Disconjugate Adaptation of the Vertical Oculomotor System

ZOI KAPOULA,*† THOMAS EGGERT,* MARIA PIA BUCCI*

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Conjugate post-saccadic eye drift can be induced in normal humans if a visual pattern is made to drift after every saccade. This study examines the ability of normal humans to create disconjugate vertical post-saccadic drift. Identical fuseable patterns were presented dichoptically, one to each eye. At the end of each vertical saccade one pattern drifted up and the other down, by 5% of the saccade amplitude. Five subjects were trained for 2–3 hr. Eye movements were recorded with eye coils. Normal vertical saccades along the midline were remarkably conjugate and post-saccadic drift was minimal. Training produced only small disconjugate post-saccadic drift (0.14 deg) but substantial saccade amplitude disconjugacy (0.70 deg). For several subjects, the induced disconjugacies persisted even for saccades in the dark indicating that adaptive changes occurred in the binocular coordination of vertical saccades. Apparently vertical disparate post-saccadic retinal slip is not sufficient to stimulate significantly the saccade pulse-step matching mechanism which is believed to control post-saccadic eye drift. The changes we observed aimed to reduce position disparity and not retinal slip in each eye. Copyright © 1996 Elsevier Science Ltd.

INTRODUCTION

Lesions of the extra-ocular muscles or central pathways are often unilateral and can cause saccade dysmetria as well as post-saccadic drift in only one eye; such disorders can compromise single binocular vision. Disconjugate adaptive mechanisms are needed to correct dysmetria and suppress the retinal slip in the affected eye only. The present study examines the capability to make disconjugate adaptations in post-saccadic eye drift.

Several recent studies demonstrated slow and fast disconjugate adaptations in saccade amplitude (e.g. Lemij & Collewijn, 1991a,b; Oohira et al., 1991; Oohira & Zee 1992; Schor et al., 1990; van der Steen & Bruno 1995; Kapoula et al., 1995). However, altering the amplitude of the saccade between the two eyes may be a different adaptive mechanism than altering post-saccadic drift. Disconjugate adaptation in saccade amplitude may be obtained by readjusting the pulse command separately for each eye. Post-saccadic eye drift is believed to be due to inappropriate matching of the amplitudes of the pulse and step of the saccadic neural signals. Disconjugate post-saccadic drift may be created by readjusting the matching of the pulse-step signals differently in the two eyes.

One error signal used to control conjugate post-saccadic eye drift is the retinal slip of the images. When ocular drift is simulated by causing the visual scene to move transiently after every saccade, the adaptive mechanism is stimulated to produce post-saccadic eye drift that reduces the retinal slip; this drift persists after spontaneous saccades made in the dark. This has been demonstrated in the monkey (Optican & Miles, 1985) and in humans (Kapoula et al., 1989).

Kapoula et al. (1990) attempted to induce disconjugate post-saccadic drifts. A dichoptic viewing arrangement allowed the provision of a different image to each eye. The two visual images (random dots) were similar but not fuseable. Post-saccadic eye drift was induced by holding the image still for one eye and drifting it for the other. Only conjugate changes were obtained, with both eyes responding to the mean retinal slip in the two eyes. The cause of this failure could be that the two images were not fuseable.

It is hypothesized that disconjugate post-saccadic drift adaptation is driven by the process of obtaining binocular fusion of disparate images. Consequently, in the present study fuseable images are used. Fusion is challenged at the end of each saccade by drifting the images in opposite directions. In addition to the retinal slip velocity this sort of visual stimulation provides a position disparity signal. To avoid complications arising from the contribution of
the horizontal disparity-vergence system and stereopsis, this study examines the capability to create vertical disconjugate drift following vertical saccades. The range of vertical disparity-fusional movements is limited and vertical disparities alone have no input to the stereoscopic depth system. We found only moderate vertical disconjugate post-saccadic drift adaptation. Instead, significant adaptive disconjugacy occurred in the amplitude of the saccades.

**METHODS**

**Subjects**

Eye movements were recorded from four subjects before, during, and after they experienced optically imposed, disconjugate post-saccadic retinal image motion. Ages ranged from 19 to 35 yr. Each subject underwent a neuro-ophthalmological examination. Four subjects were emmetropes with normal binocular vision (TNO test for stereoscopic vision was 60 sec arc or better). They all had right eye dominance. This study was approved by the French ethics committee CCPRPB No. 15. Subjects participated in our experiments after giving informed consent.

**Eye movement recording**

Stimulus presentation and data collection were directed by REX, a UNIX software developed for real-time experiments and run on a PC (HP RS/20). Before and after training, movements of both eyes were recorded with the search coil-magnetic field method (Robinson, 1963; Collewijn _et al._, 1975). Subjects sat in a dark room, 100 cm in front of a translucent screen onto which could be rear-projected a laser dot for calibration. Their head was stabilized by a bite bar (with individually fitted dental impression of the subject's upper teeth) and a forehead support. Horizontal and vertical movements of each eye (L—left, R—right) were recorded simultaneously. Calibrations were determined for each individual eye when it alone viewed the laser dot that stepped to ±10, ±15 and ±20 deg vertically along the midline and horizontally. The eye-position signals were filtered with a bandwidth of 0–200 Hz, digitized with a 12-bit analogue-to-digital converter sampling each channel 500 times per second and stored on digital tape for off-line use.
Adaptation paradigm

Two identical slide projectors were used to rear-project on the screen two slides of a pattern consisting of a circle (white on a black background) with a central fixation point and three horizontal lines [a central line and two lines symmetrically placed at 8 deg up and down, Fig. 1(A)]. The pattern subtended 32 deg at 1 m viewing distance, the fixation points were 0.67 deg across and pattern lines were 0.36 deg wide. Except for these patterns the room was dark and no stationary frames were visible. The beams of the projectors were polarized 90 deg apart. Subjects viewed through filters also polarized 90 deg apart mounted on a frame attached to the forehead rest (Dubois-Poulsen, 1979); thus each eye saw a different image. Two X–Y mirror-galvanometers (General Scanning CX660) were used to drift the patterns at the end of each saccade [Fig. 1(A)].

At the beginning the patterns were superimposed and we made sure that subjects fused and saw a single pattern. Subjects were asked to saccade between the different points of the pattern located in the midline. A typical sequence was: from the centre to the upper line, then to the top of the pattern and then back to the centre; similarly for bottom half. At the end of each saccade, detected by the computer, one pattern drifted up the other down by the same amplitude, 5% of the vertical component of the antecedent saccade; this produced a vertical disparity of 10% of the saccade (typically <1.5 deg). Drift of the patterns was exponential (time constant of 50 msec). The pattern of the left eye drifted upward (up after up saccades, down after down saccades), while the right eye pattern drifted downward [Fig. 1(B)]. This required a different change in the pulse-step ratio for each eye but the change was the same for up and down saccades.

During training eye movements were recorded continuously by the electro-oculogram (EOG). Subjects were instructed to try to maintain fusion. To keep the disparity within a fuseable range (<1.5 deg), a computer algorithm evaluated the amplitude of the disparity resulting from the opposite drifts of the patterns after each saccade. If the disparity exceeded 1.5 deg (due to the accumulation of unequal vertical motions over successive saccades), a step of opposite sign was applied to the mirror galvanometers during the next saccade to recentre the patterns on the screen. The rate of occurrence of such resets was modest (24% of the saccades in the training condition); the direction of the resetting mirror movement was not coupled with the direction and amplitude of the ongoing saccade. Thus, the actual disparity encountered at the end of such a saccade was not strictly proportional to the saccade amplitude, but neither was it statistically dependent on eye position. Retinal slip per se was proportional to the saccade amplitude. The EOG signal was adequate for detecting saccade onset and its direction. It was recalibrated after each pause (every 30 min). For subject EB, more frequent recalibrations were required (at about 20 min interval). Head stabilization and calibration procedures were the same as for the eye coil recordings.

In three pilot experiments run on subjects EB, JL, YL, training periods of 1.5 hr were applied. No consistent adaptation occurred. Thus, in all experiments presented here subjects were trained for 2.5–3 hr using short rests every 30 min.

Before training we also tested static (non-saccadic) vertical fusion responses. Subjects were asked to fixate at the central fixation point. Then disparity was introduced by moving the two patterns in opposite directions. The left eye pattern moved up, the right moved down, exponentially (time constant 50 msec). In consecutive trials, the amplitude of disparity produced was increased from 0.5 to 1 deg and then to 1.5 deg. Subjects were asked to indicate when fusion was lost and their eye movements were recorded.

Data analysis

Calibration factors were extracted from saccades to the laser dot. They were obtained for each eye individually by matching eye position with target position when the eyes were steadily fixating the target (usually after the corrective saccade). A polynomial function with five parameters was used to fit the data. Measured eye position data were thus corrected for the intrinsic sine nonlinearity of the coil system and for the tangent screen effect. Off-line computer algorithms were used to determine the times of saccade onset and offset. To determine saccade onset the algorithm looked for a saccade when the peak velocity exceeded 100 deg/sec. It then found peak saccade velocity and, scanning backward, onset was determined as the time when eye velocity reached 5% of the peak velocity. Saccade offset was taken as the time when eye velocity of either eye dropped below 15 deg/sec [Fig. 1(C)]. The placement of these computer-generated marks was corrected by a human operator. Post-saccadic eye drift was determined for a period of 160 msec after saccade offset. This value was chosen to be near that of the ocular drift in lesioned animals (Optican & Robinson, 1980); the time constant
FIGURE 2. Saccades in the presence of the adapting moveable patterns for subject JL together with the corresponding disconjugacy (left–right vertical eye position difference). LE and RE are the left and right eye position traces. Lower traces are the transducer outputs of the mirror galvanometers and show the instantaneous position of the pattern seen by each eye. (A) and (B) show up saccades, (C) and (D) down saccades. At the beginning (A, C), eye motion in the direction of the drifting patterns is seen at the points marked by the tics. After 3 hr of training an up saccade (B) shows noticeable inequality in its amplitude between the two eyes; a slow disconjugate motion is also visible about 170 msec after the end of the saccade. A down saccade (D) is yoked in the two eyes but is followed by a small disconjugate drift that starts immediately after the end of the saccade. An enhancement of this response occurs about 100 msec later.

of such drift is 50 msec, requiring approximately 160 msec for the eye to reach the steady-state position.

In contrast to prior studies the vertical disconjugacies induced in the present study were poorly correlated with saccade size. Consequently, disconjugacy was expressed in degrees rather than in percentage of the saccade size. For each saccade we measured the vertical disconjugacy (L–R eye difference) of the amplitude of the saccade, of post-saccadic drift and the total steady-state disconjugacy (see below). Positive values indicate adaptive disconjugacies in the appropriate direction regardless of the saccade direction.

RESULTS

Qualitative observations

Changes in sensory fusion. Before training, the threshold of vertical disparity beyond which subjects
reported diplopia was 1 deg for all four subjects tested (EB, JL, YS and SC). During training sensory fusion was evaluated regularly by asking subjects to indicate when they experienced double vision. Towards the end of training, subjects SC and YS claimed to be able to fuse even the largest post-saccadic disparities of 1.3–1.5 deg occurring after saccade amplitudes of 13–15 deg.

**Changes in saccade amplitude and post-saccadic drift.** Figure 2 shows ocular responses in the presence of the adapting moving patterns recorded at various times for up and down saccades during training. Initially, disconjugate movements in the direction of the pattern motions occurred only 45% of the time. The latency of these movements was measured for two subjects. The saccade traces and the corresponding disconjugacy trace were displayed on the computer screen. The investigator marked the time point when the most abrupt change in the disconjugacy trace occurred [vertical ticks, Fig. 2(A) and (C)]; the disconjugacy trace was displayed on a high resolution scale. This point was taken as the latency of the disparity fusion. For subject SC this latency was 190 ± 5 msec (±SEM, n = 108); for subject JL this value was 205 ± 7 msec, n = 55. These latencies are in the range of the latency of fusional disparity movements. Furthermore, similar to fusional movements seen by Houtman et al. (1981) and Perlmutter and Kertesz (1978), the delayed disconjugate movement shown in Fig. 2(A) is small in amplitude and asymmetric in the two eyes. Such movements are presumably fusional responses to the disparity resulting from the opposite drifts of the patterns. After 3 hr of training, the disparity-driven response for up saccades was still delayed but the amplitude of the saccade itself was larger in the left eye that was exposed to onward slip [Fig. 2(B)]. Down saccades exhibited a consistent but small disconjugate eye drift that started immediately after the end of the saccade [Fig. 2(D)]. This was enhanced by the disparity fusional system entering the response later.

Figure 3 shows typical examples of vertical saccades before and after training made in the dark, precluding any visual disparity fusional response. Normal saccades recorded before training were almost perfectly yoked [Fig. 3(A) and (C)]. Note in the disconjugacy trace a transient change in the vertical eye alignment that is restored at the end of the saccade. Post-saccadic drift, if any, was also largely conjugate in the two eyes. After training, binocular yoking of the saccades was altered. Even in the dark, up saccades were larger in the left eye which was exposed to onward retinal slip [Fig. 3(B)]. Note, however, the small monocular corrective movement in the right eye that almost cancels the intrasaccadic adaptive disconjugacy of the primary saccade and realigns the eyes. This was typical for this subject. Down saccades in the adapted state exhibited small disconjugate drift in the direction of the former pattern motion used for training. All subjects showed mainly disconjugacies in saccade amplitude and/or some disconjugate post-saccadic eye drift with zero latency. The direction for which adaptive disconjugacy occurred mainly in the amplitude of the saccade, instead of the expected disconjugacy in post-saccadic drift, varied with subjects.

**Quantitative data**

Table 1 shows individual mean disconjugacies in the pulsatile component of the saccade ΔP, in post-saccadic drift ΔD and the total, steady-state disconjugacy ΔS. These values are shown for normal vertical saccades in the dark and after training for both saccades in the dark and in the presence of the adapting patterns. Since saccades were spontaneous, their sizes varied. Before training, individual mean amplitude of saccades varied from 17 to 22 deg; after training the range of the mean amplitude of saccades in the dark was 13–25 deg. During training this range was smaller: 14–16 deg.

Normal saccades in the dark were well-yoked in the two eyes. With one exception (YS upward saccades), the total saccade disconjugacy was <0.5 deg. There was no consistent bias in the sign of the disconjugacy for upward and downward saccades. In several cases (five out of eight) post-saccadic drift disconjugacy reduced or cancelled the intrasaccadic disconjugacy. Thus, the disconjugacy in normal vertical saccades along the midline was rather transient. Only two out of the eight normal total disconjugacy measures, which show the disconjugacy of the eyes 160 msec after the end of the saccade, were significantly different from zero (indicated by an *). The group mean total disconjugacy was zero.
TABLE 1. Intrasaccadic $\Delta P$, post-saccadic $\Delta D$ and total disconjugacy $\Delta S$ (in deg) before and after training

<table>
<thead>
<tr>
<th>Subject</th>
<th>Normal Dark</th>
<th>Dark</th>
<th>After training</th>
<th>With adapting stimulus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\Delta S$</td>
<td></td>
<td>$\Delta D$</td>
<td></td>
</tr>
<tr>
<td>EB</td>
<td>0.19±0.83</td>
<td>0.04±0.22</td>
<td>1.02±0.67†</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.47±0.92* (44)</td>
<td>0.00±0.33† (93)</td>
<td>1.02±0.66† (185)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-0.27±0.3*</td>
<td>0.03±0.36†</td>
<td>0.01±0.15†</td>
<td></td>
</tr>
<tr>
<td>JL</td>
<td>0.06±0.21</td>
<td>0.41±0.44†</td>
<td>0.47±0.55†</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.16±0.30* (21)</td>
<td>0.81±0.46† (46)</td>
<td>0.52±0.53† (140)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-0.10±0.22*</td>
<td>-0.41±0.38†</td>
<td>-0.06±0.23</td>
<td></td>
</tr>
<tr>
<td>SC</td>
<td>0.46±0.91†</td>
<td>0.65±0.71</td>
<td>1.12±0.97†</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.55±0.89* (81)</td>
<td>0.53±0.60 (31)</td>
<td>0.66±0.92 (58)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-0.09±0.43</td>
<td>0.12±0.21†</td>
<td>0.46±0.38†</td>
<td></td>
</tr>
<tr>
<td>JL</td>
<td>-0.82±1.53*</td>
<td>0.20±0.70†</td>
<td>0.60±0.61†</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-0.66±1.48* (81)</td>
<td>0.24±0.68† (129)</td>
<td>0.59±0.61† (433)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-0.16±0.25*</td>
<td>-0.04±0.29†</td>
<td>0.02±0.20†</td>
<td></td>
</tr>
<tr>
<td>SC</td>
<td>0.34±1.39</td>
<td>0.59±0.54</td>
<td>1.73±1.51†</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.24±1.27 (35)</td>
<td>0.38±0.53 (26)</td>
<td>1.42±1.51† (48)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.10±0.34</td>
<td>0.21±0.18</td>
<td>0.31±0.33†</td>
<td></td>
</tr>
<tr>
<td>YS</td>
<td>0.02±0.75</td>
<td>0.35±0.65†</td>
<td>0.53±0.51†</td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.10±0.79 (58)</td>
<td>0.50±0.69† (65)</td>
<td>0.39±0.49† (397)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-0.09±0.24*</td>
<td>-0.15±0.28</td>
<td>0.14±0.20†</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>-0.00±0.40</td>
<td>0.26±0.31</td>
<td>0.84±0.46†</td>
<td></td>
</tr>
<tr>
<td>means</td>
<td>$\Delta P$</td>
<td>0.10±0.40 (8)</td>
<td>0.24±0.42 (8)</td>
<td>0.70±0.40† (8)</td>
</tr>
<tr>
<td></td>
<td>$\Delta D$</td>
<td>-0.10±0.11*</td>
<td>0.01±0.22</td>
<td>0.14±0.17†</td>
</tr>
</tbody>
</table>

Values are means in deg±1 SD; each mean is based on the number of saccades $n$ indicated in parentheses. The typical value of $n$ is 102 but in some cases, especially for baseline normal saccades in the dark, $n$ dropped to as low as 14. Positive values indicate that the amplitude of the saccade, or the final step amplitude is larger in the left eye or that the left eye has more onward drift than the right eye.

*Indicates normal disconjugacies that are significantly different from zero ($t$-test). Total means are algebraic ($n = 8$).

†Change from normal that was statistically significant at the level $P<0.05$ ($t$-test comparing means before and after training).

‡Indicates a significant change from normal but in the wrong direction. Note that, except for round-off errors, $\Delta S$ is the sum of $\Delta P$ and $\Delta D$.

The group mean disconjugacy in the amplitude of the saccade was 0.10 deg; this is not statistically different from zero. The mean disconjugacy in post-saccadic drift was also very small: -0.10 deg. These results are in agreement with prior reports on visually guided saccades (Collewijn et al., 1988) and show that the binocular yoking of vertical saccades along the midline is maintained even in the dark.

After 3 hr of exposure to disconjugate retinal slip, binocular yoking of vertical saccades was significantly altered for all subjects. While still viewing the drifting patterns, all disconjugacies were in the direction of the patterns' motion; 20 of the 24 measures differed significantly from normal values (Table 1, With adapting stimulus, dagger). Subject JL for up saccades and subject EB for down saccades showed a significant disconjugacy in the amplitude of the saccades only. In contrast, subject SC's up saccades and subject JL's down saccades showed a significant disconjugacy in the good direction in post-saccadic drift only. In the remaining cases disconjugate changes in the good direction occurred in both the amplitude of the saccade and post-saccadic drift. The former was always larger. Prominent disconjugacy in post-saccadic drift (>0.20 deg) occurred in two subjects only, JL and SC. The rate of occurrence of disconjugate drift for subject SC was 93% and 87% for up and down saccades, respectively. The group mean total disconjugacy was 0.84 deg; this is 57% of the required disconjugacy. The group mean disconjugacy in saccade amplitude was 0.70 deg, i.e., 47% of the requirement. The group mean disconjugacy in post-saccadic drift was 0.14 deg, that is, only 10% of the requirement. Thus 82% of the induced disconjugacy occurred during the saccade itself. All group values were significantly different from normal values in the dark. It should be noted that saccade amplitude disconjugacy was not consistently observed in the preliminary study using shorter training (1.5 hr): only 23% of EB's downward saccades showed a disconjugacy in the appropriate direction, and the same was noted for 68% of JL's upward saccades. In the present study these
values were 96 and 87%, for EB and JL, respectively. Thus, saccade amplitude disconjugacy and the disconjugacy in post-saccadic drift in the first 160 msec after the saccade were both adaptive, open loop phenomena in the sense that they developed progressively and could not be influenced by immediate visual feedback. To test for further evidence of their adaptive nature we examined their persistence for saccades in the dark.

Seventeen of the twenty-four measures of disconjugacy in the dark (i.e., 71% of the measures, Table 1, After Training, Dark) changed in the direction of the former motion of the patterns used for training. Statistically significant adaptive changes in post-saccadic drift disconjugacy (ΔD) occurred in four of the eight cases (EB, SC, YS up saccades, JL down saccades). The rate of occurrence of disconjugate drift in the appropriate direction was measured in three cases: JL, down saccades 93%, EB and SC up saccades 76 and 74%, respectively. Thus in these cases post-saccadic drift disconjugacy in the dark, was significantly and consistently in the direction of the former adapting stimulus but its amplitude was small. Statistically significant changes in saccade amplitude (ΔP) occurred in three out of the eight cases; they were all larger in amplitude than the disconjugacy in post-saccadic drift (JL, YS up saccades, YS down saccades, Table 1). Note that in the preliminary studies in which the duration of the training was briefer no persistent saccade amplitude disconjugacy was observed.

In general, the changes from normal values were in the same direction for saccades in the presence of the adapting stimulus and for saccades in the dark, both recorded after training. There were three exceptions, however. Subject JL showed an unexpected disconjugacy in the wrong direction for saccades in the dark; this occurred in post-saccadic drift for up saccades and in saccade amplitude for down saccades. These disconjugacies reduced or even reversed the disconjugacy in saccade amplitude and post-saccadic drift that was in the direction of the adapting stimulus [see also Fig. (3B)]. Similar conflicting disconjugacies in the rapid part of the saccade and in post-saccadic drift, as already mentioned, occurred frequently for normal saccades in the dark. They allowed the eyes to realign as quickly as possible after the saccade. Subject EB’s up saccades in the presence of the adapting stimulus exhibited marked disconjugacy in the amplitude of the saccade. In the dark, this disconjugacy vanished. Thus, the adaptive changes were not always sustained in the dark.

In the remaining cases the changes in the dark, particularly those in saccade amplitude disconjugacy, were, in general, smaller than those in the presence of the drifting patterns. This phenomenon was seen in prior studies (Kapoula et al., 1989, 1993) and suggests context specificity or a visual enhancement of the adaptive mechanism. The group mean of the total disconjugacy of the saccades in the dark was 0.26 deg; this value was significantly different from zero and its change from the normal value tended towards statistical significance (P < 0.11). The mean disconjugacy of the amplitude of the saccades was 0.24 deg, and that of post-saccadic drift was only 0.01 deg; neither value differed significantly from normal values.

In summary, in the presence of the adapting stimulus, all subjects showed statistically significant and appropriate changes in post-saccadic drift and/or in saccade amplitude. In contrast, in the dark, significant changes only occurred for a few subjects. However, the majority of the disconjugacy measures in the dark (71%) showed small changes from normal values in the appropriate direction; in contrast to baseline values, all individual means and the group mean of the total disconjugacy were significantly different from zero.

Disconjugate drift in the presence of the adapting stimulus adaptive?

Busettini et al. (1994) reported ultra-short latency horizontal vergence movements to steps of convergent or divergent disparity delivered with a variable delay (30–300 msec) after the end of a saccade. Latencies as short as 50–60 msec were observed in the monkeys and somewhat longer in humans (about 70–80 msec). The existence of a similar phenomenon for vertical disparity fusional movements is not yet known. However, to exclude such a possibility we measured the disconjugacy in the average velocity over the first 80 msec after the end of the saccade after training with the adapting stimulus. For normal saccades, the group mean (n = 8, four subjects measured with up and down saccades) of the initial velocity was -0.21 ± 1.44 deg/sec (± SD, range -2.33–2.11 deg/sec). After training drift velocity disconjugacy in the first 80 msec was consistently in the direction of drifting patterns. The group mean value was 1.17 ± 1.36 deg/sec (range of individual means: -0.7–3.72 deg/sec). This group mean value differed significantly from the normal value (t-test significant at the P < 0.05 level). The most prominent changes in initial drift velocity occurred for subjects SC up saccades, JL, SC, YS down saccades. We conclude that in the presence of the drifting patterns, disconjugate motion of the eyes in the first 80 msec after the end of the saccade is part of the adaptive response. Sensory-driven disparity fusional movements probably did account for extending the eye drift after this period.

Additional observations

Disconjugate vs disjunctive post-saccadic drift. Disjunctive movements are a special type of disconjugacy in which the eyes move in opposite directions. Such movements were necessary to reduce both the retinal slip in each of the individual eyes and the position disparity resulting from the opposing pattern drifts. Before training, in most cases, both eyes were drifting in the same direction but the drift was larger in the right eye. The group mean drift was 0 ± 0.29 deg (± SD) and 0.10 ± 0.34 deg for the left and the right eye, respectively. Adapted saccades in the presence of the drifting patterns showed disjunctive post-saccadic drift in only four cases:
subject SC up saccades, subjects JL, SC, YS down saccades. In the remaining cases the eyes were drifting in the same direction. The group means were $-0.01 \pm 0.23$ and $-0.15 \pm 0.11$ deg for the left and right eye, respectively (negative sign indicates backward drift). For saccades in the dark disjunctive movements in drifts were absent: the group means of drift was $-0.03 \pm 0.26$ deg for the left eye and $-0.04 \pm 0.28$ deg for the right eye. These findings show a limited capability to create disjunctive, vertical post-saccadic eye drift. The small drift disconjugacy we induced succeeded better in reducing position disparity than retinal slip of each eye.

**Time course of post-saccadic drift.** Prior studies (Kapoula et al., 1989) induced conjugate post-saccadic eye drift that had a simple exponential time course. In contrast, for all testing conditions of the present study, the large majority of the disconjugacy of post-saccadic eye motions (about 70% of the saccades after training) was not exponential. The post-saccadic drift for each individual eye was not exponential either.

**Vertical disconjugate adaptation in microstrabismus.** Subject SR had a long-standing convergent microstrabismus and performed the experiment with her habitual glasses (+5 D in both eyes). Her deviation was 4 prism D with her glasses on and 16 prism D without; she also had a vertical right eye hyper-deviation of 2 D. Orthoptic examination revealed the presence of a 2 deg central, suppression scotoma of the image of one eye that switched with the fixating eye. This subject had perifoveal and peripheral but not foveal fusion. Corrected visual acuity was 20/20 for both eyes but stereoaquity was below normal (200 sec arc). Her results were similar to those of normal subjects. For up saccades she showed statistically significant changes in post-saccadic drift only: the mean post-pre-training change was 0.48 deg for saccades in the presence of the adapting drifting patterns, and 0.28 deg for saccades in the dark. For down saccades she showed significant changes in saccade amplitude only: 0.31 deg with the patterns, 0.71 deg in the dark. Thus, foveal fusion is not necessary to achieve disconjugate adaptations.

**Vertical disparity fusional movements.** Were the dynamics of the small post-saccadic disconjugate motion similar to those of static (nonsaccadic) fusional move-
ments to vertical disparities? Disparity movements were recorded from subject YS on a different day. The procedure was similar to that described in Methods for static fusion responses.

The maximum vertical disparity that could be fused was 1 deg both before and after 30 min of recording vertical fusional movements. Thus, the sensory component of the vertical fusional system did not change after performing repetitively vertical fusional movements. Figure 4(A) shows typical vertical disparity fusional responses. All responses are asymmetric, the right eye is drifting downward while the contribution of the left eye could be almost zero. The latency of these fusional responses was long and variable (200–400 msec). The time required by the right eye to reach 63% of its final amplitude was also long and variable: 500–1000 msec. Figure 4(C) shows the difference between the left and right eye for several disparity fusional movements. The mean time required to reach 63% of the total fusional response is long, approximately 700 msec. In Fig. 4(B) the disconjugacy traces are shown for a group of down saccades in the presence of the adapting drifting patterns. The post-saccadic motion seemed composed of two parts (between the two arrows) with an approximate time constant of 80 msec and a second component (beyond the second arrow) with an average time constant of approximately 160 msec. Thus, the induced disconjugacy of post-saccadic eye drift, although small in amplitude and slower than the retinal slip, was faster than the normal, static vertical disparity fusional movements.

**DISCUSSION**

*Limits in disconjugate control of vertical post-saccadic drift*

The present study was designed to test for the capacity of the oculomotor system for disconjugate vertical post-saccadic eye drift. After 3 hr of training and while still viewing the adapting stimulus, a significant change in drift in the stimulus direction occurred for most of the subjects. The amplitude of this change, however, was small: 0.24 deg (Table 1, total means Normals vs After training); the group mean change consisted of an inversion of the sign of the baseline drift disconjugacy rather than an increase of the amplitude of the disconjugacy. Despite the fact that the change in eye velocity was small it was apparent during the first 80 msec after the end of the saccade. The long latency of the vertical motor fusional system or other visual following systems exclude their contribution during this early post-saccadic period. Thus, in the presence of the adapting stimulus, the early part of the post-saccadic drift was part of the adaptive response. In the dark, the change in post-saccadic drift was even smaller (total mean change: 0.11 deg); statistically significant changes occurred only for a few subjects.

An increase of the zero-latency post-saccadic drift with a visual stimulus was observed in prior studies dealing with the conjugate post-saccadic drift adaptation mechanism (Kapoula et al., 1989, 1990, 1993). There are, however, fundamental differences in the vertical disconjugate post-saccadic drift examined here. In the former studies, the induced conjugate post-saccadic drift was much larger [10% for saccades in the light and 6% in the dark, Kapoula et al. (1989)] and it was exponential and positively correlated with the amplitude of the saccade. In the present study, drift disconjugacy was not correlated with the amplitude of the saccade. Neither the post-saccadic drift of individual eyes nor their difference was exponential. Thus, the main result of this study is that although disconjugate change in vertical post-saccadic eye drift can be induced, its amplitude is limited and does not exceed the range of the naturally occurring small disconjugacy in drift. Evidently, our experiments did not significantly stimulate the pulse-step matching adaptive mechanism which is believed to control post-saccadic eye drift and retinal slip. That the drift was not systematically disjunctive (in opposite direction in the two eyes) suggests that the principal effect of the small drift disconjugacy is to reduce position disparity and not retinal slip in each of the two eyes.

It may be important that our subjects’ proprioceptive signals would be in conflict with the retinal slip and visual disparity information. The conjugate post-saccadic drift mechanism can be efficiently stimulated by retinal slip information alone (see Optican & Miles, 1985; Kapoula et al., 1989). In contrast, the vertical disconjugate post-saccadic eye drift adaptive mechanism may depend more on proprioceptive information. Lewis et al. (1994), have presented evidence for the contribution of proprioceptive signals in the long-term adaptive mechanisms that control the alignment of the eyes during fixations and saccades. Thus, although our study in normals shows only a limited adaptive capability of vertical post-saccadic drift, long-standing pathological drifts in cases of vertical unilateral paresis may still be efficiently correctable by plastic adaptive mechanisms receiving both visual and proprioceptive signals.

*Significance of adaptive disconjugacy in saccade amplitude*

We found substantial disconjugacy in the amplitude of the saccades. The average disconjugacy in saccade amplitude for all subjects was 0.70 deg in the light and 0.24 deg in the dark (Table 1). Saccade amplitude disconjugacy is adaptive in the sense that it reduced, in a predictive way, the final position disparity resulting from the pattern drifts thereby lessening the need for post-saccadic drift adaptation. As mentioned previously, with only 1.5 hr of training it was not possible to induce saccade amplitude disconjugacy consistently in the direction of the drifting patterns, or to induce persistence of the disconjugacy in the dark. Thus, the consistent disconjugacy obtained with longer training and its persistence, found in a few subjects, confirms the existence of adaptive changes in the binocular coordination of vertical saccades. However, this form of adaptation, despite its larger amplitude, was more context
specific or visually dependent than the adaptation in post-saccadic eye drift.

Mechanisms for making disconjugate vertical adaptations

There is neuroanatomical evidence for the substrate of Hering's law of equal innervation of the eyes during vertical saccades (Moschovakis et al., 1990). Moschovakis et al. (1991) found that upward, medium-lead, burst neurons in the rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF) contact motoneurons innervating both the superior rectus and the inferior oblique muscles of both eyes. Downward, medium-lead, burst neurons in the same area project to motoneurons that innervate the ipsilateral inferior rectus muscle and the contralateral superior oblique muscle (Moschovakis et al., 1991). Vertical, medium-lead, burst neurons also project to the interstitial nucleus of Cajal which is believed to perform the velocity to position integration for vertical movements.

The binocular coordination of normal vertical saccades in our study reveals an extraordinary degree of yoking of the eyes even during spontaneous vertical saccades in the dark. This is consistent with the anatomical evidence of Moschovakis et al. (1990) for a single vertical generator controlling both eyes. However, this high degree of binocular yoking is presumably assured by disconjugate adaptive mechanisms operating continuously to compensate for asymmetries in the oculomotor plant or other adaptive mechanisms operating continuously to compensate for asymmetries in the oculomotor plant or other inevitable changes due to development, diseases, etc. Our study does show that vertical yoking can be altered after only 3 hr of experience of disconjugate post-saccadic retinal slip.

If so, in what structures could disconjugate adaptation take place? Our finding of larger disconjugate adaptation in saccade amplitude than in post-saccadic drift suggests that adaptive modification occurred downstream from the saccade pulse-step generator, most likely at the motoneuron pools innervating individual eye muscles. The gain of the motoneuron populations in the ipsilateral and the contralateral oculomotor nucleus innervating respectively the inferior rectus and the superior rectus of one eye would change while those of the other eye would remain unchanged. A parametric adjustment at that level would modulate both the pulse and the step components. Consequently, saccades may become unequal but they will not show marked post-saccadic drift.

Another way to obtain adaptive disconjugacy of vertical saccades could be a differential change in the contribution of the superior and inferior oblique muscles who also have important vertical actions, as depressor and elevator, respectively. Recent studies reported substantial conjugate torsion during disparity-induced vertical fusional movements. Enright (1992) attributed torsion to muscular constraints and emphasized the role of the oblique muscles, while Van Rijn and Collewijn (1994) suggested a central link between torsion and vertical fusional movements.

Finally, adaptive disconjugacy of the vertical saccadic system could be produced by coupling the conjugate vertical saccadic system with the adaptive, three-dimensional map proposed by Ygge and Zee (1995). Such a map would serve to overcome the natural vertical disparities occurring for proximal targets away from the midline (since lateral targets subtend a larger visual angle in the closer eye). This map determines the required vertical eye alignment for all possible gaze positions (see also Schor et al., 1994). We suggest that in our experiment the disparity due to the opposing pattern drifts led to an adaptive reconstruction of this map. Thus, intrasaccadic and to a lesser extent post-saccadic disconjugacy was made possible even for saccades along the midline. To allow fusion to occur immediately after a saccade this map-mechanism would produce a rapid disconjugacy during the saccade itself, thereby lessening the need for disconjugate post-saccadic eye drift. In agreement with other authors (Houtman et al., 1981; Perlmutter & Kertesz, 1978) we found vertical fusional responses to disparity changes to be slow, requiring about 700 msec to reach 63% of their final amplitude. Thus, responding to the final position disparity with an adjustment of the saccade amplitude allowed fusion to occur more rapidly. This behavior is also understandable from a functional viewpoint. Under natural conditions the need to reduce vertical disparities is invariably associated with saccades or other conjugate movements.

In summary, this study was designed to induce subjects to create disconjugate vertical post-saccadic eye drift. Such adaptive capability is needed in case of unilateral vertical paresis creating disconjugate post-saccadic eye drift. Simulation of the visual consequences of such pathological drift is not sufficient to stimulate significantly the adaptive mechanism of pulse-step readjustment which is believed to control post-saccadic drift. Disconjugate adaptation of vertical post-saccadic drift is small; instead larger disconjugate adaptation can occur in the amplitude of vertical saccades. The main signal driving such adaptations is position disparity and not retinal slip in each of the eyes.

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