Disconjugate oculomotor learning caused by feeble image-size inequality: differences between secondary and tertiary positions

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Abstract

In order to examine the minimum value of image-size inequality capable of inducing lasting disconjugacy of the amplitude of saccades, six normal emmetropic subjects were exposed for 16 min to 2% image size inequality. Subjects were seated at 1 m in front of a screen where a random-dot pattern was projected and made saccades of 7.5 and 15 deg along the horizontal and vertical principal meridians and to tertiary positions in the upper and lower field. During the training period, compensatory disconjugacy of the amplitude of the saccades occurred for the principal horizontal and vertical meridians; such increased disconjugacy persisted after training, suggesting learning. In contrast, for horizontal saccades to or from tertiary positions made in the upper and lower field, no consistent changes in the disconjugacy occurred, either during training or after the training condition. In an additional experiment, three subjects read sequences of words with the 2% magnifier in front of their dominant eye: in such a task, horizontal saccades to or from tertiary positions at the upper or lower field showed appropriate and lasting disconjugacy for two of the three subjects. We conclude that even a 2% image size inequality stimulates oculomotor learning, leading to persistent disconjugacy of saccades. The small disparity created by the image-size inequality is thus compensated by the oculomotor system rather than tolerated by the sensory system (e.g. by enlarging the Panum’s area). © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Normal emmetropic subjects can rapidly change the natural binocular coordination of their saccades when they view an image uniformly magnified for one eye (aniseikonic image): saccades become disconjugate in the two eyes after only a few minutes. Such disconjugacy reduces the disparity due to the aniseikonia and provides single bifoveal fixation immediately after each saccade. Saccade disconjugacy persists under subsequent monocular viewing (in the absence of disparity), which indicates oculomotor learning (e.g. Kapoula, Egger, & Bucci, 1995; Van der Steen & Bruno, 1995). The above cited studies used a relatively important image size inequalities (8–10%); the disparity of such images corresponds to that created by a difference of about 4–5 Diopters (D) for spherical lenses (see Rubin, 1974). There are a few studies dealing with smaller image-size inequalities (of the order of 2 D), but these studies examined relatively longer-term disconjugate learning. Erkelens, Collewijn, and Steinman (1989) showed that normal subjects exposed for 8 h to +2D of aniseikonia can produce compensatory disconjugacy of the amplitude of saccades. Lemij and Collewijn (1991) reported that after 1 h of wearing aniseikonic spectacles of −2D, normal subjects were able to produce disconjugate changes in the amplitude of saccades. In monkeys, Oohira and Zee (1992) used a combination of positive and negative prisms of 2 D such as to elicit discrete position specific adaptive changes (different for different parts of the visual field). Saccades and adaptation were assessed by recording eye movements 4–15 days after wearing that combination of prisms. Position-specific saccade adaptation was found, albeit not as discrete, as required by the prisms.
Our interest here is to examine in normal humans whether a small value of aniseikonia is able to activate fast disconjugate oculomotor learning and to assess better the interplay between sensory and motor aspects of such learning. Would the sensory system tolerate or learn to fuse disparities resulting from image size inequalities smaller than 2 D, or would such a disparity cause fast disconjugate oculomotor learning? It should be noted that a small image-size inequality (< 2 D) frequently occurs in subjects wearing spectacles.

The second goal of the study is to examine whether learned saccade disconjugacy occurs for horizontal saccades to or from tertiary eye positions in the upper and lower fields. To our knowledge, such eye positions were extensively studied for vertical phoria adaptation (see Schor, Gleason, & Lunn, 1993a; Schor, Gleason, Maxwell, & Lunn, 1993b; Schor, Maxwell, & Stevenson, 1994; Maxwell & Schor, 1996; Schor & McCandless, 1997). Nevertheless, as shown by Schor et al. (1993a), adaptation of phoria involves a different mechanism and does not transfer to saccades. The only human study dealing with tertiary positions is the study of Lewis et al. (1995) on patients with paresis of the superior oblique muscle. They showed an improvement of both vertical saccade conjugacy and vertical phoria after strabismus surgery for both secondary and tertiary positions.

In our study, subjects were exposed for 15 min to a 2% image-size inequality and made saccades along the horizontal and the vertical principal meridians, as well as horizontal saccades in the upper and lower field. This led to a lasting disconjugacy of the amplitude of the saccade that was appropriate for the disparity. This, however, occurred only for the principal horizontal and vertical meridians. In contrast, for horizontal saccades to or from tertiary positions made in the upper and lower field, no consistent changes in the disconjugacy occurred, either during training or after the training condition. Nevertheless, a second experiment suggests an improvement in disconjugate oculomotor capability for tertiary positions when using a more demanding task such as reading sequences of words.

2. Methods

2.1. Subjects

Six emmetropic subjects were studied. Visual acuity was 20/20 for each eye, and binocular vision was normal (the TNO test for stereoscopic vision was 60 sec arc or better). For all but one subject (SP), the right eye was dominant; subjects participated in the experiment after giving their consent.

2.2. Stimulus

In a dark room, subjects were seated 1 m in front of a flat translucent screen. Their head was stabilized with a bite bar (with an individual fitted dental impression of the subject’s upper teeth). Subjects wore an afocal magnifier of 2% in front of their dominant eye. At the beginning of the session, one eye was covered, and the subject looked monocularly to avoid any binocular visual stimulation with the magnifier. It should be observed that the magnifier was afocal and had no effect on the accommodation. Consequently, this was a reduced situation where disparity was almost the only stimulating cue.

Subjects looked at a random-dot pattern (30 × 30 deg) projected onto a translucent screen; this stimulus is very efficient because of the absence of any important conflict between disparity and monocular depth cues (Bucci, Kapoula, & Eggert, 1999).

2.3. Eye movement recording

A detailed description on recordings and data-analysis techniques can be found in previous studies (e.g. Kapoula et al., 1995; Bucci et al., 1999). Data collection was directed by REX, software developed for real-time experiments, and run on a PC. The horizontal and vertical movements of both eyes were recorded simultaneously by a magnetic-field search coil (Robinson, 1963; Collewijn, Van der Mark, & Jansen, 1975). The eye-position signals were filtered with a bandwidth of 0–200 Hz and digitized with a 12-bit analog-to-digital converter sampling each of the four channels 500 times per second.

2.4. Bidimensional calibration

At the beginning of the experiment, subjects were asked to explore, step by step, a grid (subtended 30 deg) including tertiary positions. The grid was formed by five horizontal and vertical lines with letters at their intersection; subject was asked to fixate each letter at each intersection of the grid. Subjects performed this task twice: once by saccading laterally from one letter to the other and another time by saccading vertically from one letter to the other. This calibration test was performed under monocular viewing (right- and left-eye viewing, respectively). Calibration was performed with the magnifier in front of the dominant eye; consequently, the amplitude of the grid for the dominant eye viewing condition was corrected for the 2% magnification. From the complete sets of eye position data, fixation periods of at least 350 ms duration were extracted, during which, the eye position stayed within a circle of 1.2 deg from the fixated position. A bidimensional calibration in Helmholtz coordinates was estab-
lished from these fixation data using a bidimensional spline extrapolation. Recall that the coordinate system described by Helmholtz uses a head-fixed horizontal axis for the vertical component of eye position and an eye-fixed vertical axis for the horizontal component (Schor et al., 1994).

2.5. Testing conditions

2.5.1. Baseline recordings (6 min)

This control condition was used to determine the natural binocular coordination of saccades before the training. Under monocular viewing with the eye wearing the magnifier (absence of disparity), the subject was asked to saccade back and forth between the center and different points of the random-dot image along the horizontal and vertical meridians: the extreme edge points of the image or the points half-way, which were indicated by markers placed upon the random-dot pattern. These points corresponded to 7.5 and 15 deg from the center of the image. Previous studies (Kapoula et al., 1995; Kapoula, Bucci, Lavigne-Tomps, & Zambrescu, 1998) have shown that the amplitude of the disconjugacy induced by 10 or 8% magnification was not correlated with the amplitude of the saccade, despite the fact that the magnification caused disparity increasing with the amplitude of the saccade. We wondered whether the small magnification (2%) used in the present study would also produce a similar uncorrelated disconjugacy. To test for this, we used the aforementioned two saccade amplitudes. Furthermore, in the present study, for the first time, saccades from secondary to tertiary positions are included; it is interesting to examine if and how the central induced disconjugacy for such axis would be correlated with the size of the saccade.

The axis along which saccades were made was changed every 1.5 min: (i) horizontal saccades at eye level, (ii) vertical saccades along the midline, (iii) horizontal saccades between secondary and tertiary positions at 15 deg of constant elevation in the upper field and (iii) horizontal saccades at 15 deg of constant depression in the lower field. For the two later conditions, the markers at the tertiary positions were placed also at 7.5 and 15 deg from the corresponding (up or down) secondary position. Thus, the amplitudes of the saccade tested were the same for all four axes. Note that the term “principal meridian” refers to meridians that cross the center of the image, and the term “primary position” refers to the straight-ahead fixation of the center of the image.

2.5.2. Experiment I: training (16 min)

Viewing was binocular with the 2% magnifier in front of the dominant eye. Consequently, the dominant eye viewed each point of the image 2% further than the other eye (disparity). Subjects were asked to make saccades for 16 min between the same points indicated by the markers; the training period was 4 min for each axis (horizontal at eye level, vertical along the midline, horizontal at 15 deg up, horizontal at 15 deg down).

2.5.3. Experiment II: reading words along tertiary positions with a 2% magnification over the dominant eye

To explore further the ability of normal subjects to exert disconjugate learning on the binocular coordination of their saccades to or from tertiary positions, we ran a second experiment in which subjects read from left to right a sequence of words projected (i) at 15 deg up, (ii) at eye level, or (iii) 15 deg down.

Word identification is an automatic process, albeit highly cognitive. Rapid word recognition most likely relies on accurate alignment of both eyes within the word in order to obtain single clear binocular vision. This task was rendered perceptually more difficult because of the 2% binocular disparity due to the magnifier.

Three of the subjects (MPB, ZK, and SP) participated in this study. Words were written in Microsoft PowerPoint 97 and directly projected onto the screen via an overhead projector connected to the PC. Each line of words was presented for 2 s. The length of the words was either seven or nine characters. In some trials, the sequence contained three words, in others, five words. In the former case, we elicited saccades of approximately 12.5 deg, and in the latter case, we elicited saccade sizes of about 6 deg. These sizes are similar to those of the first experiment and also close to habitual saccade sizes during reading.

Subjects were invited to read each word, searching for words meaning an animal’s name. We did not ask them to report manually or verbally the animal’s name detected after every sequence read in order to avoid head or body movement. However, to make the task meaningful, at the end of the experiment, subjects should have reported the names of the animals they read. All subjects reported the names correctly in 100% of the cases.

As in the first experiment, three testing conditions were run: reading sequences of words under monocular viewing (before), reading with both eyes viewing and the magnifier 2% on (training), and reading under monocular viewing (after training). During training, the axis where the sequence of words was presented (eye level, up or down) alternated every 2.5 min, and each axis was run twice; the total training time devoted for each axis was 5 min. For the before- and after-training recording conditions, saccades along each axis were recorded for 2 min.
3. Experiment I: results

3.1. Horizontal and vertical saccades to secondary positions

3.1.1. Qualitative data

Fig. 1 shows typical binocular recordings for horizontal saccades, leftward movements (A–C) from subject MPB, and for downward saccades (D–F) from subject ZK. Before training, horizontal as well as vertical saccades were fairly conjugate for the two eyes. Horizontal saccades show a small intrasaccadic divergent movement due to the well-known abducting–adducting asymmetry (e.g. Kapoula, Hain, Zee, & Robinson, 1987; Collewijn, Erkelens, & Steinman, 1988a). Vertical saccades were almost perfectly yoked, as reported by Collewijn, Erkelens, and Steinman (1988b). During training, horizontal as well as vertical saccades became unequal in the two eyes: the right eye, which was wearing the magnifier, made larger saccades than that of the left eye. The disconjugacy reached at the end of the saccade was sustained during the post-saccadic fixation period. Under subsequent monocular viewing after the training period, horizontal and vertical saccades retained a similar sustained disconjugacy.

Note that for all conditions tested, the post-saccadic drift amplitude was smaller than the intra-saccadic amplitude. This confirms previous studies (e.g. Kapoula et al., 1995; Bucci et al., 1999), showing that the most prominent change induced by such paradigm is the intra-saccadic disconjugacy. Next are presented quantitative data for both the disconjugacy of the amplitude of the saccades and of the post-saccadic eye drift for horizontal and vertical saccades to secondary positions.

3.1.2. Quantitative data

3.1.2.1. Saccades to secondary positions. Fig. 2 shows individual means of the disconjugacy measured at the end of the saccade for each subject, and the group mean for horizontal (A) and vertical saccades (B) before, during and after training. The during-training value is based on all saccades made during the 15 min training period. The requirement due to the magnifier is shown by the horizontal segments: it is 2% of the amplitude of the saccade towards the target point aimed by both eye (the target point for the eye with the magnifier was corrected for the 2% of magnification). This measure of requirement was almost identical to 2% of the amplitude of the saccade averaged over the two eyes. It should be noted that the amplitude of the disconjugacy of the saccade induced was not correlated with the amplitude of the saccade, even though the requirement increased with the saccade size, either for horizontal or for vertical saccades. During training, a reliable positive correlation between saccade amplitude and induced disconjugacy occurred for subject MPB, horizontal saccades ($r = 0.48$, $n = 325$) and, to a lesser extent, for subject MA, horizontal saccades ($r = 0.28$, $n = 220$), and for subject ZK, vertical saccades ($r = 0.26$, $n = 215$). This is in agreement with several prior studies (e.g. Kapoula et al., 1995, 1998). Consequently, quantitative data presented in Figs. 2–5 show, in degrees, the mean disconjugacy of all saccades made in each condition; the mean size of the saccades was kept the same for the three tested conditions and are indicated in the legends.
The baseline values of disconjugacy were small for all subjects for both horizontal and vertical saccades. The group mean disconjugacy value was $0.10 \pm 0.19$ deg for horizontal saccades (range $-0.07$ to $0.31$ deg) and $0.02 \pm 0.19$ deg for vertical movements (range $-0.07$ to $0.30$ deg). During training, the disconjugacy changed in the appropriate direction for all subjects; the change was significant for 10 of the 12 cases (MPB vertical saccades, NA horizontal saccades showed no change). The group mean disconjugacy was statistically different with respect to the baseline measure for horizontal saccades (difference $0.26 \pm 0.28$ deg, $P < 0.05$); for vertical saccades, the group mean difference was $0.17 \pm 0.23$ deg and tended towards significance ($P < 0.07$).

For the majority of the subjects for both horizontal and vertical saccades, the disconjugacy persisted under monocular viewing recorded after the training condition. The after-training disconjugacy value was statistically different from the baseline value for four subjects (MPB, MG, ZK and SP) for horizontal saccades and for three subjects (MG, NA, ZK) for vertical saccades. The group mean difference of the after-training value from the baseline value was $0.24 \pm 0.23$ deg for horizontal saccades and $0.17 \pm 0.25$ deg for vertical saccades. Both these differences were statistically significant (at $P < 0.05$).

![Fig. 1. Typical binocular recordings of saccades before, during and after training. The solid line is the position trace of the left eye, and the dashed line is that of the right eye; the lower trace is the vergence (difference between LE and RE); (A–C) rightward saccades from subject MPB (positive values show convergence, negative values show divergence); (D–F) downward saccades together with the corresponding disconjugacy from subject ZK (negative value show right eye hypodeviation). Both subjects had the magnifier in front of the right eye.](image-url)
Was the change in disconjugacy of appropriate amplitude for the requirement? As shown in Fig. 2, individual subjects show a large variability: subject MG, for all saccades, and subject ZK, for vertical saccades, developed a disconjugacy larger than that required by the disparity of the aniseikonic image. On average, however, the group mean changes were equal to, or slightly smaller than, those required.
Fig. 3. Individual means of disconjugacy of saccades before, during and after the training period; vertical lines are standard deviations. Horizontal lines indicate the disconjugacy required by the magnifier during the training period. (A) Horizontal saccades at 15 deg in the up field; (B) horizontal saccades at 15 deg in the lower field. The mean amplitude of saccades analysed was 9.9 ± 3.7, 10.2 ± 2.2 and 9.9 ± 2.3 for saccades made before, during and after training in the upper field and 10.3 ± 3.1, 10.1 ± 3.4 and 9.8 ± 3.4 deg for saccades made in the lower field. Before- and after-training means are based on 58–91 for horizontal saccades in the upper field and on 65–107 for horizontal saccades in the lower field; means during training are based on 93–194 and on 85–201 for saccades made in the upper- and lower field, respectively. Asterisks indicate the difference from the disconjugacy of saccades in the before-training condition that was appropriate for the disparity due by wearing the magnifier, and significant at level $P < 0.05$. Crosses indicate a significant change in the opposite direction.
3.1.3. Changes in post-saccadic eye drift

3.1.3.1. Horizontal saccades. Before training, for all subjects tested, horizontal saccades were followed by a small disconjugate drift that was usually convergent for both rightward and leftward saccades. The group mean drift amplitude (rightward and leftward saccades together) was $0.03 \pm 0.07$ deg ($n = 6$ subjects). During training, the mean drift value was $-0.01 \pm 0.08$ deg ($n = 6$ subjects); in the after-training condition, the mean drift value was $-0.01 \pm 0.1$ deg ($n = 6$ subjects). Student's $t$-test, comparing each of these means with the mean in the before-training condition, failed to reach significance.

3.1.3.2. Vertical saccades. In the baseline condition, the group mean value of vertical post-saccadic drift following vertical saccades was $0.04 \pm 0.04$ deg ($n = 6$ subjects); this value did not change significantly either during training (group mean value: $0.05 \pm 0.05$ deg) or after training ($0.06 \pm 0.1$ deg).

3.1.3.3. Horizontal saccades between secondary and tertiary positions. Fig. 3 shows individual means of the disconjugacy of horizontal saccades made between secondary and tertiary positions at 15 deg in the upper field (A), and at 15 deg in the lower field (B). Before training, the mean disconjugacy of saccades to or from tertiary positions either in the upper or in the lower field was small for all but one subject (MA, saccades in the upper field); values were similar to those observed for horizontal saccades at eye level, to or from secondary positions (< 0.5 deg for saccade amplitude below 20 deg; see Kapoula et al., 1987; Collewijn et al., 1988a). The group mean value was $-0.04 \pm 0.38$ deg and $-0.10 \pm 0.12$ deg for saccades in the upper and lower field, respectively. Note, however, the large variability of both individual means.

During training, while subjects were exposed to an image-size inequality of 2%, the disconjugacy of the saccades changed for almost all subjects in the appropriate direction and for both saccades in the upper field as well as the lower field; such changes, however, were statistically significant with respect to the control condition only in a few cases (MG, ZK, MA in the upper field and MPB, ZK in the lower filed). The group mean values did not change significantly from the baseline values (the difference was $0.09 \pm 0.55$ deg for saccades made in the upper field, and $-0.01 \pm 0.26$ deg for saccades made in the lower field). Again, there was no positive correlation between saccade amplitude and the induced disconjugacy, except for saccades in the upper-field subject MA ($r = 0.40, n = 185$) and subject SP ($r = 0.44, n = 202$).

After training, under monocular viewing, the group mean disconjugacy value was $-0.07 \pm 0.36$ deg for...
3.1.4. Additional observations

How well were the eyes aligned vertically when subjects made saccades between secondary and tertiary positions? First, saccades in the upper and lower field were purely horizontal with no significant vertical component. The vertical saccadic conjugate component was only 0.16 ± 0.30 deg and 0.15 ± 0.26 deg in the upper and lower field, respectively. Despite the fact that there was no significant vertical conjugate saccadic component, for downward gaze, there was a change in the vertical binocular eye alignment during the horizontal saccades, i.e. a mild cross-axis misalignment of the eyes. Before training, tested under monocular viewing, there was a mild hypodeviation of the covered eye associated with execution of the horizontal saccades with both up and down gazes. The mean value of this hypodeviation for the six subjects was $-0.32 ± 0.40$ deg at the up gaze and $0.19 ± 0.65$ deg at the down gaze. During training, i.e. under binocular disparate viewing with the magnifier, there was no change in this hypodeviation for horizontal saccades made at the upper visual field: the mean hypodeviation of the eye without the magnifier was $-0.25 ± 0.45$ deg ($n = 6$ subjects) during training, and remains the same $-0.40 ± 0.69$ deg ($n = 6$ subjects) in the after-training condition (monocular viewing, when this eye was covered). It should be noted that this relative hypodeviation of the eye without the magnifier and hyperdeviation of the eye with the magnifier was appropriate for reducing the disparity at up gaze. In contrast, it was inappropriate for the down gaze. Thus, when the subject looked binocularly with the magnifier on, horizontal saccades at the down gaze were coupled with vertical disconjugacy in the appropriate direction that allowed to reduce vertical disparity at down gaze as well. During the training period, the group mean vertical disconjugacy associated with horizontal saccades was $0.15 ± 0.79$ deg ($n = 6$ subjects), and this value was statistically different from the baseline value. In the after-training condition (under monocular viewing), the vertical disconjugacy was $0.01 ± 0.88$ deg ($n = 6$ subjects), and it was also statistically different from the baseline value.

The static vertical eye alignment measured at the end of the horizontal saccades showed that the eyes were aligned appropriately for the vertical disparity for the up gaze (during training: $-0.40 ± 1.25$ deg, $n = 6$ subjects) but inappropriately for the down gaze (during training: $0.15 ± 1.40$ deg, $n = 6$ subjects). Thus, the cross-axis disconjugate vertical component coupled with the horizontal saccade accentuated the appropriate alignment for the up gaze and reduced the misalignment for the down gaze. This suggests that the cross-axis disconjugate vertical disconjugacy was functional particularly for the down gaze. This is further corroborated from the observations concerning horizontal saccades at eye level: the vertical alignment of the eyes was

![Fig. 5. Individual changes in the disconjugacy of saccades for subject MPB and ZK in the two different experiments for saccades made at eye level, 15 deg in the upper- and lower fields. (A–C) Before during-training changes. (D–F) Before after-training changes. Other notations as in Fig. 3.](image-url)
almost perfect and stable in all tested conditions, and there was no significant vertical disconjugacy component: 0.02 ± 0.25 deg (n = 6 subjects) before training, 0.04 ± 0.15 deg and 0.01 ± 0.22 deg in the after-training condition.

4. Experiment II: results

Fig. 4 shows the individual mean of saccade disconjugacy in the three conditions tested for each subject for horizontal saccades at eye level (A), at 15 deg in the upper field (B) and at 15 deg in the lower field (C).

For saccades at eye level [Fig. 4(A)], the natural saccade disconjugacy was again small. During training, this disconjugacy changed to compensate for the disparity due to the magnifier; the change was significantly different from the baseline value for two subjects (MPB and ZK), and tended towards significance for subject SP (P < 0.06). After training, the disconjugacy was still in the direction required by the magnifier. The before–after training differences were significant for two of three subjects (ZK and SP, P < 0.05) and similar to the significance for subject MPB (P < 0.07).

For saccades at the upper field [Fig. 4(B)], and for saccades at the down field [Fig. 4(C)] during training, saccades became disconjugate in the two eyes, as required by the disparity due to the magnifier for two subjects (MPB and ZK) the changes were significantly different with respect to the baseline condition. Subject SP did not show any change in her saccade disconjugacy. After training, the disconjugacy was still in the appropriate direction as during the training period for subjects MPB and ZK up field, and for subject ZK down field; these before–after training differences were significant (P < 0.05). In contrast, subject SP showed no appropriate change in her disconjugacy for either field.

The role of the cognitive task on oculomotor learning can be better appreciated by comparing the amount of changes in the disconjugacy of the amplitude of the saccades for subjects MPB and ZK for the two different experiments (Fig. 5). Fig. 5A–C shows the before–during training changes in the disconjugacy of the saccade for subject MPB and ZK for horizontal saccades along the three axes examined. In all but one case (saccades in the lower field, subject ZK), the changes are significantly larger in the experiment II (t-test, P < 0.05). The before–after training changes (Fig. 5D–F) show similar results; all individual changes are larger in the experiment II, and all of them (except saccades at eye level, subject MPB) are significantly larger than the changes observed in the experiment I (t-test, P < 0.05).

In conclusion, this experiment, albeit run on three subjects, suggests that in the presence of a feeble image-size inequality, disconjugate oculomotor learning can occur even for horizontal saccades at the upper and lower visual field between secondary and tertiary positions; nevertheless, such learning appears to be subject-dependent and, for some subjects, could be facilitated by the use of a task such as reading words with an increased perceptual or cognitive load.

5. Discussion

5.1. Summary and findings

The first new finding of this study is that horizontal and vertical saccades to secondary positions become rapidly disconjugate in the two eyes, even when the aniseikonic disparity is as small as 2%, i.e. 1 D. This finding is in line with prior studies using a larger image-size inequality (8–10%; see Kapoula et al., 1995; Van der Steen & Bruno, 1995) and allows a more complete characterization of the disconjugate oculomotor learning. The disconjugate learning induced here by the feeble image-size inequality showed compatible characteristics as in the above cited studies: after a short time of exposure to feeble aniseikonia, the disconjugacy of the amplitude of saccade was retained under subsequent monocular vision in the absence of disparity cues. As has been observed previously (e.g. Kapoula et al., 1995; Bucci et al., 1999), this paradigm did not produce any significant changes in the disconjugacy of the post-saccadic eye drift.

The second new finding is that disconjugate learning or even compensatory disconjugacy in the presence of disparate aniseikonic images is more difficult to implement for horizontal saccades to or from tertiary positions at the upper and lower visual fields.

The third new finding is the suggestion that a perceptually and cognitively more demanding task, such as reading sequences of words, can improve the ability to produce appropriate disconjugacy for saccades to tertiary positions.

5.2. Exposure to feeble image-size inequality: sensory and motor aspects

The significance of the present study relies on understanding better the interplay between sensory and motor mechanisms. With the 2% magnifier in front of one eye, subjects encountered disparities of about 0.15–0.3 deg, depending on the size of their antecedent saccade. Such disparities, horizontal and vertical, could be readily fused by the sensory system. Indeed, single binocular vision occurs even though the image of an object is not projected perfectly corresponding to retinal elements, i.e. in the presence of fixational disparity. Furthermore, fixational disparity, e.g. due to interocular distance, is the basis for stereopsis and depth perception (see...
Howard & Rogers, 1995 for a recent review). The respective role of sensory and motor signals in driving adaptation or learning and the nature (sensory or motor) of learning itself is an issue of theoretical importance. This has been addressed for phoria or prism adaptation: immediately upon wearing a prism over one eye, the phoria changes, but a few minutes later, the phoria is reduced back to its normal value. According to Schor (1985, 1988), phoria adaptation is driven by a slow fusional mechanism that uses the motor output of a hypothetical, fast, disparity-fusional mechanism as an error signal. Thus, both the driving signal and the adaptation itself are motor. Our findings are consistent with these ideas, as they show that adaptation to disparity even of a small amplitude, ends up by causing oculomotor readjustment, e.g. saccade disconjugacy. The readaptation with which disconjugate oculomotor learning can occur (i.e. within a few minutes) is probably the reason why the CNS operates by modifying the oculomotor binocular coordination rather than by learning to tolerate or fuse at the sensory level disparities, i.e. by enlarging Panum’s area, which is known to be adaptable (see Howard & Rogers, 1995).

5.3. Disconjugate learning for tertiary positions

Our findings on tertiary positions are of particular interest. First, we observed that the yoking of such saccades is not as good as that of saccades to secondary positions (for comparison, see Figs. 2 and 3, hatched bars, subjects MPB, ZK, SP). Second, in the first experiment, subjects failed to develop a disconjugacy appropriate for the disparity due to the magnifier, suggesting a smaller capacity for disconjugate oculomotor readjustment for saccades to tertiary eye positions. With an afocal magnifier in front of one eye, subjects encountered both vertical and horizontal disparities when fixating at tertiary positions; the vertical disparity was constant for a given axis (up and down gaze). In contrast, the horizontal disparity increased with the eccentricity of the target-marker aimed by the saccade.

The additional analysis of the vertical eye alignment provides evidence that for up and down gazes, there was a higher load of sensory and motor control, and this could be the reason why disconjugate learning for horizontal saccades driven by the horizontal disparity was less systematic for these axes.

Extensive investigations of vertical phoria adaptation (see Schor et al., 1993a,b; Schor et al., 1994; Maxwell & Schor, 1996; Schor & McCandless, 1997) indicate that the sensory system is capable of dealing efficiently with, and adapting to, disparities at tertiary positions. In particular, Schor and McCandless (1997) showed that vertical phoria adaptation can occur within 1 h and can be specific to horizontal and vertical conjugate positions, to horizontal vergence angle, and to any combination of two of these parameters. Thus, there is no limitation for the sensory system to deal with disparity and associate vertical disparity with different gaze positions. Nevertheless, in an earlier study, Schor et al. (1993a) reported that vertical phoria adaptation does transfer to vertical pursuit eye movements but not to vertical saccades. The authors suggest the presence of distinct learning mechanisms for slow and rapid eye movements. In our experiment, we concentrated on horizontal saccades to or from tertiary positions, and the most appropriate mechanism would be a disconjugate learning mechanism that would adjust the alignment of the eyes within the course of a saccade. Perhaps, it is more difficult to program horizontal disconjugate saccades when the innervation should be distributed to all six extra-ocular muscles of each eye as is required to keep the eyes elevated or depressed. Such difficulty, however, would be particularly disastrous in a reading task where horizontal saccades and fixations to tertiary positions at the upper or lower field are readily involved.

Our additional study on reading sequences of words, albeit on three subjects only, suggests that in such a situation, disconjugate oculomotor learning can also occur (for two of the three subjects tested). Therefore, these observations refute the existence of an absolute limitation in dealing with disparities and tertiary positions. We attribute the improvement in the ability to perform disconjugate oculomotor learning for tertiary positions in the reading task to the increased perceptual demand and cognitive load related to word recognition: single clear binocular vision of each word is presumably a prerequisite for rapid word recognition, thereby creating additional stress for the oculomotor system to deal with the small, but bothersome, disparity. Nevertheless, there are other possible explanations. For instance, in this task, subjects performed a sequence of saccades from left to right, thereby encountering the same type of disparity (e.g. consistently uncrossed or divergent disparity), and this could facilitate disconjugate learning, even for tertiary positions. Further research is needed to explore the mechanisms by which perceptual and cognitive tasks could influence the capacity of disconjugate oculomotor learning against the possibility of consistency in the type of disparity over successive saccades.

5.4. Absence of correlation between saccade amplitude and induced disconjugacy

The present study confirms prior reports (Kapoula et al., 1995, 1998), showing that the induced disconjugacy is not correlated with the saccade size, even though the disparity due to the magnifier is proportional to the size of the saccades. It seems that the absence of any correlation is an intrinsic aspect of the disconjugate
learning at least by the magnifications of 2% or 8% and 10% examined in the present and early studies, respectively. Furthermore, the present study indicates an absence of such a correlation also for saccades from secondary to tertiary positions. The disparity of the magnifier most likely induces a command of disconjugacy attached automatically to the saccade rather than a parametric readjustment of the amplitude of the saccade (see also Kapoula et al., 1995, 1998). In other words, this paradigm seems to induce a context-specific disconjugacy. Context specificity of oculomotor adaptation has been studied, e.g. by Deubel (1995). Here we use the term context-specific to express the hypothetical mechanism of associative oculomotor learning based on the coupling between saccades and disparity (mentioned above).

This hypothetical associative mechanism produces a disconjugacy that is coarsely related to the requirement from one trial to another, even though, on average, the change in the induced disconjugacy was equal to, or slightly larger than, the requirement. Then, the question arises whether, in cases of a larger-than-necessary disconjugacy at the end of the saccades, subjects were exposed to disparity of an opposite sign. To gain some insight, an additional analysis was performed of the horizontal vergence angle in the reading task for subjects MPB and ZK (see Fig. 5). Recall that rightward saccades of these subjects showed a change in the divergent disconjugacy larger than required. The results show that prior to training with the magnifier, subjects tended to converge closer in front of the screen. For subject MPB, the measured vergence angle was $3.6 \pm 0.5$, $3.6 \pm 0.8$ and $3.8 \pm 0.4$ deg, respectively, for saccades at eye level, at the upper field, and at the lower field; the corresponding plane of binocular fixation was thus 96 cm during saccades at eye level and for saccades made in the upper field and about 90 cm for saccades made in the lower field. For subject ZK, these measures were $3.7 \pm 0.4$, $3.9 \pm 0.4$ and $4.2 \pm 0.6$ deg. The corresponding planes of binocular fixation were 91, 88 and 81 cm for saccades made at eye level, at the upper field, and at the lower field, respectively. The measure of vergence angle in the training period, i.e. during reading with the magnifier, for subject MPB, was $3.4 \pm 0.3$, $3.2 \pm 0.8$ and $3.3 \pm 0.7$ deg for saccades at eye level, at the upper field, and at the lower field, respectively; these angles corresponded quite closely to viewing distances of 1, 1.03 and 1.07 m. For subject ZK, the values were $3.3 \pm 0.2$, $3.10 \pm 0.3$ and $3.2 \pm 0.5$ deg, corresponding to viewing distances of about 1.04, 1.02 and 1.10 m. Thus, despite the fact that the change in the disconjugacy was larger than the disparity of the magnifier, the eyes were closer to the correct viewing distance during training than before.

In conclusion, this study shows, for the first time, that disconjugate oculomotor learning occurs even for a feeble image-size inequality (of approximately $+1$ D). It also shows for the first time that disconjugate learning for horizontal saccades to or from tertiary positions is more difficult to stimulate. Finally, it provides some indication that disconjugate oculomotor learning for tertiary positions can improve in tasks with increased perceptual and cognitive demands such as reading of words.

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