Visually Induced Cross-Axis Postsaccadic Eye Drift

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SUMMARY AND CONCLUSIONS

1. It has been previously shown that, if a visual pattern is tran-
siently moved just after every saccade, it is possible to induce
horizontal, postsaccadic, ocular drift after horizontal saccades that
persist in the dark. In this study, we show that horizontal ocular
drift can also be created after vertical saccades. Five human sub-
jects viewed binocularly the interior of a full-field hemisphere
filled with a random-dot pattern. They were encouraged to make
frequent vertical saccades. During training, eye movements were
recorded by the electrooculogram. A computer detected the end of
every saccade and immediately moved the pattern to the left after
up saccades and right after down saccades. The motion was expo-
nential, its amplitude was 25% of the vertical component of the
preceding saccade, its time constant was 50 ms. Before and after
2-3 h of training, movements of both eyes were measured by the
eye-coil/magnetic-field method while subjects were instructed to
make vertical saccades in the dark, in the presence of the movable
adapting pattern, and between stationary targets for calibration.

2. After training (~20,000 saccades) all subjects developed a
zero-latency, exponential ocular drift to the left after up saccades
and to the right after down saccades. The amplitude of the horizon-
tal drift, expressed as a percentage of the vertical component of the
preceding saccade, was 2.7% in the dark. This rose to 10.2% in the
presence of the movable adapting stimulus. The latter rise is not
due to visual following systems but to a zero-latency increase in
initial drift velocity.

3. The horizontal drifts were usually unequal between the two
eyes, indicating the presence of dissociated movements. We
measured intrasaccadic and intersaccadic horizontal movements of all
subjects. In agreement with studies by others of saccades in the
light, we measured a divergence during up saccades (1.3°) and a
convergence for down (0.4°), but in this case for spontaneous
saccades in the dark. After training, these values increased for
saccades in the dark but decreased in the light in the presence of the
adapting stimulus. These changes were largely idiosyncratic and
statistically significant in only a few subjects.

4. The cross-axis postsaccadic drifts were separated into their
conjugate and disconjugate components. The disconjugate compo-
nants were small and idiosyncratic, and the means were small for
saccades in the dark. The only consistent trend was in the presence
of the adapting stimulus where up saccades were often followed by
convergence. The presence of these vergence components did not
interfere with our conclusion that this paradigm demonstrated
cross-axis plasticity in postsaccadic drift.

5. The induced drift was specific to the stimulus pattern. The
horizontal induced drift became smaller for oblique saccades, de-
creased as their vertical components became smaller, and disapp-
peared for horizontal saccades. There was no induced vertical drift
after horizontal saccades.

6. We suggest a hypothesis of crossed innervation. During a
vertical saccade, horizontal burst neurons are known to be bilater-
ally coactivated by a signal presumably from vertical burst neu-
rons. Normally, these activities cancel each other to produce no
net horizontal movement. Thus the lack of a horizontal compo-
nent would seem to be not passive (no signal at all) but active and
determined by a balance between opposing forces. The same argu-
ment can be made for the step of innervation. Plastic modification
of synapses between the horizontal burst neurons and the horizon-
tal neural integrator could therefore create, during a vertical sac-
cade, a step of innervation to horizontal motoneurons in the ab-
sence of a pulse. This hypothesis, with the use of only demonstra-
ble neural pathways, shows how one might create a step of
innervation without a pulse and thus a horizontal postsaccadic
drift without a horizontal cascade.

INTRODUCTION

Saccadic eye movements are made by a pulse, slide, and
step of innervation (e.g., Goldstein 1983; Robinson 1964;
Robinson et al. 1990).Lesions of the extracocular muscles or
brain stem can disrupt the match between these compo-
ments and cause postsaccadic eye drift and motion of
images across the retina. It is generally accepted that such
retinal slip acts as an error signal for plastic, motor-learning
mechanisms that can alter the pulse-slide-step ratios to
minimize postsaccadic eye motion. Kapoula et al. (1989)
showed that adaptive changes in postsaccadic drift can be
induced in normal humans by exponentially drifting the
visual scene immediately after each spontaneous saccade.
After 3 h of exposure to such viewing, all subjects developed
zero-latency, postsaccadic, ocular drift that decreased the
optically induced retinal slip. This drift persisted in the dark
and can be explained by parametric adjustments of the
pulse, slide, and step of saccadic innervation.
So far, only horizontal saccades have been examined. Ear-
er studies, in which saccadic adaptation was probe by
creating or utilizing disconjugate eye drifts and then requir-
ing the subject or the animal to view chronically with only
one eye, also concentrated largely on horizontal saccades
(Abel et al. 1978; Kapoula et al. 1987; Kommerell et al.
1976; Optican and Robinson 1980; Viirre et al. 1978).Sac-
cades, however, are made by three pairs of muscles in each
eye, and the CNS must innervate all of them in such a way
that after every saccade there is little drift in any direction.
Conjugate drifts are relatively small in normal subjects: the
average velocity over the first 100 ms is <1°/s after both
horizontal and vertical saccades (Collewijn et al. 1988a,b).
Presumably, plastic, adaptive mechanisms are ensuring
such drifts to be minimal. It occurred to us that an equally
important task of these mechanisms is to prevent orthogo-
nal drifts; that is, prevent horizontal drifts after vertical sac-
cades and vice versa, should the need arise. For example,
Viirre et al. (1987) patched one eye of a monkey for 1 wk

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and induced, among other things in that eye, vertical post-saccadic drift after horizontal saccades. After only 1 day of normal binocular viewing, monkeys were able to suppress this drift. If this is the case, it must be possible to induce orthogonal, or cross-axis drift.

Consequently, the present study examines cross-axis post-saccadic drift plasticity of normal humans, by asking them to adapt to horizontal, optically induced retinal slip, coupled with vertical saccades. The results demonstrate that horizontal eye drift can be induced after vertical saccades in humans within 3 h of training.

METHODS

Subjects

Eye movements were recorded in five subjects with ages ranging from 18 to 32. Each underwent a neuro-ophthalmological examination with normal findings. All subjects but one were emmetropes. Subject DM was myopic and wore habitual corrective spectacles (7 diopters) during the experiment. Subjects DN and RT had left eye dominance, the others right eye dominance. ZK was the only non-native subject. She first tested this paradigm on herself, and her measurements were made only after training.

Eye movement recording

Details of the methods are given elsewhere (Kapoula et al. 1989). Briefly, stimulus presentation and data collection were directed by REX, a UNIX-based software system, and run on a PDP 11/73 microcomputer. Before and after training, eye movements were recorded with the search-coil/magnetic-field technique (Collewijn et al. 1975; Robinson 1963) with 6-f-torr field coils (CNC Engineering). Subjects sat in the center of a hemispheric screen, with a radius of 92 cm and an edge-to-edge distance of 2 m, onto which could be projected red light-emitting diodes (LEDs) for calibration, or a random-dot pattern for training. Their heads were stabilized with a chin and forehead rest. Vertical and horizontal movements of each eye were recorded simultaneously. Calibrations were determined for each eye when it alone viewed the LEDs. Care was taken that the magnetic fields were aligned and phased while subjects fixated targets up, down, left, and right to eliminate any cross talk between horizontal and vertical movements. The eye-position signals were filtered with a bandwidth of 0–240 Hz and digitized with a 12-bit analog-to-digital converter, sampling each channel 600 times per second. These data were stored on digital tape for offline analysis. Overall system sensitivity was 0.1°. To measure post-saccadic drift before and after training, the subjects were instructed to make saccades in a variety of directions but especially many vertical saccades, as well as they could, of various sizes in complete darkness. After training, saccades were also recorded in the presence of the adapting stimulus that drifted, as described below, after every saccade.

Adaptation paradigm

Subjects were asked to continuously explore, with saccades, a random-dot pattern projected with a fish-eye lens onto the interior of the hemisphere. Viewing was binocular. Eye movements were recorded during the 2-3 h of training with the direct-coupled electrode electrooculogram. Subjects were asked to include many vertical saccades. The computer detected the end of each spontaneous saccade and drifted the pattern horizontally across the hemisphere. Upward saccades triggered the pattern to slide to the left and downward saccades to the right (Fig. 1). The excision of the pattern was always 25% of the amplitude of the vertical component of the antecedent saccade. An exponential waveform with a 50-ms time constant was used for the postsaccadic pattern motion. Subject BL was exposed to this visual experience for 2 h, producing 12,000 saccades; the other subjects were trained for 3 h, producing 18,000–25,000 saccades.

Analysis of data

Offline analysis was performed on the eye-coil recordings obtained before and after training. Saccades were selected by the investigator scrutinizing a graphics monitor showing horizontal and vertical eye position and velocity traces. During such tests, subjects usually made well over 100 saccades in all directions. These files were then inspected with the object of finding, if possible, 40-50 saccades that could be considered vertical. Saccades (usually > 10°) with a small, net, conjugate horizontal component (points 1-6, Fig. 3) of ±3° (e.g., Fig. 2F) were excluded, as were vertical saccades with irregular waveforms (velocity too low or with closely spaced multiple peaks). Typically, 40 such saccades (37% of the total on average) could be found, but for some subjects, especially for down saccades, it was not possible to find this
FIG. 2. Typical binocular eye movements during vertical saccades to light-emitting diode targets recorded before training, showing the small, strange horizontal wiggles that usually occurred. Note the difference in scale between horizontal and vertical eye position traces. In each section, vertical eye movements are above, horizontal below. A: a small, monocular, phasic movement. B: an oscillation in one eye, a pulse in the other. C: small, binocular pulses. D: disjunctive oscillations at different frequencies. E: small, conjugate, horizontal component during a 20° vertical saccade. Recordings such as in E were excluded from the analysis as not being sufficiently vertical.
many acceptable vertical saccades. Table 1 gives the number of
saccades actually used for each subject in each condition.

During vertical saccades, there were frequencies as high as
50% by analysis) strange, intriguing, small horizontal movements or oscillations
with waveforms that were usually different between the two
eyes (Fig. 4A, B). Such movements occurred at similar rates for
two types of saccades (up, down, in the dark, or in the light),
before and after training. Because these waveforms were not reproducible,
no attempt was made to analyze them.

Cross-axis drift adaptation was assessed as follows (Fig. 3).
First, the times of onset and offset of the vertical pulse and step
components were identified automatically by a template-matching
method described elsewhere (Kapoula et al. 1989). The investiga-
tor verified the accuracy of these computer-generated marks
and placed time markers in the corresponding points of the hori-
zontal eye position traces. We then measured the amplitude, direc-
tion, and time constant of horizontal drift during the first 250 ms
after the end of the vertical saccade (points a to f for displacement
Sh, Fig. 3). Records with intersaccadic intervals <250 ms were
discarded. As the amplitude of the pattern motion was propor-
tional to the size of the vertical saccade, horizontal cross-axis drift
was expressed as a percentage of the vertical pulse amplitude; in
the terminology of Fig. 3, cross-axis drift = (Sh/Pv) x 100. Left-
ward drift is negative, rightward drift positive, regardless of the
saccade direction. After training, the drift almost always started at
the end of the vertical saccade, although sometimes it could appear
to start slightly before or after because of interference from the
highly variable intrasaccadic wiggles. Because there was no
consistent pattern, we defined the end of the vertical saccade as
the start of the interval to be examined for horizontal drift. The time
constant of the drift was taken as that of a single exponential
waveform with the data used with negative drift, regardless of the
saccade direction. Binocular recordings were also analyzed for their
congjugate and disconjugate components. If L and R were the cross-axis ratios, or angular displacements, of the
left and right eye, the conjugate part was taken to be (L + R)/2,
the disconjugate part as (L - R).

RESULTS
Qualitative observations

Figure 4A shows examples of responses to the adapting
pattern motion recorded in the presence of the movable
adapting stimulus, at different times during the training.
Early in the training (Fig. 4A, left), subjects followed the
pattern with a pursuit or ocular following mechanism. Im-
nediately after the saccade (4), the eyes drift about weakly,
in no consistent direction, until, at the second tick, a clear
inflection marked the start of ocular following. At this stage,
in training, no adapted response (zero-latency drift) would
be expected, and none was seen. It would obviously be inap-
propriate to try and fit the horizontal waveform in Fig. 4A
with an exponential. Instead, the beginning of the ocular
following was marked, by eye, by the experimenter (2nd
tick) and taken as the latency for ocular following.

This initial latency was measured for two subjects.
Subject RT had latency commonly accepted as in the range of
the pursuit system (117 ± 12 ms, mean ± SE). Subject RT
had shorter latencies (68 ± 9 ms); these responses may be
due to the short-latency ocular following system reported
by Miles and Kawano (1986). This ocular following is inci-
dental to our investigation because, at this time, no learning
has yet occurred. After 3 h of training, saccades were fol-
lowed reliably by exponential ocular drift, whose onset
seemed time locked to the end of the vertical saccade (Fig.
4A, right). This zero-latency drift was always in the direc-
tion of the pattern motion; upward saccades were followed
by leftward drift, downward saccades by rightward drift (Fig.
4B).

Figure 5, A and B, shows typical examples of vertical
saccades made in the dark, precluding any ocular following
reflex. Small horizontal drifts are frequently seen before
each saccade (73%), especially in the dark. One should note
the sensitivity with which these movements are measured.
These small drifts fall within the range of the drifts of nor-
mal miniature eye movements of fixation in the light and
dark and are to be expected. These drifts are known to be
partially conjugate and partially disconjugate as illustrated
in Fig. 5, B and C. Vertical saccades, recorded before train-
ing, were usually followed by similar small horizontal drifts
(Fig. 5A, left); they could be in either direction with similar
rates of occurrence. After training, horizontal postasaccadic
drifts in the dark increased in amplitude and were almost
always in the direction of the pattern motion used to train
subjects (90% by analysis of individual drifts: upward
saccades were followed by reliable, leftward drift (Fig.
5A, right); downward saccades by rightward drift. These
drifts had an exponential waveform, occurred in the ab-
sence of a horizontal saccade, and their onset seemed time
locked to the offset of the vertical saccade. The induced

drift was present in both eyes as shown in Fig. 5B. Figure
5C shows binocular recordings after training, while the sub-
ject made saccades between LEDs for calibration; these sac-
cades were still followed by horizontal drifts in the direction
of the former pattern motion in spite of the deterring effect
of a stationary visual pattern.

During the vertical saccades the eyes wiggled about, hori-
zontally, in unpredictable and unrepeatable ways as empha-
sized in Fig. 2, although one should note the peak dis-
placements are typically 0.5° and seldom >1.0°. Figure 5,
B and C, also shows that these wiggles are almost never
disconjugate; the eyes do different things. Also, the postas-
cadic drifts are not strictly conjugate; they can differ in am-
plitude (Table 1) and even time constants (see below).
There is usually a net horizontal displacement between the
beginning and end of the saccade (Table 2) that is typically
1-2°, and these displacements are also seldom conjugate.
Thus, when one examines the horizontal behavior of the
eyes with high sensitivity, during large vertical saccades,
one finds a variety of unusual behaviors not normally asso-
ciated with the stereotyped patterns of large saccades. Of
these phenomena, this study concentrates primarily on the
induced postasaccadic drifts after training.

Quantitative data

Table 1 shows average, cross-axis horizontal drift of each
eye, for normal vertical saccades in the dark, and for sac-
cades after training both in the dark and in the presence of
CROSS-AXIS POSTSACCADEIC DRIFT PLASTICITY

TABLE 1. Cross-axis ratios: horizontal ocular drift following vertical saccades in percent of the vertical saccade amplitude

<table>
<thead>
<tr>
<th>Subject</th>
<th>Normal</th>
<th>Dark</th>
<th>After Training</th>
<th>With Adapting Stimulus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Dark</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>After upward saccades</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BL</td>
<td>-0.71 ± 1.38 (23)</td>
<td>-2.11 ± 1.91* (33)</td>
<td>-6.65 ± 2.74* (38)</td>
<td>-11.81 ± 3.77* (38)</td>
</tr>
<tr>
<td>R</td>
<td>-2.12 ± 1.30</td>
<td>-4.10 ± 2.93* (34)</td>
<td>-10.87 ± 2.22* (61)</td>
<td>-17.40 ± 2.97* (61)</td>
</tr>
<tr>
<td>DN</td>
<td>-1.07 ± 1.96</td>
<td>-4.38 ± 1.79* (107)</td>
<td>-5.12 ± 1.53* (18)</td>
<td>-6.83 ± 2.76* (18)</td>
</tr>
<tr>
<td>R</td>
<td>0.10 ± 2.90* (34)</td>
<td>-1.24 ± 1.48* (47)</td>
<td>-5.12 ± 1.53* (18)</td>
<td>-6.83 ± 2.76* (18)</td>
</tr>
<tr>
<td>RT</td>
<td>1.43 ± 1.79</td>
<td>-1.21 ± 4.71* (67)</td>
<td>-5.12 ± 1.53* (18)</td>
<td>-6.83 ± 2.76* (18)</td>
</tr>
<tr>
<td>L</td>
<td>-3.92 ± 2.49 (60)</td>
<td>-6.92 ± 3.94* (47)</td>
<td>-5.12 ± 1.53* (18)</td>
<td>-6.83 ± 2.76* (18)</td>
</tr>
<tr>
<td>R</td>
<td>2.70 ± 2.11</td>
<td>-0.71 ± 2.43* (66)</td>
<td>-5.38 ± 1.30* (55)</td>
<td>-12.97 ± 2.73* (55)</td>
</tr>
<tr>
<td>SS</td>
<td>-1.49 ± 2.18 (28)</td>
<td>-4.17 ± 2.94* (66)</td>
<td>-5.38 ± 1.30* (55)</td>
<td>-12.97 ± 2.73* (55)</td>
</tr>
<tr>
<td>ZK</td>
<td>-1.40 ± 2.41</td>
<td>-4.98 ± 4.14 (53)</td>
<td>-7.64 ± 2.82 (44)</td>
<td>-9.21 ± 1.88 (44)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Subject</th>
<th>After downward saccades</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>BL</td>
<td>-1.34 ± 2.19 (20)</td>
<td>-3.40 ± 2.07* (30)</td>
<td>0.96 ± 1.96* (08)</td>
<td>7.22 ± 4.56* (08)</td>
</tr>
<tr>
<td>R</td>
<td>-1.56 ± 2.58</td>
<td>3.19 ± 1.71* (30)</td>
<td>13.87 ± 2.21* (30)</td>
<td>14.10 ± 4.20* (30)</td>
</tr>
<tr>
<td>DN</td>
<td>0.86 ± 4.51* (30)</td>
<td>1.33 ± 2.76 (30)</td>
<td>0.95 ± 1.52* (30)</td>
<td>3.03 ± 3.09* (30)</td>
</tr>
<tr>
<td>L</td>
<td>-1.37 ± 2.20 (31)</td>
<td>0.59 ± 1.52* (31)</td>
<td>13.87 ± 2.21* (30)</td>
<td>14.10 ± 4.20* (30)</td>
</tr>
<tr>
<td>R</td>
<td>-0.65 ± 2.49* (54)</td>
<td>5.02 ± 3.03* (54)</td>
<td>8.68 ± 3.09* (34)</td>
<td>5.33 ± 1.51* (34)</td>
</tr>
<tr>
<td>SS</td>
<td>-2.20 ± 3.45</td>
<td>1.45 ± 3.89* (54)</td>
<td>8.68 ± 3.09* (34)</td>
<td>5.33 ± 1.51* (34)</td>
</tr>
<tr>
<td>ZK</td>
<td>0.77 ± 3.08</td>
<td>4.29 ± 1.59* (50)</td>
<td>10.64 ± 2.27* (52)</td>
<td>12.12 ± 3.92* (52)</td>
</tr>
<tr>
<td>L</td>
<td>1.00 ± 3.09 (19)</td>
<td>1.40 ± 1.10 (50)</td>
<td>10.64 ± 2.27* (52)</td>
<td>12.12 ± 3.92* (52)</td>
</tr>
<tr>
<td>R</td>
<td>3.06 ± 2.66</td>
<td>0.24 ± 4.05 (45)</td>
<td>5.92 ± 2.16 (39)</td>
<td>4.84 ± 1.67 (39)</td>
</tr>
<tr>
<td>Total means</td>
<td>-0.77 ± 3.11 (538)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amplitude means</td>
<td>2.73 ± 3.32 (1.070)*</td>
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</tbody>
</table>

Values are means ± SD; each ratio is the mean of the number of saccades n indicated in parentheses. The typical value of n is 43 but in some cases, especially for downward saccades for BL, n dropped to as low as 8. Negative values indicate leftward drift; positive values, rightward drift. Most normal drifts were statistically different from 0. Total means are algebraic. Amplitude means average the subject means after multiplying those for upward saccades by -1 to provide an overall measure of the amplitude of changes independent of saccade direction. These means are weighted for the number of saccades for each subject. Recall that no data are available for ZK before adaptation. L, left eye; R, right eye. *Change from normal that was statistically significant at the level P < 0.05 (t test comparing means before and after training). |Not significantly different from 0.

the movable adapting stimulus. These saccades, before and after training, had typical mean amplitudes from 15 to 23°. Recall that no data was taken for ZK before training. Nevertheless, it was felt that her postadaptation data were worth presenting, although a pre-poststatistical significance cannot be attached to them. Before training, all subjects exhibited some small, post sacadic horizontal drifts, most of which were statistically different from zero. After upward saccades (subjects DN, RT, and SS), the eyes drifted in opposite directions; after downward saccades, the eyes could drift left (BL and RT) or right (SS) in opposite directions (DN). The total mean of these drifts was small, -0.77%. After exposure to retinal slip, horizontal drifts increased in amplitude and, in most cases, both eyes drifted in the direction of the former pattern motion. Statistically significant changes are indicated by an asterisk in Table 1. For all subjects, upward saccades in the dark created significant binocular, leftward drifts (- sign); downward saccades usually caused rightward drifts (+ sign) in both eyes. Of the eight eyes involved, five showed significant changes in the expected direction, but one (BL, L) was in the other direction. Two others (DN, L, SS, R) failed to reach significance. Although we had no normal data for ZK, her right eye also appeared to drift in the unexpected direction, although the value is not different from zero. The average of the amplitudes of the subject means (to pool up and down saccades, Table 1) rose to 2.73% for saccades in the dark, and to 10.16% when the movable adapting stimulus was present. These values show statistically significant changes from normal values. Total and Amplitude means were weighted by the number of saccades contributed by each subject.

The further increase of drift in the presence of the pattern motion occurred in all but one case (RT, right eye, upward
saccades). This phenomenon was seen in previous studies (Kapoula et al., 1989, 1990). Because the response has zero latency, it cannot be due to any visual following system and appears to be a vision-activated property of the neural mechanism undergoing modification. To illustrate this point more clearly, the average velocity of the horizontal, cross-axis drift was measured over the first 80 ms for each eye movement in Table 1. In the normal case, mean velocity, weighted by the number of saccades for each subject, was $-0.69 \pm 3.66^\circ$/s (16 eyes). After training, this rose to $5.05 \pm 5.35^\circ$/s (20 eyes, Amplitude mean). In the presence of the adapting stimulus, it rose to $14.22 \pm 9.57^\circ$/s (20 eyes). Both numbers indicated significant changes. Consequently, the increased horizontal cross-axis ratios in Table 1 with the adapting stimulus were not due simply to an ocular following reflex. Such a reflex probably did account for some of the increase by extending the eye drift after 150 ms, but the threefold increase in initial eye velocity with the stimulus present is too early to be due to following reflexes or pursuit and is, instead, an intrinsic property of the learning mechanism itself.

For adapted saccades in the dark (all cases in Table 1 where the mean exceeds 1%), the amplitude of the horizontal cross-axis drift (in deg) was usually positively correlated with the amplitude of the vertical saccade. For up saccades, for 9 out of 10 eyes, the r Bravais-Pearson coefficient was between 0.34 and 0.64, all were significant, 6 at the 0.0005 level. The correlation for one eye was not significant. For down saccades, there were too few saccades for one subject. For the remaining eight eyes, the r coefficient was significant for only four eyes, three at the 0.0005 level. Thus, just as for the cross-axis ratio itself, training had much clearer and stronger effect on up saccades than down saccades. For saccades in the presence of the movable adapting stimulus, this correlation was stronger (range of r values, 0.50–0.92) and significant in all but one eye, again, after down saccades. Thus, for most subjects, there was a strong correlation between drift amplitude and vertical saccade size, which justifies our measuring the cross-axis movements as a ratio in percent.

Before adaptation, the small horizontal drifts, following vertical saccades in the dark, had a time constant of $115 \pm 11$ ms (SD of the group mean with both eyes pooled together; range, 100–132 ms). After adaptation, the group mean time constant in the dark was $100 \pm 6$ ms (range, 92–108 ms); this decrease was statistically significant for two of the four subjects tested (DN and SS). As in prior studies (Kapoula et al., 1989), viewing the adapting pattern motion significantly increased the time constant for all subjects; the group mean rose to $166 \pm 13$ ms (range, 148–182 ms).

The drifts were also disconjugate with respect to their time constants (e.g., Fig. 5, B and C). For all subjects the time constant was larger in one eye, but there was no consistent pattern among subjects. These differences in time constants averaged out; the group mean for all left eyes did not differ significantly from that for all right eyes. The differences in time constants between the two eyes for individual saccades in the dark were measured and averaged for each subject. These means were then averaged over the group. That difference was $68 \pm 16$ (SD) ms (range, 48–99 ms).

We also noted that, for adapted saccades (in the dark or light), the amount of drift was largely unequal between the two eyes (Table 1). This inequality is presumably due to the ongoing vergence changes that can be seen in the differences in horizontal drifts between the two eyes even for normal vertical saccades (Table 1, 1st column). These differences, for normal saccades, were also statistically significant with the exceptions of subjects B1 and S5 for downward saccades. The differences were not due to unequal vertical saccade amplitudes between the two eyes. Analysis showed excellent yoking between the eyes and no significant differences in their vertical amplitudes. Such disconjugate postasaccadic drifts have been well documented for horizontal saccades (e.g., Kapoula et al. 1987) and have also been reported for vertical saccades (Collewijn et al. 1988) where intrasaccadic vergence was also measured. We felt that we should analyze the data further to see how such movements interacted with our induced postasaccadic drift. Tables 2 and 3 show the results for intra- and postasaccadic disconjugate movements.

**Horizontal vergence changes during and after vertical saccades**

Table 2 shows intrasaccadic vergence estimates based on the net change in horizontal eye position (in deg) during vertical saccades (the change from point i to d, Fig. 3). This change was measured for each eye and the difference taken. Divergence is negative; convergence, positive. For normal, upward saccades in the dark, all subjects exhibited convergence. For downward saccades, all but one exhibited convergence. These findings are in agreement with those re-
FIG. 4. Vertical and horizontal eye position traces from subject BL in the presence of the movable adapting stimulus. During the saccades, the horizontal component could oscillate and drift in a highly variable fashion. Note, however, the difference in scales; the horizontal eye movements are only a fraction of a degree. A: in these examples the pattern was drifting rightward. On the left, during the saccade, the subject made a small, horizontal, phasic movement that disappeared shortly after the end of the vertical saccade (1) similar to those shown in Fig. 2. After ~100 ms, at the 2nd tick, eye velocity increases because of visual following systems. After 3 h of training, the delay became 0, and the saccade is followed immediately by a reliable exponential drift. B: after training, upward saccades are followed by leftward drift, and downward saccades by rightward drift.

ported by Collewijn et al. (1988b) and Enright (1989). The weighted average of the amplitude of vergence (dis- and con-) over up and down saccades (Amplitude mean, Table 2) is 0.92°. Exposure to horizontal retinal slip coupled with vertical saccades, led to an apparent increase of the divergence associated with up gaze and the convergence associated with down gaze. The overall amplitude mean rose to 2.18°. This increase, however, reached statistical significance in only three of the eight cases (*) with the use of a t test. In contrast, saccades recorded after training, while looking at the adapting stimulus, usually showed a small amount of divergence, regardless of the saccade direction (total mean of −0.58°). Compared with normal saccades in the dark, the magnitude of disconjugate movements in the latter case was significantly different and smaller in four out of eight cases (1). The tendency for the intrasaccadic horizontal vergence to increase with training raised the question of whether
FIG. 5. A: spontaneous vertical saccades in the dark before (left) and after training (right). Recordings from the right eye of subject DN. Vertical ticks indicate the end of the saccade. After training, upward saccades are followed by significant downward drift. B: binocular recordings from subject SS of downward saccades in the dark after training. Note the dissociation of horizontal components during the vertical saccade. The net change in horizontal eye position is 0.5° in the right eye but 0° in the left. At the offset of the vertical saccade, both eyes began an exponential drift in the direction of the pattern motion used for training. C: binocular recordings of saccades to stationary light-emitting diode targets recorded from the same subject (SS) after training; the eyes were still drifting in the direction of the former pattern motion.
posttaccadic, vergence-related motion also increased with training. Consequently, the horizontal eye motions following vertical saccades in Table 1 were separated into their conjugate and disconjugate components and shown in Table 3. Initially, the total (weighted) mean of the conjugate component was –0.77%. After training, the conjugate component for saccades in the dark increased in the correct direction to an amplitude mean of 2.73%. The conjugate component increased significantly in all eight cases (t-test) and are indicated by an asterisk. Turning on the movable adapting stimulus increased this change to 10.16%. Again, all changes were significant. These numbers are, of course, the same as those found at the bottom of Table 1, because averaging over L and R saccades there is equivalent to saving the conjugate component and eliminating the disconjugate. They are repeated here to show what individual subjects did in this regard and to enable comparison with the disconjugate data.

Significant changes in the disconjugate component also occurred, but most were idiosyncratic. Table 2 shows that normal saccades in the dark created divergence on up saccades and convergence on down, during the saccades. In the dark, there is no obvious reason why there should then be any subsequent correction, and Table 3 shows no significant vergence either way (0.27°). After training, there is still no reason to expect a change in the dark, and the mean (0.22°) supports this. Only five of the eight means showed significant changes (indicated by * for convergence and † for divergence), but they were in no consistent direction. Although both of the group means (up, down) showed a significant change, they showed loss of convergence (†) after up saccades and increased convergence after down, just the opposite of what one might expect. Consequently, we used the total (weighted) mean. In the presence of the adapting stimulus, with visual targets at a constant distance, one might expect to see convergence to offset the tendency for intrasaccadic divergence (Table 2, column 3), but this only occurred for up saccades. The changes of only five of the eight means were statistically significant. Three of the four subjects converged on up gaze (*). On down gaze, only one subject converged, one diverged, and two had no significant change. Because no consistent behavior was apparent, we simply took the total (weighted) mean, which was 0.61° and not markedly different from that of the other two conditions.

Thus our main finding is a consistent, significant increase, after training, of the conjugate component of the horizontal drift following vertical saccades that seems not to be obscured by changes in any disconjugate, vergence-related mechanism. These results provide evidence for the existence of a cross-axis, drift-adaptation mechanism operating to reduce retinal slip orthogonal to saccades.

**Posttaccadic drifts after oblique and horizontal saccades**

After training, subjects also made oblique saccades. The horizontal components of oblique saccades made in the dark or in the light (in the presence of the adapting stimulus or stationary LED targets) were always followed by noticeable posttaccadic drifts in the direction of the pattern motion used for training. Note that, during training, horizontal pattern motion was coupled only with the amplitude of the vertical component of any eye movement that had such a component detectable. Consequently, posttaccadic drifts, in the direction of the pattern motion for oblique saccades, were expected. Such drifts could be easily explained by a pulse-step mismatch in the horizontal saccadic component, but that was not the case. As the saccade became less vertical and more horizontal, the horizontal posttaccadic drift became smaller, regardless of the size of the horizontal component, because the vertical component and consequently the pattern motion became smaller. When tested in three subjects (BL, RT, and SS), the amplitude of the cross-axis horizontal drift was better correlated with the amplitude of the vertical rather than the horizontal component of the antecedent saccade. For saccades with vertical upward components, the r Bravais-Pearson coefficient between the vertical component and the amplitude of the horizontal posttaccadic drift ranged from 0.49 to 0.81 in 5 of the 6 eyes. These values are highly significant. Significant r values for the correlation between the horizontal component and the horizontal drift occurred in only two of the six eyes, and one of them was negative.

When the saccade was almost entirely horizontal, the posttaccadic drift changes disappeared. Thus the amplitude of the horizontal drift was not proportional to the horizontal component of the saccade as would be the case if there were simply a pulse-step mismatch in the horizontal component. We looked for vertical posttaccadic eye drift after horizontal saccades. In two subjects examined (SS and DN), after adaptation, in the dark, the mean vertical drift, after horizontal saccades, was –0.68 and –0.13°, respectively, (n = 70). These are very small values (see Table 1). This result would be expected because the subjects had never been exposed to such a pattern motion. This sort of motor plasticity is usually highly context specific; it seems not to learn things not asked of it.

**Vertical drifts following vertical saccades**

Such drifts were examined for spontaneous saccades made in the dark before and after training; they were quantified as pulse-step mismatches expressed as a percent of vertical saccade size (see Fig. 3). Before training, all four subjects exhibited some vertical posttaccadic drift. It was quite conjugate in the two eyes and was mostly upward for both upward and downward saccades. [Note that for visually guided saccades, Collewijn et al. (1988b) observed a small drift following upward saccades.] The overall, group, algebraic mean in our study (4 subjects, left and right eye, and down saccades only pooled together) was –1.16 ± 3.62% (SD of the group mean). After training, vertical drift became mostly backward for both up and downward saccades. The overall, group, algebraic mean was 1.55 ± 2.09%. This change (from outward to backward drift) occurred for three out of the four subjects (BL, DN, and RT) and was statistically significant. Recordings after training from subject ZK also showed backward drifts that were particularly pronounced (8°–9°). Subject SS was the only subject showing backward
TABLE 2. Horizontal verge changes (deg) during vertical saccades

<table>
<thead>
<tr>
<th></th>
<th>Normal</th>
<th>After Training</th>
<th>With Adapting Stimulus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Dark</td>
<td>Dark</td>
<td></td>
</tr>
<tr>
<td><strong>During upward saccades</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subject</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BL</td>
<td>-1.10</td>
<td>-1.70</td>
<td>-0.28</td>
</tr>
<tr>
<td>DN</td>
<td>-1.93</td>
<td>-4.97*</td>
<td>-1.09</td>
</tr>
<tr>
<td>RT</td>
<td>-0.81</td>
<td>-1.65*</td>
<td>-0.69</td>
</tr>
<tr>
<td>SS</td>
<td>-1.94</td>
<td>-3.37</td>
<td>-0.95*</td>
</tr>
<tr>
<td>ZK</td>
<td>-1.02</td>
<td>0.28</td>
<td></td>
</tr>
<tr>
<td><strong>Means</strong></td>
<td>-1.34 (143)</td>
<td>-2.67 (366)</td>
<td>-0.55 (216)</td>
</tr>
<tr>
<td><strong>During downward saccades</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subject</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BL</td>
<td>0.24</td>
<td>0.81</td>
<td>0.16</td>
</tr>
<tr>
<td>DN</td>
<td>4.44</td>
<td>4.97*</td>
<td>-0.86*</td>
</tr>
<tr>
<td>RT</td>
<td>-0.28</td>
<td>0.15</td>
<td>-0.77</td>
</tr>
<tr>
<td>SS</td>
<td>1.04</td>
<td>1.10</td>
<td>-0.14</td>
</tr>
<tr>
<td>ZK</td>
<td>-0.73</td>
<td></td>
<td>-0.94</td>
</tr>
<tr>
<td><strong>Means</strong></td>
<td>0.44 (124)</td>
<td>1.11 (169)</td>
<td>-0.81 (174)</td>
</tr>
<tr>
<td><strong>Total means</strong></td>
<td></td>
<td></td>
<td>-0.58 (390)</td>
</tr>
<tr>
<td><strong>Amplitude means</strong></td>
<td>0.92 (369)</td>
<td>2.18 (355)</td>
<td></td>
</tr>
</tbody>
</table>

Values are stated in degrees; all means are weighted by the number of saccades for each subject followed by the total number of saccade pairs used in its determination in parentheses. The net change in horizontal eye position, in degrees, during the saccade for the left eye minus that of the right. Positive values represent convergence; negative values, divergence. Individual means are based on the same number of saccades as in Table 1. The expectation (Collewijn et al. 1988b; Erniet 1989) was divergence during up saccades and convergence during down, even though these saccades were in the dark, before and after training, so they are summarized by an Amplitude mean in which the subject means are taken as plus if in the expected direction and minus if in the opposite direction. With the moving adapting stimulus, this expectation was not confirmed, so the Total (weighted algebraic) mean is given. *An increase in magnitude from normal saccades that was statistically significant at the P < 0.05 level (t test comparing the differences before and after training). fA significant decrease.

Drift, regardless of saccade direction, before training (4%); after training, this drift was reduced but remained backward (1%). Moreover, our paradigm produced a significant decrease in the amplitudes of vertical post-saccadic drifts in three out of four subjects (DN, RT, and SS); the group mean of all four subjects averaging the magnitudes (absolute values) of drifts for all saccades in both eyes was 3.39 ± 1.79% before, and 1.18 ± 1.87% after training. We have no hypotheses for this general reversal and decrease of post-saccadic drifts after training.

**DISCUSSION**

This study shows that horizontal retinal slip coupled with vertical saccades can induce cross-axis ocular drift. Within 3 h, all five subjects developed horizontal ocular drift that would reduce retinal slip. This horizontal drift occurred in the absence of a horizontal saccade, and in many instances (Fig. 5B, right) in the absence of any sort of horizontal eye displacement. The cross-axis drift had an exponential waveform and persisted in the dark and even in the presence of stationary LED targets. Inspection of the recordings showed that the onset of the drift showed no consistent lead or lag relative to the end of the vertical saccade so that the latency may be regarded as zero. In the context of a learning neural network, this result is consistent with the notion that the network will learn only what is asked. Because we moved the random-dot pattern just at the end of the saccade, it should not be surprising that the network programmed the ocular drift to begin at that time. The amplitude of the induced horizontal drift correlated with the amplitude of the vertical saccade. After training, viewing the movable adapting pattern motion increased the amplitude of the cross-axis drift, largely by increasing its initial velocity, and lengthened its time constant from 100 to 166 ms. The latter finding can probably be explained in part because visual following systems can prolong the movement. Cross-axis adaptation occurred only for saccade-linked pattern motions to which the subject was exposed and did not generalize to other axes.

All these characteristics of the mechanism for cross-axis drift adaptation are similar to those we have observed previously, for adaptation to horizontal retinal slip following horizontal saccades, that are believed to be due to changes in the pulse-slip-segments of saccade inversion (Kapoula et al. 1989, 1990). One basic difference, however, is the amplitude of the induced drift. The amount of cross-axis drift persisting in the dark (2.7%) was considerably smaller than that induced in the previous studies (6%). Possibly the natural occurrence of cross-axis drift, resulting from a lesion, is less likely, and the repair mechanism to deal with it is slower.

Cross-axis plastic abilities have been demonstrated for several other ocuomotor subsystems, such as the vestibulo-ocular reflex (e.g., Harrison et al. 1986; Peterson et al. 1989; Schallhorn and Robinson 1983) and the ocular following reflex (Miles and Kawano 1986). The only prior evidence, suggesting a cross-axis ability in the post-saccadic drift adaptation mechanism, was the observation that the vertical drift coupled with horizontal saccades in normal monkeys caused by a week of patching that eye, was quickly eliminated when the monkey was allowed to view binocularly (Vièrre et al. 1987). Our findings are an extension of that observation and indicate that cross-axis drift adaptation can be induced optically in normal humans within 3 h.

**Complications from vergence**

Collewijn et al. (1988b) and Erniet (1989) reported a coactivation of vergence during vertical saccades that manifests itself by convergent eye motion after up saccades and divergent motion after downward saccades. One possibility is that, when we look up, we are likely to be looking at things far away. Things down tend to be near. This results in intrasaccadic divergence on up gaze and convergence on down. If, however, the targets are at the same depths, corrective vergence is needed after the saccade: convergence for up, divergence for down. These observations raised the question of whether vertical saccades in the dark would show similar vergence movements and how they might complicate our measurements of cross-axis drift. We confirmed, on the basis of measures of intrasaccadic eye dis-
### TABLE 3. Conjugate and disconjugate components of the cross-axis ratio

<table>
<thead>
<tr>
<th>Subject</th>
<th>Dark Conjugate, %</th>
<th>Dark Disconjugate, deg</th>
<th>After Training Conjugate, %</th>
<th>After Training Disconjugate, deg</th>
</tr>
</thead>
<tbody>
<tr>
<td>BL</td>
<td>-1.41</td>
<td>0.24</td>
<td>-3.11*</td>
<td>0.40</td>
</tr>
<tr>
<td>DN</td>
<td>-0.48</td>
<td>-0.15</td>
<td>-2.81*</td>
<td>-1.20*</td>
</tr>
<tr>
<td>RT</td>
<td>-1.25</td>
<td>0.64</td>
<td>4.06*</td>
<td>0.92*</td>
</tr>
<tr>
<td>SS</td>
<td>0.61</td>
<td>0.67</td>
<td>-2.44*</td>
<td>0.67</td>
</tr>
<tr>
<td>ZK</td>
<td></td>
<td></td>
<td>-3.19</td>
<td>0.75</td>
</tr>
<tr>
<td><strong>Means ± SD</strong></td>
<td><strong>-0.74 ± 1.84</strong></td>
<td><strong>0.40 ± 0.53</strong></td>
<td><strong>-3.04 ± 2.35</strong></td>
<td><strong>0.10 ± 1.00</strong></td>
</tr>
</tbody>
</table>

**After upward saccades**

<table>
<thead>
<tr>
<th>Subject</th>
<th>Dark Conjugate, %</th>
<th>Dark Disconjugate, deg</th>
<th>After Training Conjugate, %</th>
<th>After Training Disconjugate, deg</th>
</tr>
</thead>
<tbody>
<tr>
<td>BL</td>
<td>-1.50</td>
<td>0.01</td>
<td>-0.15*</td>
<td>-0.82*</td>
</tr>
<tr>
<td>DN</td>
<td>-0.26</td>
<td>0.21</td>
<td>0.96*</td>
<td>0.17</td>
</tr>
<tr>
<td>RT</td>
<td>-1.42</td>
<td>-0.20</td>
<td>3.23*</td>
<td>0.57*</td>
</tr>
<tr>
<td>SS</td>
<td>0.93</td>
<td>-0.10</td>
<td>2.88*</td>
<td>0.73*</td>
</tr>
<tr>
<td>ZK</td>
<td></td>
<td></td>
<td>1.41</td>
<td>0.62</td>
</tr>
<tr>
<td><strong>Means ± SD</strong></td>
<td><strong>-0.78 ± 2.55</strong></td>
<td><strong>0.13 ± 0.60</strong></td>
<td><strong>2.07 ± 2.27</strong></td>
<td><strong>0.49 ± 0.74</strong></td>
</tr>
<tr>
<td><strong>Total means</strong></td>
<td><strong>-0.77</strong></td>
<td><strong>0.27</strong></td>
<td><strong>2.73</strong></td>
<td><strong>0.22</strong></td>
</tr>
<tr>
<td><strong>Amplitude means</strong></td>
<td></td>
<td></td>
<td></td>
<td><strong>10.16</strong></td>
</tr>
</tbody>
</table>

Cross-axis ratios in Table 1, in percent, are broken down into their conjugate and disconjugate parts. Numbers of saccades or saccade pairs (left and right eye) are as in Tables 1 and 2. If L is the cross-axis ratio for the left eye and R that of the right eye, the conjugate entry in this table was [L - R]/2 and the disconjugate (L - R). The disconjugate component is also reported in degrees, rather than a ratio, to be comparable with Table 2. The conjugate and disconjugate components were estimated for each saccade individually; individual means here are the average of these components. Sigma * and 1 indicate a change from normal that was statistically significant at the P < 0.05 level (t test). For the conjugate components, significant changes in the correct direction should be changes in the negative direction for upward saccades and in the positive direction for downward. All changes were significant, in the correct direction, and are therefore reported as Amplitude means as defined in Table 1. For disconjugate components, *indicates a significant shift in the direction of convergence, a significant shift toward divergence from the normal. Since no trends could be clearly justified or were obvious, only Total means are given. Total and Amplitude means are weighted by the number of saccades for each subject.

placements, a divergence on up gaze and convergence on down gaze for normal saccades made in the dark, similar to that found by the authors mentioned above. Posttarsaccadic drifts, however, were small and idiosyncratic (Table 3, column 2). There was a mild trend to converge after up saccades and a very weak convergence after down gaze. This suggests that, in the dark with no stimulus, there is no consistent posttarsaccadic vergence.

Exposure to horizontal retinal slip coupled with vertical saccades had, in the dark, a mean disconjugate drift that was even smaller (Table 3, column 4). Some subjects had statistically significant changes, but they were in no consistent direction, and the effects largely canceled out. Again, these were saccades in the dark; there was no reason to expect a consistent change from normal saccades in the dark. When the movable adapting stimulus was present, there were targets to fuse, and there we did see a modest convergence after up saccades in agreement with predictions from previous studies but failed to observe significant divergence after down saccades.

We note that our definition of conjugate and disconjugate may well be overrestrictive because the "vergence system," if defined as its neural substrate, might make, by mistake or design, conjugate movements, especially when combined with saccades as is the case here. Also, the "conjugate systems," similarly defined, may also produce disconjugate movements. Unfortunately, until we can define these "systems" better with microelectrodes and understand their possible nonlinear interactions in premotor circuits, these cautions must remain theoretical. From a practical point of view, one must deal with the observables that only allow separation of conjugate and disconjugate components as we have done.

With this caveat in mind, we nevertheless feel that, although our training paradigm did alter the intra- and posttarsaccadic disconjugate movements, we were unable to see any consistent picture emerging or any way in which they might confuse our results on cross-axis plasticity or require any reinterpretation of our conclusions.

**Theoretical considerations**

Posttarsaccadic drift is generally regarded as a form of pulse-step mismatch. [The slide is also an important component of saccade innervation (Goldstein 1983), but because the pulse and step, by themselves, can produce posttarsaccadic drift, it is conceptually easier to set aside the slide momentarily and think in terms of only the pulse and step. This is done to simplify the following hypothesis.] If the neural pulse is too large (or small), the eyes will drift backward (or forward) with an exponential time course to the steady-state position dictated by the step. The main problem for cross-axis drift is how it is generated; the horizontal drift cannot be generated by a pulse-step mismatch because there is no pulse; that is, no horizontal saccade.
We suggest the existence of a form of crossed innervation in which a motor command to create a movement in one direction is also sent, in a weaker version, simultaneously to agonist and antagonist motoneurons that generate orthogonal movements, to eliminate any unwanted orthogonal motion. More specifically, when a vertical saccade is made, the lack of a horizontal component is not achieved by default; that is, the absence of any signal sent to the horizontal motoneurons. We propose that the lack of a horizontal component is active rather than passive. If it were passive, plastic learning mechanisms would have no control over it—no way to eliminate an unwanted component coming from, for example, mechanical cross talk in the periphery. Active control would leave nothing to chance. In our example it would require that the pulse and step command for a vertical saccade be sent into premotor pathways responsible for both rightward and leftward movements so that they normally cancel at the motoneurons and produce no horizontal component. With this arrangement, if any unwanted component began to appear, it could be actively eliminated by synaptic plasticity that readjusted the balance between the opposing signals.

This may be a general principle in motor control. There is very good evidence for it in the vestibuloocular reflex. When cats are oscillated in pitch synchronously with the horizontal displacement of a visual display, they develop, within 2 h, a cross-axis reflex (e.g., Schallheis and Robinson 1981). In the dark, stimulation of the vertical canals by pitch produces a vigorous (25%) horizontal eye-movement component. Presumably, in 2 h, de novo projections were not made from the vertical semicircular canals to the horizontal motoneurons. If not, then preexisting connections must have changed their synaptic weights. Because vertical head movements do not normally produce horizontal eye movements, these connections must carry signals that normally cancel each other. When challenged, they must have undergone synaptic changes that upset the balance to create the observed horizontal movements. A model for such cross connections has recently been proposed by Peterson et al. (1991). They place the modifiable synapses in the flocculus, a much debated idea, but the main idea of orthogonal plasticity through preexisting synapses is clearly laid out.

For the saccadic pulse, evidence for crossed innervation is available (Keller 1974; Luschei and Fuchs 1972; van Gisbergen et al. 1981). In the latter study in the monkey, (medium-lead) burst neurons on both sides of the brain stem, which burst most vigorously for purely ipsilateral saccades, also burst weakly (300 spikes/s) during vertical saccades. These neurons monocularly excite ipsilateral descending motoneurons and, through inhibitory burst neurons, di- or trimodally inhibit or disinhibit contralateral-due saccade motoneurons. During a vertical saccade, these signals cancel on the motoneurons that show no obvious bursting at such times. (It is unlikely that these signals cancel perfectly at each instant during a vertical saccade, and this could account, in part, for the tiny intrasaccadic horizontal pulses and wiggles seen in all our recordings.) The activity of the horizontal burst neurons must reflect a small projection from the burst cells that primarily effect both up and down saccades, crossed innervation.

The horizontal burst neurons also project to the neural integrator in the medial vestibular and prepositus hypoglossus nuclei, bilaterally, to produce the requisite step of innervation for the motoneurons (e.g., Cannon and Robinson 1987). During a vertical saccade, the horizontal burst neurons send contradictory signals to the integrator with no net result, no horizontal step. If the pathways from the burst neurons to the integrator are altered by synaptic learning, the integrator would produce a step even though the bursts still cancel out on the motoneurons and no horizontal saccade occurs. The result is a step without a pulse that creates post-saccadic drift without a saccade. The purpose of this arrangement is to prevent retinal image motion after a saccade from whatever source it might arise and in any direction.

This is one way to account for our results. Other pathways could also be involved. Excitatory and inhibitory signals, normally canceling, from vertical burst neurons could reach the horizontal integrator more directly. Similar signals from the vertical neural integrator could project to the horizontal motoneurons. The only recommendation for the arrangement we have described above is that it resembles pathways already demonstrated to exist.

It is known that the flocculus is essential for plastic control of post-saccadic drift and cross-axis plasticity of the vestibuloocular reflex, so it is very likely to be involved in cross-axis post-saccadic drift. This means that the plastic changes we observe are somehow mediated by floccular Purkinje cells projecting to the vestibular nuclei and prepositus hypoglossus nuclei (McCrea et al. 1979), but nothing is known about where such plastic synapses exist or how they might be modified.

In summary, we propose a fairly simple method by which plastic synapses can account for our results on cross-axis post-saccadic drift utilizing pathways already known to exist.

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