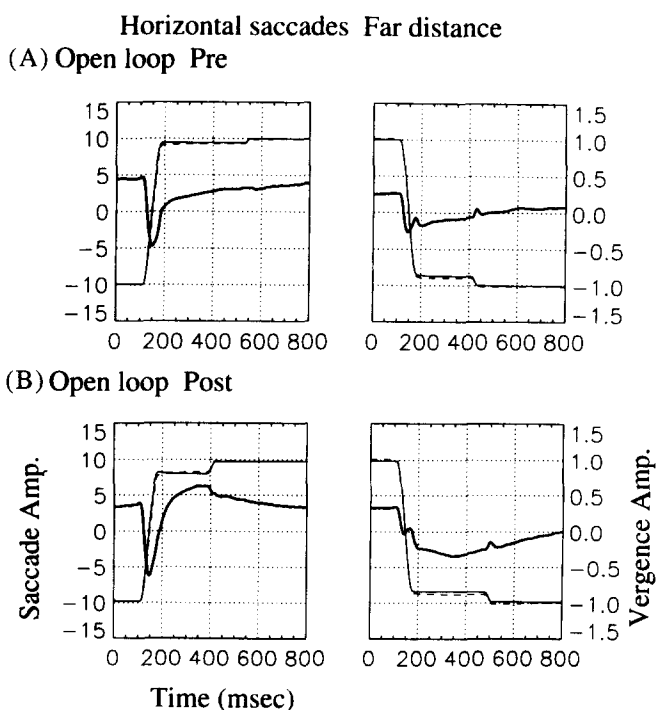
Horizontal saccades Far distance

FIGURE 5. Examples of right-and leftward saccades under open-loop conditions at a distance of 144 cm in subject G1. (A) Open-loop before the aniseikonia trials, (B) open-loop responses after 12 min of aniseikonia.
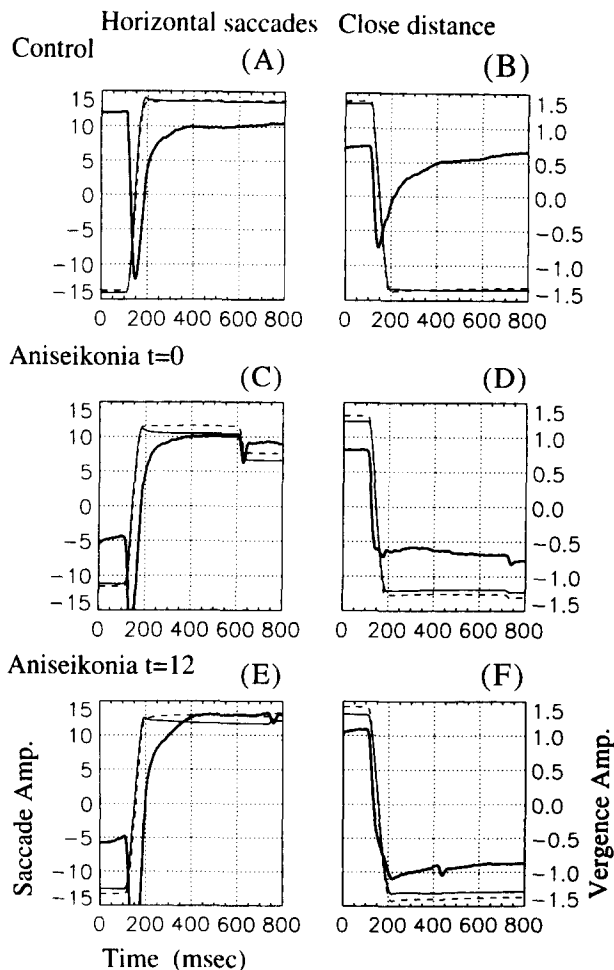
Horizontal saccades Close distance

FIGURE 6. Individual horizontal saccades with the image at a distance of 37 cm (subject PB). (A, B) Control situation, (C–F) the first saccades to the right and left in response to the aniseikonia. Note the immediate disconjugacy in the vergence trace.

FIGURE 7. Summary of the average vergence errors at close viewing distance in all four tested subjects. Also see Fig. 3 for comparison.

shows the control situation, Fig. 6(C, D) and Fig. 6(E, F) show examples of left-and rightward saccades at the start of the aniseikonia and after 12 min respectively. As soon as we introduced the aniseikonic patterns the saccades were disconjugate. The shape of the vergence trace of the first few close distance aniseikonic saccades was almost identical to that of the disconjugate saccades at the end of the far distance aniseikonia.

For rightward saccades (convergence) The mean ARV at $t = 0$ was 0.37 ($n = 4$). No systematic increase in the ARV at $t = 12$ was observed. Two subjects showed during
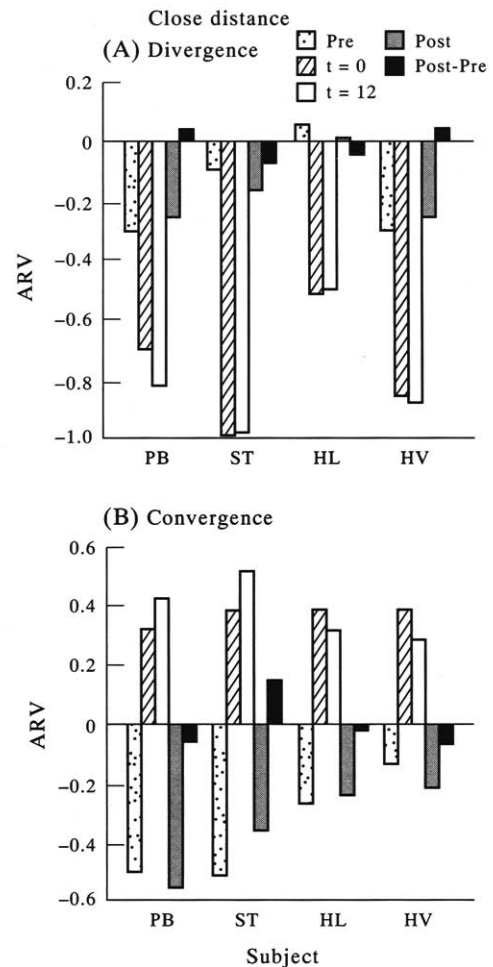
the aniseikonia a small increase in intrasaccadic convergence, two a small decrease.

For leftward saccades (divergence) the disconjugacy was almost completely accomplished within the saccade. The ARV at $t = 0$ was 0.77 ($n = 4$). There was, at close viewing distance, in contrast to the far distance condition, no significant (t-test for paired means) increase in the divergent ARV in the course of the aniseikonia. A summary of the ARV for all four subjects is presented in Table 2 and Fig. 7.

A comparison between the differences in AVE under close and far distance viewing is made on Fig. 8. As shown in this figure, at close viewing distance the intrasaccadic

TABLE 2. Mean values of the ARV for four subjects at close distance

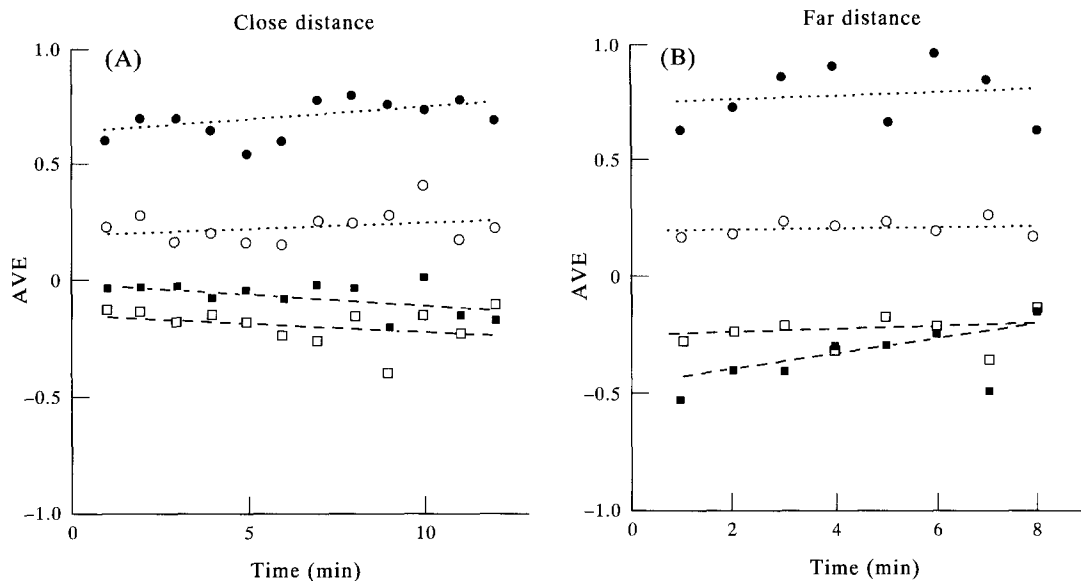|	Open-loop pre	$t = 0$	$t = 12$	Open-loop post	Post − Pre
Divergence					
PB	− 0.30	− 0.71	− 0.83	− 0.26	0.04
ST	− 0.10	− 0.99	− 0.98	− 0.17	− 0.07
HL	0.05	− 0.52	− 0.50	0.01	− 0.04
HV	− 0.30	− 0.86	− 0.88	− 0.26	0.04
Convergence					
PB	− 0.50	0.32	0.42	− 0.56	− 0.06
ST	− 0.51	0.38	0.51	− 0.36	0.15
HL	− 0.22	0.38	0.31	− 0.24	− 0.02
HV	− 0.14	0.39	0.28	− 0.21	− 0.07

FIGURE 8. A comparison of the vergence errors at close distance (A) and at far distance (B) of subject HV. Meaning of symbols as in Fig. 4.

divergent changes are immediate and the errors are smaller (A, ■) than at far distance viewing (B, ■). In contrast, few changes occurred in the intrasaccadic convergence errors [cf. ● in Fig. 8(A, B), also see Table 2]. Although in the data shown in Fig. 8, differences in vergence errors 200 msec after the saccade (AVE$_2$) can be observed between far and close distance viewing, these differences were not consistent across subjects. In two out of the four subjects these errors were smaller for close distance viewing than for far distance viewing (as is the case for subject HV shown in Fig. 8). In the other two subjects the errors were larger.

Saccade disconjugacy in open-loop trials

The open-loop responses at close viewing distance were different from those at far distance. Despite the fact that, in general, at close distance the saccades were more disconjugate during the aniseikonia than at far distance viewing, the persistence of the disconjugacy during post open loop was virtually absent. Changes in the open-loop responses before and after the aniseikonia (Table 2) were not significant (t-test, $n = 4$). An example of the open-loop pre and post response is given in Fig. 9.

Initial disconjugacy in relation to viewing distance

The relation between intrasaccadic disconjugacy and viewing distance is shown in Figs 10 and 11. In Fig. 10 each panel shows, from top to bottom, the first disconjugate right or leftward saccade at three different viewing distances (144, 55 and 37 cm).

Figure 10(B, D, F) shows that for leftward saccades (divergence), the time needed to reach the required disconjugacy for the two eyes decreases as a function of viewing distance from 400 to 100 msec. In addition, the intrasaccadic divergent ARV of the first aniseikonic trial increased from 0.37 to 0.85 with decrease in viewing distance (see Fig. 11, ■).

Figure 10(A, C, E) shows that, although for rightward saccades the intrasaccadic convergent ARV did not change as a function of viewing distance (see Fig. 11, □), the profile of the postsaccadic slow vergence becomes different in shape. At close distance the rising flank of the initial divergence peak increases, such that the required convergent disconjugacy is complete within 100 msec after the saccade, compared to 400 msec at far distance.

Simulation of close viewing distance

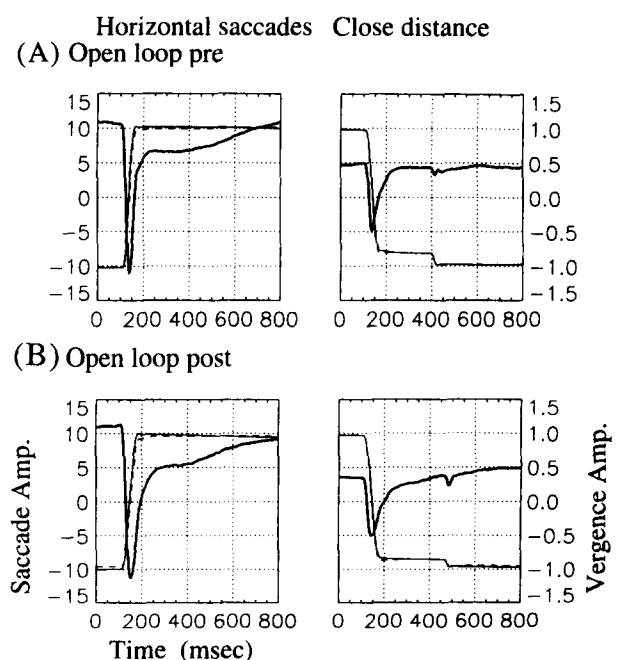In two subjects, we repeated the same experiment with the target screen at 144 cm (far distance condition).

FIGURE 9. Right-and leftward saccades under open-loop conditions at a distance of 37 cm (subject PB). (A) Open-loop before the aniseikonia trials, (B) open-loop responses after 12 min of aniseikonia.

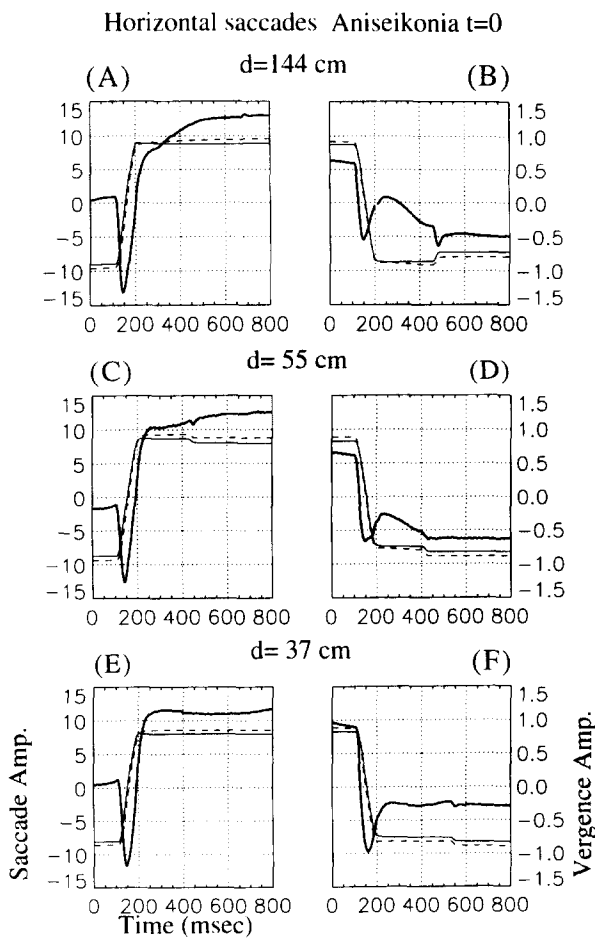Horizontal saccades Aniseikonia t=0

FIGURE 10. Example of the changes in vergence in subject HV at 144, 55 and 37 cm viewing distance. For all three distances the first saccade in the presence of aniseikonia was taken. Note the increase in intrasaccadic vergence, and the decrease in postsaccadic vergence.

However, we shifted the left eye image to the right and the right eye image to the left to simulate a close viewing distance situation [see Fig. 10(B, D, F)]. This arrangement created a stimulus situation with the same amount
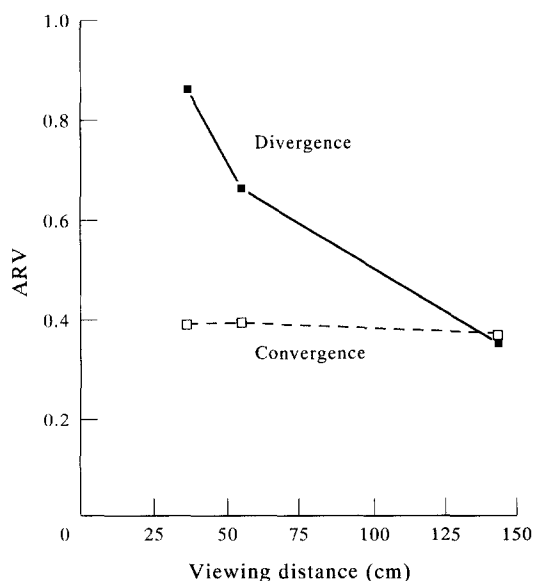

FIGURE 11. Relation between the averaged relative vergence and viewing distance of the first rightward (convergence, □) and leftward (divergence, ■) disconjugate saccade for subject HV.

of tonic convergence as under close viewing conditions, but without accompanying accommodation changes. When making horizontal saccades, the two subjects maintained good fusion both during the control (equal sized patterns) as during the trials with aniseikonia.

Figure 12(A) shows the typical responses obtained under this "simulated close viewing" condition. The top panels show the control situation, the lower panels the first disconjugate left- and rightward saccades. Like the real close distance condition, saccades were immediately disconjugate. The ARV was 0.5 for rightward saccades (convergence) and 1.05 for leftward (divergence) saccades. So, with the "simulated close viewing" there was even a small overcompensation for divergence. Similar to the real close viewing situation the AVE remained constant and was without further reduction over time.

In conclusion, the presence of aniseikonia has different effects for horizontal saccades that are dependent on viewing distance. At close distance (simulated or real) the saccades become disconjugate immediately, whereas at far distance the intrasaccadic disconjugacy is only partial and develops gradually over time. The data show that at far distance there is partial motor learning, indicative of an adaptive mechanism, whereas at close distance this mechanism does not operate, as shown by the absence of learning in the open-loop situation.

Disconjugate vertical saccades

In two subjects (HV and PB, the authors) we also tested the ability to make disconjugate vertical saccades as a function of viewing distance. For this we repeated the experiment with dichoptically presented vertical disparate images with an 8% size difference.

The behaviour of binocular vertical saccades in response to vertical size differences with these stimuli was different from the horizontal saccades in the presence of a horizontal disparity gradient. Vergence changes were slow, both at far and at close viewing distance.

Far and near distance vertical saccades

Similar to horizontal saccades, the disconjugacy was related to viewing distance. At far distance the mean ARV was 0.1 ($n = 2$), whereas at close viewing distance this value had increased to 0.2. This, however, left a large residual error that was only partially reduced with a slow postsaccadic vergence movement. The time-course of the postsaccadic vergence movement was much slower (slope 0.05–0.1 deg/sec) than for horizontal saccades.

The effects of vertically disparate images on binocular vertical saccades at a viewing distance of 144 cm are shown in Fig. 13. This subject (HV) had a small transient vertical disconjugacy for both up-and downward saccades, which is visible in the control situation [Fig. 13(A, B)]. The transient was opposite to the direction of the vertical saccade. The other subject (PB) had a small idiosyncratic transient that was only advantageous for upward saccades; for this direction the disconjugacy was immediately accomplished by suppression of the returning phase. In contrast, this subject was disadvantaged for downward saccades.

Horizontal Saccades Simulated close distance

Control

(A)

Aniseikonia t=0
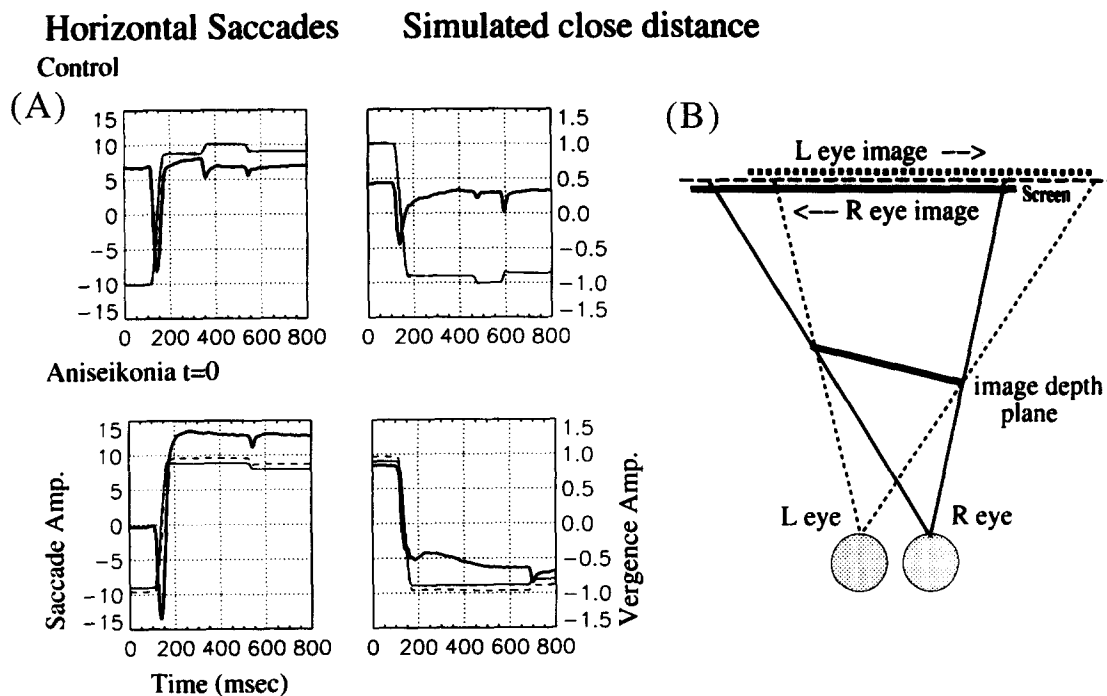

Time (msec)

(B)

FIGURE 12. Immediate disconjugate saccadic eye movements of subject PB in response to aniseikonic images at a simulated distance of 37 cm. The left and right eye images were shifted in relation to each other, see (B). (A) The top panels show the responses in the control situation, the bottom panels show the immediate disconjugate responses at the first aniseikonic trial.

In both subjects the intrasaccadic contribution to the required vertical disconjugacy remained very limited for up-and downward saccades. There was, however, an increase in the amplitude of the postsaccadic vertical vergence over time. The slope of the postsaccadic vergence increased from 0.05 deg/sec at $t = 0$ to 0.1 deg/sec at $t = 12$, both for up- and downward saccades. The other subject had a similar increase, but only for upward saccades. At far distance only 25% of the theoretical vergence was accomplished by vertical disconjugacy in both subjects. Since the subjects did not experience diplopia, the remaining vertical disconjugacy has to be accounted for by a sensory mechanism, and not by a disconjugate oculomotor mechanism.

When we repeated the same experiment at close viewing distance (37 cm), we observed small transients in the control situation in both subjects similar to the far distance viewing. Figure 14 shows the response of the same subject as in Fig. 13. The disconjugacy of the saccades in response to the aniseikonia was immediately present at $t = 0$ for upward saccades, but not for downward saccades. The final fixation disparity, however, remained relatively large. Even though after 12 min [Fig. 14(E, F)] both for up-and downward saccades, the slope and amplitude of the postsaccadic vergence had increased, only 50–60% of the required vergence had been accomplished.

In summary, exposure to vertical aniseikonia stimulated compensatory disconjugacy of vertical saccades. This disconjugacy, however, had a much slower time–course and its amplitude remained small even after 12min of training. On the other hand, vertical disconjugacy was enhanced for close viewing.

DISCUSSION

The main finding in the present experiments is that viewing distance has an effect on the metrics and dynamics of disconjugate saccades, as well on the time–course at which these take place. As we will discuss, these effects are functional in terms of their occurence under natural circumstances.

Convergent vs divergent disconjugacies

In the past, changes in the degree of conjugacy of binocular saccades in response to altered visual input for one eye have been demonstrated with the aid of anisometropic spectacles and prisms in man (Erkelens et al., 1989a; Lemij & Collewijn, 1991a,b) and monkey (Oohira & Zee, 1992), and more recently with dichoptically presented aniseikonic images (van der Steen, 1992; Eggert & Kapoula, 1992; Bush et al., 1994). For horizontal saccades, Erkelens et al. (1989a) reported an intrasaccadic change of 40–75% in a myopic subject that wore anisometropic spectacles for 40 yr. Lemij and Collewijn (1991a, b) showed that the intrasaccadic change in vergence was dependent on the magnification factor of the spectacles. For up to 4 D of interocular difference, the intrasaccadic changes for horizontal saccades were virtually complete, whereas beyond this value the intrasaccadic vergence changes were insufficient. Oohira and Zee (1992) found an intrasaccadic vergence change of 40–75% in monkeys tested with prisms (this number was estimated from the figure in their paper). In addition, these authors reported greater vergence changes for saccades associated with divergence than with convergence. The same effects, reported before
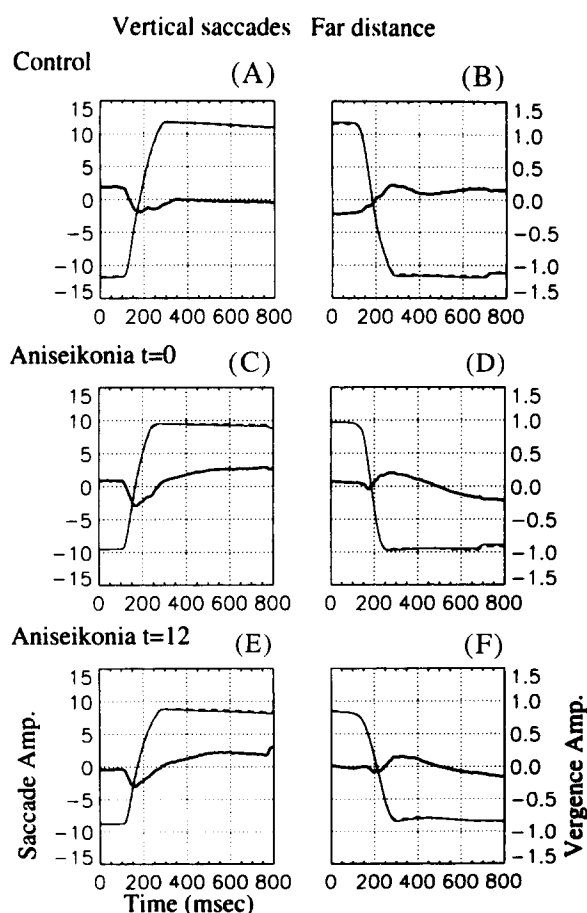
Vertical saccades Far distance

FIGURE 13. Vertical saccades at 144 cm viewing distance. Subject HV. (A, B) Control, viewing equal sized images. (C, D) Aniseikonia at $t=0$. (E, F) Aniseikonia after 12 min ($t=12$).

or less linearly over time, thereby only gradually reducing the vergence error immediately after the saccade at a mean rate of 2% per minute. Most of the remaining vergence errors diminished within 200 msec after the saccade, or if small fixation disparities remained, they were less than 0.5 deg, small enough to fall with the fusional limits of the stereopsis (Erkelens, 1988).

What is the functional significance of these differences? At both viewing distances the patterns have the same percentage of aniseikonia. Yet the responses are quite different, suggesting that disparity information is used differentially as a function of viewing distance.

To answer this question we have to realize that our stimulus arrangement, as already mentioned, creates a disparity gradient that is similar to the situation when we observe a slanted wall. Fixating parts of such a wall along the horizontal meridian requires a continuous change of vergence during saccades. To direct our gaze to a part of the wall nearby, we converge, for a part of the wall farther away we have to diverge. It has been shown by a number of investigators that under such circumstances we make a combination of saccade and vergence movements, where the necessary vergence is accomplished during the saccade (Enright, 1984, 1986, 1992; Erkelens *et al.*, 1989b; Zee *et al.*, 1992; Maxwell & King, 1992, Collewijn, Erkelens, Pizlo & Steinman, 1994) provided that the vergence requirement is modest. Two different explanations could account for this facilitation of vergence: (i) an instantaneous independent control of the two

in man when using dichoptic aniseikonic stimuli (van der Steen, 1992), are confirmed in the present experiments. In our experiments 35% of the required vergence was accomplished during rightward saccades associated with convergence, and 67% for leftward saccades associated with divergence. This quantitative difference in the amount of intrasaccadic adaptation for saccades associated with divergence and convergence could be due to the normally occurring transient divergence. This transient divergence would facilitate the acquisition of additional divergent disconjugacy, but would interfere with the acquisition of convergent disconjugacy. The fast changes in amplitude that are possible in the returning phase of the transient divergence peak, but not in the initial divergent phase, suggest an active role of this transient movement during saccades, enabling fast realignment of the eyes to a point further away in visual space, as has been suggested before (Maxwell & King, 1992; Zee *et al.*, 1992).

Effects of viewing distance on the disconjugacy of horizontal saccades

The main finding in our experiments is that the amount of intrasaccadic vergence is accomplished instantaneously when the aniseikonic images were at a distance of 37 cm. With these images at 144 cm, the intrasaccadic vergence changes were initially small, but increased more
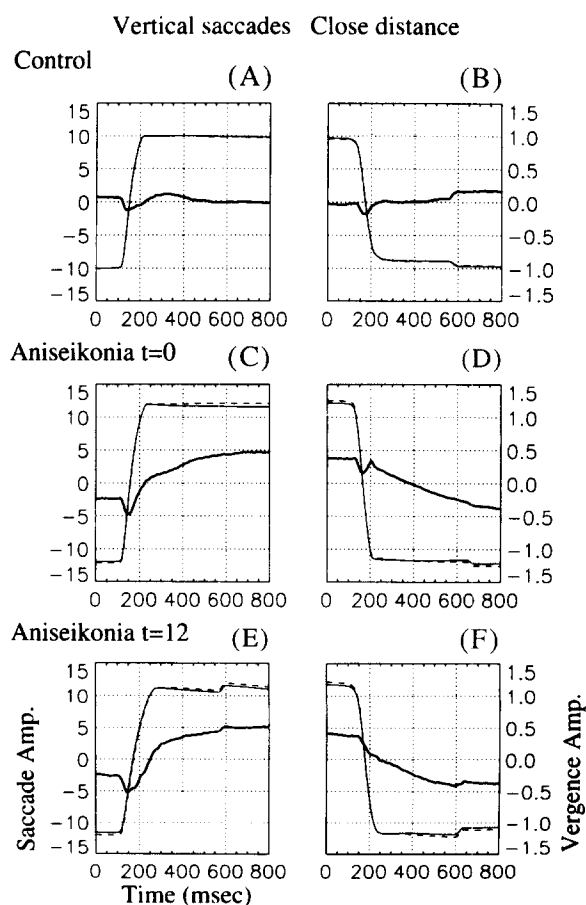
Vertical saccades Close distance

FIGURE 14. Vertical saccades at 37 cm viewing distance. Subject HV.

eyes (Erkelens *et al.*, 1989b); (ii) the existence of two independent subsystems that are neurophysiologically distinct, but that can interact as proposed by Maxwell and King (1992) and Zee *et al.* (1992).

In favour of the first mechanism, Bush *et al.* (1994) suggested that horizontal disparity is an important cue which can be used by the saccadic system to scale the relative amplitudes of the two eyes. Bush *et al.* (1994) also suggested that the binocular disparity at the time the saccade is programmed is a limiting factor. Since no known disparity detectors exist with disparity limits greater than 2 deg (Bishop & Pettigrew, 1986), the immediate disconjugate saccade control system would be limited to this value, and any larger vergence would activate the slow vergence system, that on its turn could speed up vergence during saccades through a non-linear interaction, as proposed by Zee *et al.* (1992). We propose that this particular use of the disparity information is most effective when in the operating range for nearby targets. This does not rule out that other cues, e.g. monocular cues, play a role such as shown by Eggert, Kapoula and Bucci (1994). An effective way for the CNS to keep track of disparity information in relation to viewing distance would be to use the tonic vergence angle. Evidence that the tonic vergence angle is indeed the signal that selects the use of disparity information is provided in our "simulated close viewing" experiment. In this experiment the nearby stimulus field, simulated by shifting the dichoptic images (dissociating accommo- dation from vergence), led to disconjugate saccades immediately.

The same disparity information at far distance serves a completely different purpose. With the eyes close to optical infinity the eyes essentially have to move in conjugate fashion, and there is little need for vergence. Therefore, any remaining fixation disparity after the saccade would signal to the CNS that the eyes are not properly aligned. The fixation disparity will now trigger the slow vergence system to correct postsaccadically. In our experiment, this is what initially happens when the eyes are confronted with the aniseikonic patterns. There is relatively little intrasaccadic correction, and a significant postsaccadic vergence. At far distance fixation disparity thus becomes an error signal that can be used to modify the motor program of binocular saccades on a long-term basis (see Bruno, Inchingolo & van der Steen, 1995). Our data show that this adaptive motor program starts immediately, as we and others have recently shown before (van der Steen, 1992, 1993; Eggert & Kapoula, 1992). The persistence of the disconjugacy in open-loop trials which amounted on average 25% indicate that the intrasaccadic modifications at far distance are at least partially the result of an adaptive mechanism. At this point we are not able to say if the amount of persistence is directly coupled to the reduction of the vergence error over time. Our data, however, are at least suggestive that such a relation exists. The overal slope of error reduction was 2% per minute, which amounts to about 24% over vergence error reduction in 12 min. This value is close to the 25% of persistence in the open-loop trials. Lemij and

Collewijn (1991a) reported 45% of persistence of the disconjugacy during monocular testing after 8 hr of adaptation to anisometropic spectacles. So, although our data might be suggestive of a linear relationship between open-loop disconjugacy and vergence error reduction at short-term adaptation, such a linear relation does not hold for long-term adaptation. The only partial persistence of saccadic disconjugacy during the open-loop reponse, in combination with the fact that at the onset of aniseikonia there is an immediate (albeit not complete) intrasaccadic disconjugate response, suggests that also at far distance part of the binocular alignment of the saccades during aniseikonia is under direct visual control, as was suggested before by Lemij and Collewijn (1991a). This visual contribution varies form subject to subject.

In conclusion, the information provided by retinal disparity to generate horizontal disconjugate saccades is used differentially as a function of viewing distance. At close viewing distance the information is effectively used to generate disconjugate saccades instantaneously, leaving little vergence error immediately after the saccade. Perhaps due to this small residual error there is no need for an adaptive response. In fact, in daily life when we look at objects at close distance we not only change our direction of gaze but also the vergence angle between the eyes. Any permanent modification of the binocular saccadic system is unwanted in this situation. However, at far distance any remaining vergence error after the saccade signals a binocular misalignment that calls for a motor learning process. Our data show that this motor learning process starts immediately, but is most effective for disconjugate saccades that require divergence.

Effects of viewing distance on the disconjugacy of vertical saccades

A number of investigators have investigated the adaptive capabilities of the vertical saccades. For conjugate saccadic adaptation experiments symmetrical vertical gain changes have been shown to be indistinguish- able from horizontal gain changes (Deubel, 1991). Based on these findings a simple adjustment of a common gain parameter has been assumed (Deubel, 1987) for conjugate adaptations. Whether a similar common mechanism applies to horizontal and vertical disconjugate adaptation is at this moment unclear. Disconjugate adaptation of vertical saccades has been shown to occur (Schor *et al.*, 1990). Henson and Dharamshi (1982) reported vertical phoria adaptation using anisometropic spectacles in a few hours. Erkelens *et al.* (1989a) reported a better adaptation with a higher degree of conjugacy for vertical saccades than for horizontal saccades within a short time span. These differences were explained in terms of a critical fusional limit of vertical disparities. In contrast, Lemij and Collewijn (1991a) found no differences between horizontally and vertically adapted saccades in long-term adaptation experiments, using anisometropic spectacles. In a related study, looking at short-term adaptation, the same authors (Lemij & Collewijn, 1991b) reported a slower and less complete adaptation for vertical saccades than for horizontal saccades

after 1 hr of adaptation. Downward saccades adapted better than upward. In agreement with the study of Lemij and Collewijn (1991b), our findings indicate that the time–course of adaptation of vertical saccades is much slower than for horizontal saccades and the intrasaccadic vertical disconjugacy is far from complete. This argues against a simple parametric gain adjustment for disconjugate horizontal and vertical saccadic adaptation.

We also found differences in the degree of adaptation to vertical aniseikonia that were, as for horizontal aniseikonia, related to the viewing distance. At short viewing distance the vergence changes were faster for upward than for downward saccades. In addition, the postsaccadic vergence change for both up- and downward saccades in near viewing conditions were faster and larger. One possibility is that the horizontal tonic vergence signal not only influences horizontal disconjugate saccades, but also vertical disconjugacy. Another explanation is that cognitive aspects play a role. Oohira *et al.* (1991) and Ygge and Zee (1992, 1994) claimed context specific vertical vergence changes. Their observation was based upon experiments where subjects had to look between two vertically separated nearby targets. Nevertheless, even for context selective switching, a signal that provides the right context is necessary. The horizontal vergence signal could aid in providing this information.

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