Position Dependency of Rapidly Induced Saccade Disconjugacy
THOMAS EGGERT, ZOI KAPOULA
Received 28 December 1994; in revised form 2 May 1995

We tested the ability of normal subjects to alter the conjugacy of their saccades in a position-specific manner. Five subjects dichoptically viewed a stereogram produced by two random-dot patterns. They immediately perceived a three-dimensional wedge with its apex closer to them. They were asked to saccade for 15 min back and forth between the apex and two lateral dots of the wedge. For fixation sequences between centre-right-centre, saccades immediately became larger in the right eye. For sequences between centre-left-centre, saccades immediately became larger in the left eye. For two subjects this non-monotonic position-specific disconjugacy compensated for the disparity of the stereogram almost perfectly. The disconjugacy persisted even under monocular viewing of one of the random-dot patterns. It diminished or disappeared immediately, however, when the random-dot pattern was shifted on the screen. We suggest the existence of a fast learning mechanism capable of producing position-specific disconjugacy by associating saccades with disparity. Such a mechanism would use a visual reference rather than the position of the eyes in the orbit.

INTRODUCTION

When looking at infinity or at an isovergence surface, horizontal saccades are usually conjugate (Collewijn, Erkelens & Steinman, 1988). Conjugacy of the saccades, despite asymmetries of the oculomotor plants or changes due to development or aging, is probably maintained by disconjugate adaptive mechanisms. Several studies (e.g. Erkelens, Collewijn & Steinman, 1989a; Schor, Gleason & Horner, 1990; Oohira, Zee & Guyton, 1991; Lemij & Collewijn, 1991a,b) have demonstrated such disconjugate adaptive mechanisms responding to changes in the visual input alone.

Saccade dysmetria and static eye misalignment resulting from unilateral oculomotor pathologies are frequently orbital position dependent and need position-specific adaptive changes. Position-specific adaptive changes in the static ocular alignment were demonstrated by Henson and Dharamshi (1982), Oohira and Zee (1992), Schor, Gleason and Lunn (1993). In the study of Oohira and Zee (1992), monkeys were fitted with a combination of prisms in front of one eye which produced a monotonic but stepwise distribution of disparity: relative convergence, no change in vergence, or relative divergence was required depending on the position of the eyes in the orbit. Monkeys were able to compensate for a considerable amount of the disparity within 1 day: their eyes were realigned quickly during each saccade to allow binocular fixation immediately after the saccade. The static eye alignment was adjusted to the disparity encountered at each fixated position. The change in static alignment, however, was not as discrete as required by the prism combination, suggesting, as pointed out by the authors, some limitations in this mechanism.

Much faster, visually induced, changes of saccade conjugacy were found by van der Steen and Bruno (1995) as well as by Kapoula, Eggert and Bucci (1995). It was found that emmetropic subjects, when exposed to a size inequality between the images seen by the left and the right eye, are able to change the conjugacy of horizontal saccades immediately. The disparity produced by the image size inequality is the main stimulus driving such changes. Other sensory cues, however, seem to be involved. Thus, van der Steen and Bruno (1995) demonstrated the role of viewing distance. Kapoula et al. (1995) emphasized the influence of monocular depth cues in their experiments that were conducted at intermediate viewing distance. They proposed a fast learning mechanism that associates saccades with disparity and monocular depth cues, and is capable of producing intrasaccadic disconjugacy even without disparity as an immediate visual cue.

The goals of the present study were three-fold. First, it aimed to examine whether fast disconjugate changes in the amplitude of the saccades can be induced on the basis of disparity alone, without monocular depth cues. The second goal was to test whether such changes can persist in the absence of disparity and, if so, whether they can be
appropriate for the non-monotonic disparities of the image we used for training. Fast changes in saccade disconjugacy could be due to oculomotor adaptation or to a high-level learning mechanism. To gain some insight, we examined whether the changes observed are related to the position of the eyes with respect to the orbit or to the image used for training.

METHODS

Subjects

Five subjects participated in the experiments. Their ages ranged from 19 to 33 yr. Four subjects were naive with respect to the purpose of the experiment, only subject MB was aware of it. Two subjects were emmetropic. Subject MB had a small hyperopia of +0.5 D in the left eye that stayed uncorrected during the experiment. Subject SF wore her habitual, negative glasses during the experiment (RE -1.25 D; LE -1.25 D). For all subjects, corrected visual acuity was 20/20 in both eyes. Stereoacuity was normal (TNO random-dot test for stereopsis, 60 sec arc or better). This study was approved by the French ethics committee CCPPRB No. 15. Subjects participated in the experiment after giving informed consent.

Stimulus

Subjects sat 57 cm in front of a flat, translucent screen. The head was stabilized by a bite bar (with individually fitted dental impression of the subject’s upper teeth), and a forehead support. Two projectors were used to project a black and white random-dot pattern to each eye. Each pattern consisted of 128 x 128 dots; the sizes of the dots were 0.49 deg at the centre of the pattern and 0.20 deg at its edges. The beams of the projectors were polarized 90 deg apart. Subjects viewed through filters also polarized at 90 deg apart. The room was completely dark. The image viewed was a stereogram of the black and white random-dot patterns. The two random-dot patterns were superimposed on the screen. The random-dot patterns seen by the right and the left eye [Fig. 1(A)] were monocular projections of a virtual three-dimensional object onto the plane of the translucent screen. This simulated the disparity field that would have been present under natural viewing of the three-dimensional object. Figure 1(B) illustrates the perceived object, which had the depth profile of a wedge. Its central edge formed an angle of 90 deg and was in the head median plane pointing towards the subject. This central edge was at 57 cm viewing distance and the sides of the wedge were at 77 cm. The width of the base of the wedge was 40 cm [see Fig. 1(C)]. Under monocular viewing the random-dot pattern appeared flat, under dichoptic viewing subjects got rapidly a vivid perception of a three-dimensional wedge.

Training paradigm

A red laser dot was projected onto the centre of the screen. The light of the dot was not polarized and was viewed by both eyes. Subjects were instructed to repeat a sequence of saccades between the laser dot and two black dots of the pattern each at a lateral eccentricity of about 8 deg. At the beginning of each session, the experimenter indicated the location of these two lateral dots within the random-dot pattern. During training these dots were perceived as being more distant from the subject than the central dot. The sequence of the saccades originated at the central dot and alternated between the left and right dots. The time interval between saccades was about 700–900 msec. This task was performed under three conditions: first, the baseline conjugacy of saccades was measured for about 1–2 min under monocular viewing of the right random-dot pattern. For the following 15 min (the training period), subjects viewed the stereogram binocularly. The red dot was placed on the perceived apex of the wedge. After training the monocular viewing condition was repeated to test for changes in the binocular
position dependent saccade disconjugacy

Changes between binocular and monocular viewing testing conditions were made quickly by covering and uncovering the light of one of the two projectors. For two subjects two additional monocular viewing control conditions were run that will be described in the Results. Changing fixation between any two dots of the stereogram required a change of the static eye alignment in order to compensate for the relative disparity (difference between the absolute disparities between any two dots). If such realignment could be done intrasaccadically, this would achieve accurate binocular fixation immediately after the saccade. Figure 2 shows the saccade disconjugacy required for fixations of the three dots on the image. Centrifugal saccades from the centre to 8 deg to the left or to the right. Centripetal saccades required 1 deg of divergent disconjugacy, centripetal saccades 1 deg of convergent disconjugacy. The curved arrows and letters (CR, RC, CL and LC) show the direction of the saccades.

To estimate the static eye alignment we measured the vergence angle (left — right eye difference) at the final position of the eyes after centrifugal and after centripetal saccades. Final eye position was taken as the position of the eyes at the onset of the next saccade. To estimate the change in static eye alignment we computed the difference in the vergence angle after centrifugal saccades from centre to right, and after centripetal saccades from right to the centre. The same analysis was done for saccades from centre to the left, and from left to centre. Negative values indicate divergent disconjugacy or a divergent change.

Results

Saccade disconjugacy and slow vergence movements

Brief exposure to the stereogram induced a rapid realignment of the eyes during the saccade. This allowed disparity to be reduced at the new fixation point. Figure 3(A, B) illustrates this point with individual binocular
recordings of saccades together with the disconjugacy trace, i.e., the left—right eye difference. Before training the centrifugal saccades [Fig. 3(A)] showed a small divergent disconjugacy, while centripetal saccades [Fig. 3(B)] showed even smaller convergent disconjugacy. During training centrifugal saccades increased their intrasaccadic divergent disconjugacy, and centripetal saccades increased their convergent disconjugacy. After training the saccades maintained increased disconjugacy in the same direction. Figure 3(C–F) shows disconjugacy traces only. For all traces saccades begin at 50 msec, and end at approx. 100 msec. For all these examples (before during and after training) the change in the disconjugacy before the saccade was almost zero indicating a stable eye alignment. The disconjugacy occurred during the saccade and in some cases extended slightly during the post-saccadic period [e.g., Figure 3(E), “Training”]. All subjects showed saccade-related disconjugacy and there

![Figure 3](image-url)

**FIGURE 3.** (A, B) Typical binocular recordings of saccades before, during and after exposure to the stereogram. The solid line is the position trace of the left eye, the dashed line is that of the right eye; the lower trace in (A) and the upper trace in (B) are the disconjugacy of the saccade (the difference between the left and the right eye × 2). Data are from subject MB, centrifugal (A) and centripetal (B) saccades in the right field. (C, D) Disconjugacy traces from several saccades from subject MB. (E, F) Disconjugacy traces from subject VJ. Traces in (C) and (E) correspond to saccades from centre to right; traces in (D) and (F) correspond to saccades from right to centre. All disconjugacy traces are offset at zero. Saccades start at 50 msec and end at approx. 100 msec. During training subjects viewed the stereogram; before and after training they monocularly viewed one of the random-dot patterns used to produce the stereogram. For all the examples, the change in the disconjugacy starts with the saccade and its major part is accomplished within the saccade.
Position-dependent sacode disconjugacy

Actual disconjugacy. Figure 4 shows the intrasaccadic disconjugacy from subject MB plotted over time. Each + in these graphs shows the disconjugacy of a single saccade. Saccades are divided into four groups according to their direction and position. For each group saccades are shown under monocular viewing before and after training (Fig. 4, “Monocular before” and “Monocular after”), and during training (Fig. 4, “Binocular”). To emphasize the immediacy of the change in the disconjugacy only the first 5 min of training are shown.

Most baseline saccades showed a small divergent disconjugacy (Fig. 4, “Monocular before”). When the subject viewed the stereogram binocularly, this intrasaccadic disconjugacy changed immediately in the appropriate direction, compensating for the absolute disparity encountered at the end of each saccade: centrifugal saccades showed divergent disconjugacy, centripetal saccades showed convergent disconjugacy (Fig. 4, “Binocular”). The amplitude of the disconjugacy was close to that of the requirement (horizontal lines). From one saccade to the next, the disconjugacy alternated between convergence and divergence, e.g. for a saccade starting at the right side and ending at the centre (RC) the eyes converged, for the following saccade from centre to the left (CL) they diverged, although both these saccades were leftward and had the same amplitude.

For most groups of saccades (Fig. 4, CL, CR and RC) the position-specific disconjugacy occurred from the first saccade. For saccades from left to centre (Fig. 4, LC) there was also evidence for a progressive change in the disconjugacy during the 5 min.

Interestingly, however, centripetal saccades under monocular viewing recorded after training demonstrated increased convergent disconjugacy (Fig. 4, LC and RC “Monocular after”). The variability of the disconjugacy was larger in this condition than for the baseline saccades. The disconjugacy returned abruptly to its baseline value after about 2 min of monocular viewing.

Changes from baseline. Table 1 shows the changes from baseline of the intrasaccadic disconjugacy for all five subjects. While viewing the stereogram, subjects...
VJ and MB showed statistically significant changes from baseline that were appropriate for all fixated positions. The amplitude of their changes, particularly those made by subject MB, matched that of the stimulus (1 deg) quite well. Subject ML also showed statistically significant changes but these were divergent for all rightward saccades (centrifugal as well as centripetal); her changes for leftward saccades were all convergent. Subject SF showed significant convergent changes for centripetal saccades only (RC and LC). Subject AS showed a significant convergent change only for centripetal from right to centre (RC). For both these subjects the changes were small (<0.3 deg).

Thus, two of the five subjects were able to change the disconjugacy of their saccades from one saccade to the next so as to compensate for the non-monotonic distribution of disparities of the stereogram. The other three subjects made mostly convergent changes for centripetal saccades that allowed reduction of the disparity mainly for the central fixation.

Persistence of the disconjugacy

Most changes persisted under subsequent monocular viewing (Table 1, columns $\Delta_s$). With one exception (subject MB, saccades CL) the changes under monocular viewing and during training were in the same direction (sign of $\Delta_t$ and $\Delta_s$ values). Under monocular viewing, persistence of position-specific changes was best for subjects VJ and MB who showed almost perfect changes during training.

In summary, brief exposure to the non-monotonic distribution of disparity contained by the stereogram produced immediately, at least for a few subjects, substantial position-specific changes in the disconjugacy of the saccades. Such changes persisted even under subsequent monocular viewing.

Static eye alignment

An important question is whether the final static eye alignment (700–900 msec after the end of the rapid part of the saccade) improved the compensation of disparity, particularly for the subjects who did not show intrasaccadic disconjugacy for all fixated positions. As explained in the Methods, to evaluate the static alignment of the eyes we measured the difference in the vergence angle between central and peripheral fixations. These differences for successive fixations in the right field (centre–right–centre) and in the left field (centre–left–centre) are shown in Table 2. For baseline saccades under monocular viewing (Table 2, “Before”) the change in static eye alignment between the central and the peripheral fixations was divergent. This was true for saccades in both fields except in the case of subject MB. Individual values are close to the change in static eye alignment required for accurate binocular fixation of targets presented onto a flat screen in the frontal plane (Fig. 2).

Viewing the stereogram led to increased negative values indicating that the static eye alignment became even more divergent for peripheral fixations. Two subjects (VJ and ML) showed large asymmetry between the left and the right field. Comparison of the individual means of intrasaccadic disconjugacy (Table 1) with the individual measures of the static eye alignment measures (Table 2) shows that in most cases the change in static eye alignment was in extension of the intrasaccadic disconjugacy. Thus, subsequent motion after the saccade improved the compensation of the disparity. This was particularly true for subjects ML, AS and SF who showed weak or

<table>
<thead>
<tr>
<th>Subject</th>
<th>Left field, centrifugal saccades (CL: -)</th>
<th>Left field, centripetal saccades (LC: +)</th>
</tr>
</thead>
<tbody>
<tr>
<td>VJ</td>
<td>Training - Pre $\Delta_t$</td>
<td>Post - Pre $\Delta_s$</td>
</tr>
<tr>
<td>MB</td>
<td>-0.56*</td>
<td>-0.38*</td>
</tr>
<tr>
<td>ML</td>
<td>-0.78*</td>
<td>0.58†</td>
</tr>
<tr>
<td>AS</td>
<td>0.31†</td>
<td>0.22†</td>
</tr>
<tr>
<td>SF</td>
<td>0.10</td>
<td>-</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Subject</th>
<th>Left field, centripetal saccades (RC: +)</th>
<th>Right field, centrifugal saccades (CR: -)</th>
</tr>
</thead>
<tbody>
<tr>
<td>VJ</td>
<td>0.56*</td>
<td>0.31</td>
</tr>
<tr>
<td>MB</td>
<td>0.99*</td>
<td>0.41*</td>
</tr>
<tr>
<td>ML</td>
<td>1.33*</td>
<td>0.85*</td>
</tr>
<tr>
<td>AS</td>
<td>0.17*</td>
<td>-</td>
</tr>
<tr>
<td>SF</td>
<td>0.24*</td>
<td>0.09</td>
</tr>
</tbody>
</table>

$\Delta_s$ difference between the mean value of intrasaccadic disconjugacy over the 15 min of training and the mean value in the baseline monocular viewing condition. $\Delta_s$ difference between the post-monocular viewing condition and the baseline, pre-monocular viewing condition. Positive values indicate convergent changes of disconjugacy. Individual means are based on 10–50 saccades for the monocular viewing conditions. Individual means during the training period are based on 20–200 saccades. Standard errors of $\Delta_t$ and $\Delta_s$ are <0.1 deg.

*A significant change from baseline in the direction which reduces the disparity experienced in the training period or a persistence of this change into the monocular post-training period (t-test at P < 0.05).

†A significant change in the opposite direction.
inappropriate intrasaccadic disconjugacy. Subject VJ's right field viewing is the only exception to the generalization that the disconjugacy produced by the first saccade was sustained or developed further in the post-saccadic period. Her value of change in static eye alignment was almost zero (Table 2, "Right field"), indicating that in this case, the intrasaccadic disconjugacy was not sustained (see Table 1, "Right field"). Nevertheless, she did not complain of diplopia. Five of the individual means ranged from -0.7 to -1.09 deg. These means were close to the requirement (-1 deg.), showing that the static eye alignment was, in these cases, well adjusted to the non-monotonic distribution of disparity of the stereogram. Even under subsequent monocular viewing the change in static eye alignment was more divergent than for monocular viewing before training: six of the eight individual differences between these two conditions (Table 2, A) were negative, three of them reached statistical significance. Thus our study shows that the static binocular eye alignment can also, at least for some subjects, undergo position-specific changes that persist under monocular viewing.

Relation between intrasaccadic disconjugacy and static eye alignment

Are the mechanisms adjusting the intrasaccadic and the static eye alignment coupled? To address this question we looked for a correlation between the intrasaccadic disconjugacy and the change in static eye alignment. In Fig. 5, individual mean values of intrasaccadic disconjugacy are plotted against the corresponding individual mean values of the change in static eye alignment; for each subject four means are shown corresponding to the four classes of the saccades. Before training, under monocular viewing [Fig. 5(A)], the intrasaccadic disconjugacy and the change of static eye alignment were not correlated (r = -0.03). In contrast, during training the coefficient of correlation was high: r = 0.89. For all subjects except VJ the disconjugacy was almost proportional to the change of static eye alignment [Fig. 5(B)]. After training, under monocular viewing [Fig. 5(C)], the coefficient of correlation was also significant (r = 0.73). For both these conditions the coefficient of correlation was estimated for the data of four subjects. As shown in Fig. 5(B, C) the data from

![Image of Figure 5](image-url)

**FIGURE 5.** Individual means of intrasaccadic disconjugacy plotted against the individual mean of change of static eye alignment. (A) Baseline condition under monocular viewing. (B) Viewing the stereogram binocularly. (C) Subsequent monocular viewing. For each subject four means are shown, corresponding to the four classes of saccades (CR, RC, CL and LC). Positive values indicate that the intrasaccadic disconjugacy or the change in static eye alignment are in the direction required by the stereogram. m_l and m_s are the group amplitude means of the intrasaccadic disconjugacy and of the change in static eye alignment. The coefficient of correlation r and the covariance ellipse with its main axis are shown for each scatter plot. In (B) and (C) means and correlation coefficients are for data from four subjects; data from subject VJ were excluded.
subject VJ were far beyond the distribution of the rest of the population and therefore were excluded.

In summary, our training paradigm produced a coupling between the intrasaccadic disconjugacy and the change in static eye alignment. This coupling persisted even under subsequent monocular viewing.

**Dependency of intrasaccadic disconjugacy on the position of the image on the screen**

The persistence of the intrasaccadic disconjugacy for saccades under monocular viewing could be attributed either to oculomotor plasticity or to a high level, associative learning mechanism (see Discussion). To gain some insight we examined whether the induced disconjugacy was acquired with respect to the position of the eyes in the orbit or with respect to a visual reference.

For two of the subjects (MB and ML) who developed persistent disconjugacies, we examined whether their disconjugacies under monocular viewing depended on the position of the random-dot pattern on the screen.

A mirror galvanometer was used to shift the random-dot pattern horizontally. Both the pattern and the central red dot stepped simultaneously 8 deg to the right. The head of the subject remained stabilized by the bite bar. As in all other testing conditions the subject was instructed to saccade back and forth between the laser dot and about 8 deg to the left or to the right. This condition was performed before and after training. Thus, the whole sequence of conditions for these two subjects was as follows: monocular viewing; monocular viewing with the random-dot pattern shifted; training for 15 min; monocular viewing; retraining for about 1 min; monocular viewing with the random-dot pattern shifted. The short retraining period between the two monocular viewing testing conditions aimed to avoid temporal decaying of the learned disconjugacy. Indeed, for subject MB, the mean disconjugacy during the 15 min of training was $-1.11$ and $1.01$ deg for the centrifugal and for centripetal saccades between the critical orbital eye positions (straight ahead and 8 deg to the right, see below); when viewing the stereogram again for 1 min these values were $-0.85$ and $0.83$ deg. For subject ML, mean values during training were $-1.34$ and $1.36$ deg; after retraining for 1 min recovery was complete, $-1.31$ and $1.32$ deg.

Figure 6 shows the sequence of the monocular viewing conditions and the results obtained. We compared the intrasaccadic disconjugacy for saccades that started and ended at the same orbital eye positions: straight ahead and 8 deg to the right. However, the positions of these saccades with respect to the random-dot pattern were different: when the random dot was centred on the screen, these saccades were made in the right part of the pattern; when the random dot was shifted, these saccades were made in its left part. Each monocular viewing condition lasted 1–2 min.

The bar graphs in Fig. 6 show the individual means of disconjugacy for centrifugal and centripetal saccades between the two critical orbital eye positions. Before training the centrifugal saccades from centre to the right side showed small divergence for both subjects, and the centrifetal saccades from right to the centre were almost yoked [Fig. 6(A), bar graphs]. These disconjugacies were not affected by the shift of the random-dot pattern [Fig. 6(B)].

After training the centrifugal saccades starting from the centre and going to the right showed divergence. Centripetal saccades from right back to the centre showed a convergent disconjugacy of a similar amount [Fig. 6(C)]. These disconjugacies were in the direction required by the former training.

Figure 6(D) shows the result of the critical test condition: with the random-dot pattern shifted to the right side, the centripetal saccades of subject MB that now ended at the left part of the random-dot pattern (and not at its centre), lost the acquired convergent disconjugacy. Instead, these saccades showed divergent disconjugacy even though their initial and final orbital positions were the same as in Fig. 6(C). For the centrifugal saccades of subject MB, the divergent disconjugacy disappeared completely. For subject ML, shift of the random-dot pattern produced similar diminishing effects on the acquired disconjugacy ($t$-test, significant at $P < 0.05$). Thus, the induced intrasaccadic disconjugacy persisted under monocular viewing only when the random-dot pattern remained centred on the screen as during training.

**DISCUSSION**

This study shows that dichoptic viewing of two random-dot patterns, creating a disparity field that corresponds to that produced by a three-dimensional object, can induce significant changes in the conjugacy of the saccades and of the static eye alignment.

Similarly to the studies using unequal images (Kapoula et al., 1995), the intrasaccadic disconjugacy appeared, in most cases, immediately and persisted, at least for some subjects, for 1–2 min under subsequent monocular viewing. The change in static eye alignment also persisted under subsequent monocular viewing. Before training the small intrasaccadic disconjugacy was not correlated with the small change in static eye alignment. After training these two measures of oculomotor alignment were positively correlated.

**Saccade–vergence interaction**

It seems unlikely that the induced disconjugacy was produced by slow vergence movements additively superimposed on the saccades. There were no visible slow vergence movements before the saccade. Most of the disconjugacy occurred during the saccade (see Fig. 3). Several studies reported immediate saccade disconjugacy for saccades to targets that differ both in direction and in distance (Enright, 1984, 1986, 1992; Erkelens, Steinman & Collewijn, 1989b; Zee, Fitzgibbon & Optican, 1992). In such situations, saccade disconjugacy mediates most of the vergence changes required for fixations of targets located in different depth. An equivalent description of this disconjugacy is to say that vergence is accelerated during saccades. Zee et al. (1992) developed a model of
the saccade–vergence interaction based on the idea that the omnipause neurons (OPN) serve as a crucial link between the saccade and the vergence bursters. Mays and Gamlin (1992) demonstrated a decrease in vergence velocity when the OPN activity increases, which supports the Zee et al. model. Although the saccade disconjugacy stimulated by our protocol could also be produced at the brainstem by the same saccade–vergence interaction mechanism, the sensory cues to distance are reduced in our situation. For saccades to targets in depth, changes in accommodation and accommodative vergence are involved as one changes fixation from distant to more proximal targets. By contrast, in our protocol the stereogram was projected onto a flat frontal screen and no changes in accommodation were required. Thus our study shows for the first time that disparity alone can induce saccade disconjugacy similar to that observed in the more natural situations of saccades to targets differing in depth.

Normal horizontal saccades to equidistant targets show small disconjugacy which is usually divergent (see Collewijn et al., 1988). Zee et al. (1992) attributed this disconjugacy to differences in the mechanical properties of the lateral and medial rectus. Normal baseline saccades in our experiment also showed usually small divergent disconjugacy. Exposure to the stereogram caused for all five subjects, centripetal saccades to develop substantial convergent disconjugacy. In the examples shown in Fig. 3(F), “Training” and “After”, the initial phase of the intrasaccadic disconjugacy is divergent but the return convergent phase is increased considerably. Such observations provide persuasive evidence for a capability to modify the saccade disconjugacy pattern in any direction, even opposite to the natural divergent disconjugacy.

Position specificity

The most important new finding of this study is that the immediately induced saccade disconjugacy can be position specific. Two of the five subjects were capable of making appropriate disconjugate changes for all three
fixated positions of the stereogram. Two other subjects attempted position-specific changes and succeeded in compensating, at least partially, for the disparity of one or two of the fixated positions of the stereogram. Other studies (Oohira & Zee, 1992; Schor et al., 1993) showed some limitations in position-specific changes even though much longer training periods were used (weeks and hours respectively). As mentioned, Oohira and Zee (1992), used a prism arrangement that required a monotonic but stepwise change of the vergence angle for distinct eye positions. A gradual position-specific change was found rather than an abrupt change. Schor et al. (1993) used a wedge-like position-specific distribution of vertical disparity. They also found a smooth profile of phoria adaptation and suggested a spatial spread out of the adaptation. Thus, our finding of two subjects capable of producing non-monotonic and persistent position-specific changes in intrasaccadic disconjugacy and/or in static eye alignment within 5 min only is remarkable.

Finally, the induced intrasaccadic disconjugacy persisted under monocular viewing only when the random-dot pattern was centred on the screen as during training. This finding, admittedly based on two subjects, sheds light both on the mechanism underlying this disconjugacy and on the reference system used by the CNS to produce such disconjugacy.

**Saccade adaptation vs conditioning**

Persistent disconjugacy could result from an adaptive mechanism such as a parametric adjustment of the saccade signals differently in the two eyes, based on continuous reduction of an error function (i.e. post-saccadic disparity). Such an idea is not compatible with our findings. In most cases the disconjugacy induced appeared immediately. There was no progressive increase of the disconjugacy over the training period. For some subjects (e.g. MB) the immediately induced disconjugacy compensated for the disparity almost 100%. Consequently there was no disparity error to drive adaptation. Clearly these aspects argue against the hypothesis of a slow, progressive parametric saccadic adaptation. The genuine individual differences in the ability to make position-specific disconjugate changes are also not compatible with a low-level oculomotor learning mechanism.

What is the mechanism involved? Kapoula et al. (1995) suggested a multiple conditioning mechanism that associates disparity with the saccade command and monocular depth cues.

In the present study we used random-dot patterns that did not contain monocular cues to depth. Particular care was taken to minimize effects of linear perspective induced by the border of the random-dot pattern. The persistence of the induced disconjugacy under monocular viewing suggests that association of saccades with disparity is sufficient to produce intrasaccadic disconjugacy that becomes independent from immediate disparity input. The hypothesis of associative learning rather than a parametric adaptation of the saccadic system, is supported by the finding that intrasaccadic disconjugacy was reproducible only when the random-dot pattern remained centred on the screen.

A permanent general association between saccade disconjugacy and disparities might be established by continuous exploration of our natural three-dimensional visual world. However, in order to produce large, appropriate disconjugacy for the non-monotonic disparities of the stereogram, associative learning must have operated during our experiment.

Finally, it should be pointed out that our findings do not contradict the existence of slower adaptive mechanisms. Oculomotor parametric adjustments specific to the position of the eyes in the orbit are needed to compensate for oculomotor pareses or other peripheral deficits. Furthermore, as suggested by van der Steen and Bruno (1995) parametric adjustments are more likely to occur for far viewing than for close or the intermediate viewing distances such as those used in the present study.

**Changes in static eye alignment**

Schor et al. (1990, 1993) observed that vertical phoria-adaptation does not transfer to the disconjugacy of vertical saccades. These studies tested specifically phoria adaptation and eliminated stimulation of the saccadic system. Consistent with this result, we observed that the small baseline intrasaccadic disconjugacy is not correlated with the small change in static eye alignment. The training paradigm, however, did produce a positive correlation between these two values and this correlation was present even under subsequent monocular viewing. In contrast to the study of Schor et al. (1990), in the present study binocular disparity was continuously present before, during and after the saccade. Consequently this stimulated both mechanisms, the one adjusting the intrasaccadic disconjugacy and the mechanism controlling the static eye alignment. Thus, the correlation reported here suggests a functional coupling between these two aspects of binocular oculomotor control that aimed to reduce post-saccadic disparity. Our findings are also in agreement with the study of Findlay and Harris (1993) who used disparate targets and observed larger vergence movements after saccades with marked disconjugacy.

**Reference systems**

We found that the shift of the random-dot pattern on the screen reduced the acquired disconjugacy. This result suggests that the disconjugacy was acquired with reference to the position of the saccades on the random-dot pattern and not with reference to the position of the eyes in the orbit. In other words, the CNS would use a visual reference to acquire and memorize the saccade disconjugacy.

In conclusion, our results suggest the existence of a fast associative learning mechanism, working on a higher level than brainstem oculomotor adaptive mechanisms. Interestingly, the associative mechanism proposed here is capable of making non-monotonic position-specific disconjugate changes of the saccades. Such ability might be particularly useful when viewing close objects differing...
in depth. Disparities contained by such stimuli are usually not specific to the position of the eyes in the orbit. Rather, they are closely linked to the position of the objects in the visual space. This might explain the importance of the visual reference in acquiring and memorizing the position-specific saccade disconjugacy presented in this study.

REFERENCES


Acknowledgements—The authors thank Dr Findlay for helpful comments on the manuscript and Dr T. Hain for providing the initial PC version of the REX, MARK and PRINT software. This research was supported by the European Community contract SCI*-CT91-0747 (TSTS) and a grant from the French CRAMIF.