

Binocular motor coordination during saccades and fixations while reading: A magnitude and time analysis

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Reading involves saccades and fixations. Misalignment of the eyes should be small enough to allow sensory fusion. Recent studies reported disparity of the eyes during fixations. This study examines disconjugacy, i.e. change in disparity over time, both during saccades and fixations. Text reading saccades and saccades to single targets of similar sizes (2.5°) are compared. Young subjects were screened to avoid problems of binocular vision and oculomotor vergence. The results show high quality of motor binocular coordination in both tasks: the amplitude difference between the saccade of the eyes was approximately 0.16° ; during the fixation period, the drift difference was only 0.13° . The disconjugate drift occurred mainly during the first 48 ms of fixation, was equally distributed to the eyes and was often reducing the saccade disconjugacy. Quality of coordination regardless of the task is indicative of robust physiological mechanisms. We suggest the existence of active binocular control mechanisms in which vergence signals may have a central role. Even computation of saccades may be based on continuous interaction between saccade and vergence.

Keywords: binocular coordination, eye movements, reading

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Introduction

Reading involves a succession of saccades and fixations. During a saccade, both eyes move quickly in the same direction with the same amplitude. Visual analysis is only possible during the fixation following the saccade. To allow binocular fusion of the fixated word, both foveas should be aligned on the same location, or at least have a small enough misalignment (i.e. inside the Panum's area), particularly at the beginning of the fixation (parafoveal processing of the next word, determining the upcoming saccades, may then occur). Lack of binocular coordination of saccades would cause fixation disparity and could interfere with visual processing of the word, particularly if disparity exceeds the limits of Panum's area. In such cases, a disparity-driven slow vergence movement should be activated to re-establish binocular eye alignment.

Binocular coordination of saccades is not perfect. When saccading to single visual targets, e.g. luminous points, the abducting eye makes a larger and faster movement than the adducting eye at the beginning of the saccade; these differences are small but measurable (Collewijn, Erkelens, & Steinman, 1988a, 1988b; Fioravanti, Inchingolo, Pensiero, & Spanio, 1995). They cause a transient divergent disconjugacy during the first part of the saccade; this is reversed toward the end of the saccade by a convergent disconjugacy. The residual divergent misalignment

between the eyes decreases further thanks to a disconjugate, convergent post-saccadic drift during the fixation. This pattern is the most commonly found in healthy young adults (Collewijn et al., 1988a; Yang & Kapoula, 2003). However, at a lower rate, saccades could end with a convergent or a null vergence error. Moreover, this pattern evolves during childhood. The binocular coordination of children is poorer than that of adults, and reaches the adult level at the age of 10–12 years. A divergent or convergent pattern of saccade disconjugacy occurs at similar rates in children (Yang & Kapoula, 2003). These studies typically involve saccades toward luminous points and the size of these saccades is generally about 5° or more. On the other hand, in reading, saccades tend to be much smaller. The present study bridges this gap as it examines binocular coordination of small size saccades in two tasks: reading and a standard oculomotor task involving saccades to single targets.

Most studies of the eye movements during reading are focused on cognitive aspects (for a review see Rayner, 1998) and the issue of binocular coordination has been largely ignored. However, some recent studies have addressed the issue of binocular fixation during reading and have involved the evaluation of fixation disparity at two single time points during the fixation—beginning and end (Blythe et al., 2006; Kirkby, Webster, Blythe, & Liversedge, 2008; Liversedge, Rayner, White, Findlay, & McSorley, 2006; Liversedge, White, Findlay, & Rayner,

2006). These studies showed that during reading, the eyes do not always fixate the same character (disparity at the end of the saccade of 1.1 characters, i.e. 0.32° , in the study of Liversedge, White et al. (2006) and 1.26 characters, i.e. 0.24° , in the study of Blythe et al., 2006). Yet, diplopia was not experienced and saccade metrics were computed on the basis of a unified binocular perceptual representation of the word. Indeed, using a dichoptic presentation, Liversedge, Rayner et al. (2006) showed that the process by which the visuo-motor system attains a unified visual percept of the non-foveal target word is one of fusion rather than suppression. Whether, in natural reading, fusion of the fixated word occurs systematically, remains to be explored. If fusion occurs despite relatively large disparities, it would suggest that the Panum's fusional area can extend up to at least 30 min of arc. The size of Panum's area (defined by some researchers as the area where single vision and stereoscopic vision is possible and by others as the lower limit of the disparity that will elicit fusional movements) strongly depends on the tested situation, extending from 6 minutes of arc up to 3° (for a review see von Noorden, 1996). Moreover, Panum's area may extend and shift with growing sensory adaptation (London & Crelier, 2006). The study of Liversedge, Rayner et al. (2006) showed that Panum's area during reading can be larger than the size of one character.

Yet, measuring binocular disparity at single time points (e.g. the beginning and the end of the fixation) does not reflect the entire period of visual analysis. Moreover, the criteria used to determine the beginning and the end of the saccade and fixation influence the measure of disparity. For instance, in the study of Liversedge, White et al. (2006), there were systematic disparity differences between the beginning and end of fixation, whereas this was not the case in the study of Blythe et al. (2006). The latter attributed these different findings to the different criteria used for identification of saccade onset and offset: the starting point and the end point of a fixation were marked as occurring later and earlier respectively in the study of Liversedge, Liversedge, Rayner et al. (2006), and due to transient disconjugacy during saccades (Collewijn et al., 1988a, 1988b), disparity can vary very fast during the saccade.

The present study was aimed to obtain a more complete view of the binocular motor control during reading. Thus, we examined the binocular motor coordination over multiple time periods during the saccade and during the first 160 ms of fixation. The goal was to understand how convergent and divergent movements of the eyes can create, compensate or maintain the crossed (closer than the target) and uncrossed (farther than the target) disparities found in previous studies (Blythe et al., 2006; Liversedge, Rayner et al., 2006; Liversedge, White et al., 2006). The rationale for examining the first 160 ms was the following. The average fixation duration during reading is

between 200 ms and 250 ms (O'Regan & Levy-Schoen, 1978); reading studies suggest that visual information is processed at the beginning of the fixation (see Bouma & De Voogd, 1974). More importantly, the time constant of physiological drift related to saccade control, i.e. the time constant describing the pulse-slide-step activity recorded in abducens neurons, is below 160 ms (Leigh & Zee, 2006). Thus, examining the first 160 ms of fixation is valid both physiologically and for perception and cognitive analysis. *A posteriori*, the results of the present study validate this choice as the time constant of disconjugate post-saccadic drift was even shorter.

Another novelty of the study concerns the recruitment of the subjects. We recruited young adults with perfect binocular vision (their stereoacuity was better than 40 seconds of arc). On the one hand, mild deficits of binocular vision can be reflected in poor binocular oculomotor control (Kapoula, Vernet, Yang, & Bucci, 2008), on the other hand, the coordination is developing with age during childhood (Yang & Kapoula, 2003). We consequently expect optimal binocular motor control from these subjects. Our results show rather excellent binocular coordination during reading, i.e. very small disconjugacy during the saccade and during the first 160 ms, both for the reading task and the single-target task. During the fixation, the disconjugacy was present only for a short time period, it was symmetrically distributed to the eyes, and it was often compensating the saccade disconjugacy.

Methods

Subjects

Nine young adult subjects (six women and three men) were tested. They were all native French speakers. Their age ranged from 22 to 30 years (mean 24.3 ± 2.8 years). All subjects had completed at least 4 years of university and had normal reading ability. They were healthy without any neurological, neuro-otological or ophthalmological symptoms. They had normal or corrected-to-normal vision. Binocular vision was assessed with the TITMUS test of stereoacuity. All individual scores were normal, 40 seconds of arc or better. Eye dominance was evaluated by asking the subject to look, through a hole formed with his/her hands, at a target located 5m away and then close alternatively each eye to judge the eye for which the alignment was the best. The dominant eye was the right eye for seven subjects and the left eye for one subject (s2); one subject (s8) displayed an alternating eye dominance. Each participant gave informed consent to be a subject in the experiment. This investigation was approved by the local ethics committee and consistent with the Declaration of Helsinki.

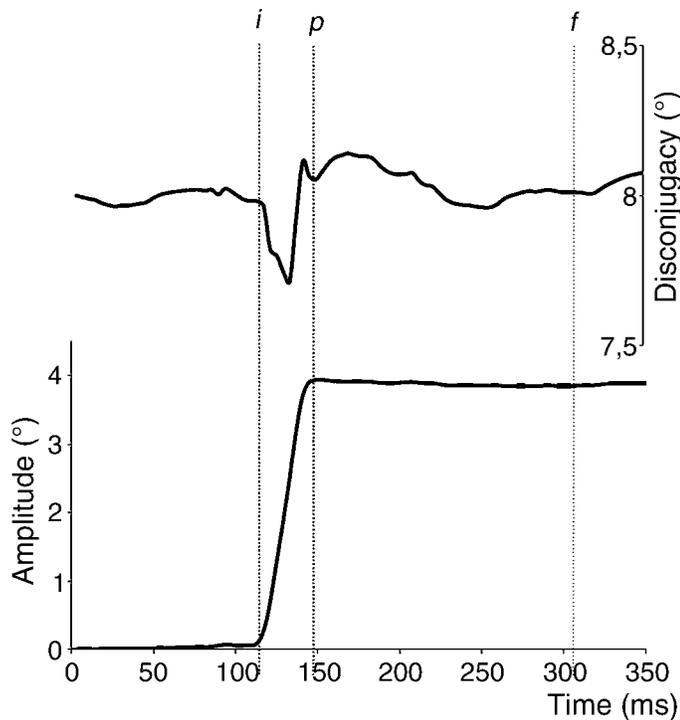


Figure 1. Determination of the saccade and the first 160 ms of fixation. Sample traces during the single target task (subject 6): saccade toward the 4° right. Lower trace: horizontal conjugate position. Upper trace: horizontal disconjugate position. *i* and *p* indicate, respectively, the beginning and the end of the saccade. *f* indicates the end of the first fixation period, 160 ms after the end of the saccade.

Eye movement recording

Horizontal and vertical eye movements were recorded binocularly with the EyeLink II device. Each channel was sampled at 250 Hz. The system has a resolution of 0.025°. The 9-point EyeLink calibration was always performed, followed by a second calibration at the beginning of each block.

Procedure

The subject was comfortably seated in an adapted chair, the head was stabilized with a chin rest. He/she viewed binocularly the visual display, on a PC screen placed 40 cm away from him/her and performed two tasks: a reading task and a single target task. The order of the tasks was pseudo-random.

Reading task

During the reading task, a text in French appeared, “L’alouette”. This text is commonly used in France for the evaluation of reading capacity in dyslexia. It contains

non-frequent words and the order of the words is unusual in French; the reader cannot use anticipation. The text was written in courier font size 12 and each letter was about 0.3° of angular size. Three text panels of 8° × 8° were presented on the screen for 30 s each, covering the complete “L’alouette” text. The subject was asked to read silently the text. To ensure that subjects actually read the text, they were asked to briefly comment on it. All subjects highlighted the strangeness of the text and quoted few words and sentences. At the beginning of the reading task a calibration sequence was run: a target (two segments 0.93° × 0.7°, aligned vertically, with offsets of 0.14° vertically and 0.7° horizontally) jumped between five positions on the screen, at the center and at ±8° horizontally and vertically. The subject was asked to follow accurately the center of the target (at the offset space).

Single target task

During the single target task, each trial started with the lightening of a central dot (angular size 0.2°) for 1000 ms. Simultaneously with the extinction of the central dot, an eccentric dot (angular size 0.2°) was turned on and remained lightened for 1000 ms. When the eccentric dot was turned off, the central dot was turned on again, starting the next trial. The apparition order of the eccentric dots was the following: left 2°, left 4°, left 6°, left 8°, right 2°, right 4°, right 6°, right 8°, up 2°, down 2°. This sequence was repeated 8 times. The instruction given to the subject was to fixate the target as accurately as possible.

Data analysis

Calibration was run on the vertical and horizontal eye position signals with second order polynomial functions. Cross-talk compensation was performed with the EyeLink calibration, preceding our second calibration procedure, with a non-linear function (coefficient computed from nine calibration points) described in the article of Stampe (1993). From the two calibrated eye position signals, we derived the horizontal conjugate signal (mean of the two horizontal eye positions) and the horizontal disconjugate signal (left-right eye horizontal position difference). We also derived the vertical conjugate signal (mean of the two vertical eye positions).

The onset, or offset, of horizontal saccades were defined as the time when the eye velocity of the conjugate signal exceeded, or dropped below respectively, 10% of the maximum velocity. The onset and the offset of the saccade are noted *i* and *p* in Figure 1. Similar criteria have been used in several other studies (e.g. Bucci, Gomes, Paris, & Kapoula, 2001; Yang & Kapoula, 2003). The end of the first fixation period of 160 ms following the saccade was marked with an *f*. The automatic placement of the markers

was verified by visual inspection of the individual eye movement traces.

From these markers, we measured the amplitude of the saccade and the amplitude of the post-saccadic drift during the first 160 ms. We then calculated the disconjugacy (change of disparity) during the saccade (between i and p) and the disconjugacy (change of disparity) during the first 160 ms of the post-saccadic drift (between p and f). The same analysis was applied to saccades during the reading task and during the single-target task.

Comparison between tasks: Selection

In both tasks, rightward saccades with amplitude equal or larger than 1° were considered. During the reading task, the average saccade amplitude was 3° and rarely exceeded 5° ; we removed the outliers, i.e. amplitudes larger than 8° (0.7% of the saccades). To consider saccades of similar direction and amplitude in the single target task, we selected saccades to targets presented at $+2^\circ$ and $+4^\circ$ positions. Saccades with amplitude larger than 150% of the required amplitude were rejected (0.8% of the saccades). In both tasks, fixation periods with a change in amplitude larger than 1° were rejected, because in such cases, a corrective saccade probably occurred (19.2% of the fixations). Thus, fixations shorter than 160 ms were not considered.

For the reading task, we considered three types of saccades: saccades starting with an elevation of the eyes lower than $\pm 1^\circ$ (eye level saccades, on average 31 saccades per subject), saccades starting with an horizontal eccentricity of the eyes lower than $\pm 1^\circ$ (midline saccades, on average 27 saccades per subject) and saccades made over the whole text (on average 157 saccades per subject). The rationale of considering eye level saccades and midline saccades in addition to considering all saccades is to take into account possible effects of vertical and horizontal eccentricity on binocular coordination. Moreover, considering only the eye level saccades or the midline saccades allows us to compare similar numbers of saccades with the single target task (on average 15 per subject). As the results were always the same for the eye level reading, the midline reading and the whole text reading, we will only present the results with the whole text.

Quantitative and statistical analysis

Magnitude

One-way ANOVA was applied on the conjugate amplitude of the saccade and on the conjugate amplitude of the drift. The fixed factor was the task (reading/single target) and the random factor was the subject. As the disconjugacy can be positive (convergent) or negative (divergent), one-way ANOVA was applied on separate

convergent and divergent disconjugacies. The effect of the task on the rate of each type (divergent/convergent) was also checked with the nonparametric test of Friedman.

Time analysis

To characterize the time development of the disconjugacy during reading, it was calculated during multiple time periods. The time periods included: (1) one period before the saccade, (2) three periods during the saccade, and (3) twenty periods during the first 160 ms of fixation. All periods lasted 8 ms except for the middle period of the saccade (lasting 16 ± 4 ms). For each subject and each period, a Student's t -test was used to examine if the disconjugacy was significantly different from 0. As disconjugacy can be divergent (negative) or convergent (positive), absolute values were also calculated to estimate the magnitude of disconjugacy.

Saccade-fixation correlation

To search for a possible correlation between saccade disconjugacy and drift disconjugacy, a Spearman correlation analysis was conducted for each subject on the individual reading saccades.

Distribution of the drift between the two eyes

To quantify the relative movement of each eye during the drift, an ocular index was calculated as the ratio $(|LE| - |RE|) / (|LE| + |RE|)$ where LE is the drift of the left eye and RE is the drift of the right eye. An ocular index of 0 indicates a pure binocular movement (either pure version or pure vergence), an ocular index of 1 indicates a movement of the left eye only and an ocular index of -1 indicates a movement of the right eye only.

Results

Binocular control of the eyes during reading: Qualitative observations

Figure 2 shows a recording of saccades and fixations during the reading of 10 lines of text in XY coordinates. Note the quality of recording, namely capacity to maintain the eyes accurately on the line, without significant vertical deviations. Figure 3 decomposes the same data in horizontal and vertical conjugate positions; the horizontal disconjugate signal is added at the top of Figure 3. The horizontal conjugate position shows that horizontal saccades over each line are almost always rightward saccades

Sous la mousse ou sur le toit, dans les haies vives ou le chêne fourchu, le printemps a mis ses nids. Le printemps a nids au bois. Annie amie, du renouveau, c'est le doux temps. Annie Annie, au bois jol gagne le pinson. Dans les nids, gîte une biche, au bois chantant. Annie ! Annie ! au d'igt vli, une églantine laïse du sang : au bout du temps des heries viendra l'emui. L'aloquette fait ses jeux ;

Figure 2. Path of the eyes during reading. Conjugate eye positions in XY coordinates during the reading task (subject 1, first panel). Circles correspond to the fixations and segments to saccades.

(one case of leftward regressive saccade, see arrow). The vertical conjugate position shows high stability of the eyes in the vertical plane during each line reading and accurate vertical component of the saccades to the next line. Moreover, the trace of the horizontal disconjugacy on the

top of the figure shows the remarkable stability of the vergence angle over 10 lines of the text: after each small transient change coupled with saccades, the vergence angle returned approximately to 8.6°, which is the vergence angle corresponding to the viewing distance for

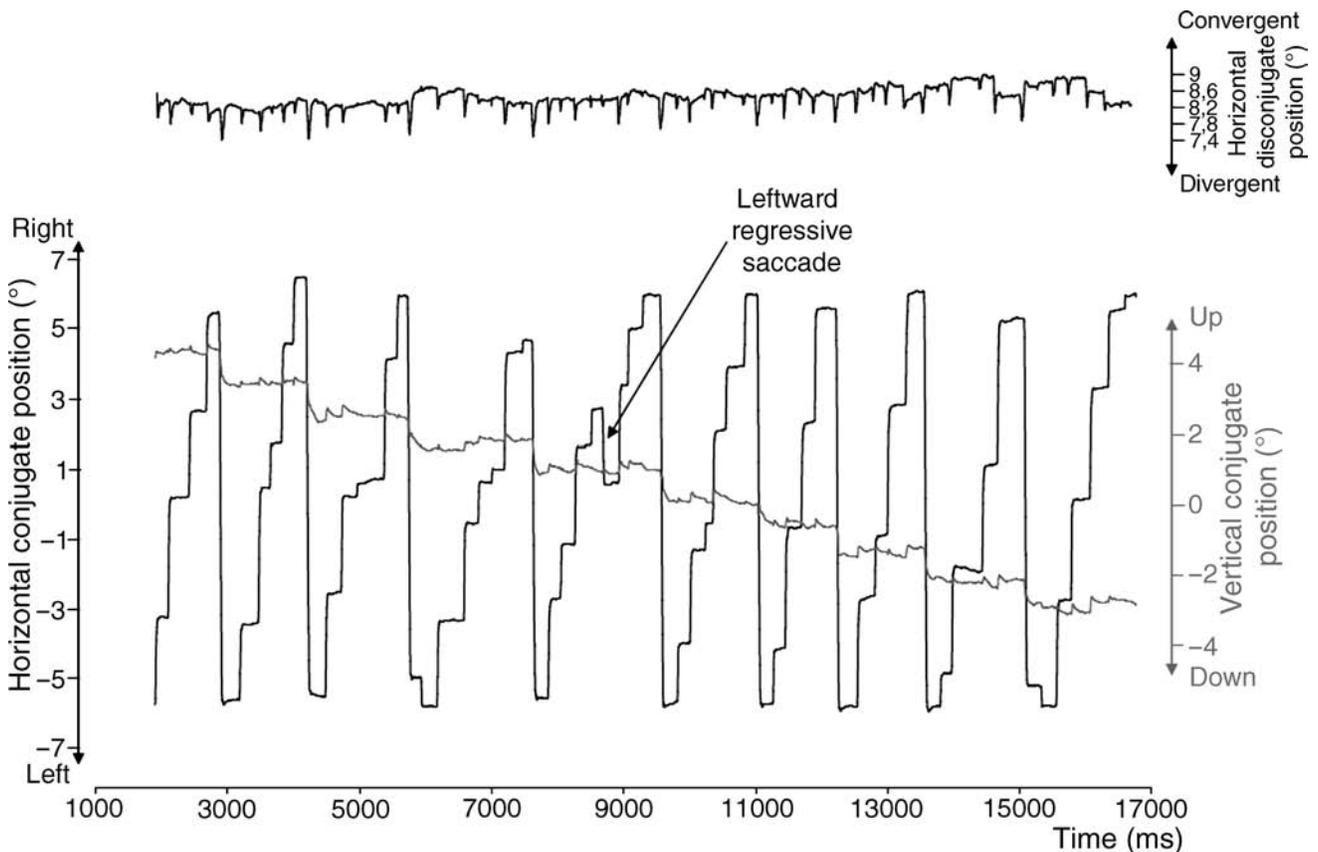


Figure 3. Evolution of conjugate and disconjugate position of the eyes over time. Sample traces during the reading task (subject 1, first panel) as a time function. Lower black trace: horizontal conjugate position. Lower gray trace: vertical conjugate component. Upper black trace: horizontal disconjugate component.

an inter-ocular distance of 60 mm. Thus there is no sustained misalignment of the eyes.

Conjugate amplitude of saccades and of post-saccadic drift

To compare the reading task to the single target task, we selected saccades of similar direction and amplitude. The conjugate amplitude of the saccades was similar in the two tasks ($2.48^\circ \pm 0.19^\circ$ during the reading task, i.e. about 8.3 characters, and $2.6^\circ \pm 0.5^\circ$ during the single target task). The conjugate amplitude of the post-saccadic drift was $0.04^\circ \pm 0.10^\circ$ during the reading task and $0.09^\circ \pm 0.14^\circ$ during the single target task. The ANOVA did not show any significant effect of the task neither on the conjugate amplitude of the saccade ($p > 0.66$), nor on the conjugate post-saccadic drift ($p > 0.33$). Thus the disconjugate parameters presented below concern saccades and drift of similar conjugate amplitude.

Disconjugacy of saccades and post-saccadic drift

Disconjugacy can be either divergent (negative value) or convergent (positive value). Figure 4 shows the separated group means for divergent and convergent disconjugacy of the saccade and of the post-saccadic drift for the reading task and the single target task. The rates of each type of disconjugacy for each task are indicated in Figure 4 above each bar. The non-parametric test of Friedman did not show any effect of the task on these rates ($p > 0.73$). Saccade disconjugacy is predominantly divergent and drift disconjugacy is predominantly convergent, but this difference was not statistically significant ($p > 0.73$). The ANOVA did not show any significant effect of the task neither on convergent saccade disconjugacy nor on divergent saccade disconjugacy. Similarly, the ANOVA did not show any significant effect of the task neither on convergent drift disconjugacy nor on divergent drift disconjugacy ($p > 0.26$).

In summary, the analysis did not identify any significant difference between the reading and the single target tasks. Note that in both tasks, the disconjugacy during saccade and post-saccadic drift were very low: on average 0.16° during saccade and 0.13° during fixation, i.e. less than one character.

Development in time of the disconjugacy

During reading, the average saccade duration was 32 ± 4 ms and the average fixation duration was 304 ± 57 ms. In the following, we examined disconjugacy during multiple time periods from 8 ms before the saccade to

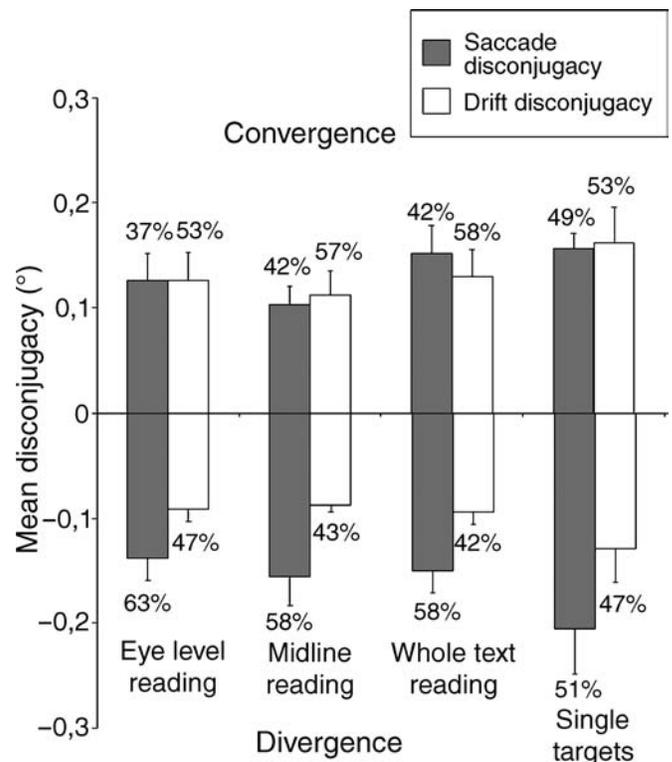


Figure 4. Saccade and fixation disconjugacy. Separate mean and standard error for convergent (positive) and divergent (negative) saccade disconjugacy and drift disconjugacy for the reading task (eye level, midline, and whole text) and the single target task. The percentages of the convergent and divergent disconjugacy are indicated next to each bar.

160 ms after the end of the saccade. Figure 5A shows examples detailing the dynamics of the disconjugacy just before, during, and after the saccade. For all subjects but one (s5), the disconjugacy during the 8 ms preceding the saccade (first measure) was not significantly different from 0 ($p > 0.24$). Even for the subject s5 the disconjugate pre-saccadic drift was very low (on average -0.007°). On the contrary, for all subjects but one (s6), the disconjugacy during the first 8 ms of the saccade (second measure) was significantly different from 0 ($p < 0.05$), and divergent for 7 of the 8 subjects. Subsequently, for all subjects but two (s5 and s9), during the main part of the saccade (third measure, lasting on average 16 ± 4 ms), the disconjugacy was significantly different from 0 ($p < 0.05$), either divergent (5 subjects) or convergent (2 subjects). During the last 8 ms of the saccade (fourth measure), the disconjugacy was significantly different from 0 for all subjects ($p < 0.05$), and convergent for 7 of the 9 subjects.

Then, during each of the first six periods of the subsequent fixation (first 48 ms of fixation), depending on the time period, 5 to 8 subjects, (on average 6.3) had a disconjugacy significantly different from 0 ($p < 0.05$), mainly convergent. In contrast, during the ten subsequent

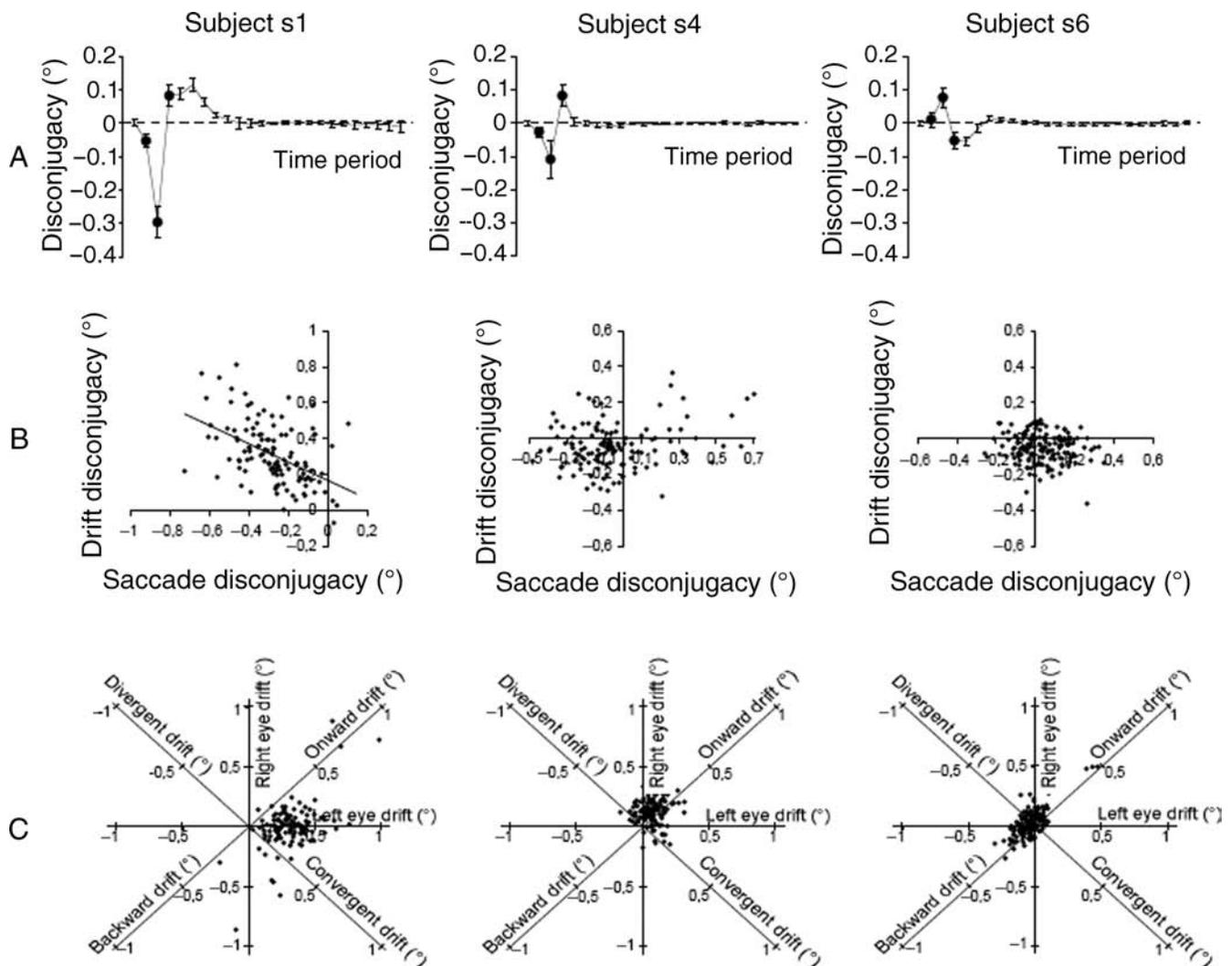


Figure 5. Characterization of drift disconjugacy: dynamics, compensation of saccade disconjugacy, ocular dominance. Examples from subject 1 (left), subject 4 (middle) and subject 6 (right), during the reading task (whole text) of: (A) Evolution of disconjugacy as a function of time period, from 8 ms before the beginning of the saccade until 160 ms after the end of the saccade. Each period lasts 8 ms except the 3 saccadic period (large dots) which are defined as follows: first 8 ms of the saccade; middle part of the saccade (lasting $16 \text{ ms} \pm 4 \text{ ms}$); last 8 ms of the saccade. Vertical bars represent ± 3 standard-errors. (B) Drift disconjugacy plotted against saccade disconjugacy. Line indicates a significant correlation (C) Right eye drift plotted against left eye drift. Values on horizontal and vertical lines would indicate a monocular movement of the right eye (RE) or left eye (LE); values on oblique lines would indicate that both eyes moved equally, either in the same direction (version) or in opposite directions (vergence).

periods (fixation from 48 ms to 128 ms), 2 to 6 subjects (on average 2.9), showed a disconjugacy significantly different from 0 ($p < 0.05$), either divergent or convergent. During the four last periods (fixation from 128 ms to 160 ms), none of the subjects had any disconjugacy significantly different from 0 ($p > 0.05$).

Considering the fact that disconjugacy can be convergent (positive) or divergent (negative), an average zero disconjugacy can still hide an important disconjugacy in absolute value. To further assess that disconjugacy occurred mainly during the saccade and the first 48 ms, we calculated its absolute value. On average, the absolute disconjugacy was: $0.020 \pm 0.002^\circ$ in the period before the

saccade; $0.118 \pm 0.062^\circ$ in the periods during a saccade; $0.027 \pm 0.019^\circ$ in the periods during the first 48 ms of fixation; $0.012 \pm 0.003^\circ$ in the periods during the remaining fixation (up to 160 ms). On average, the absolute value of disconjugacy was similar in the 48 to 128 ms period of fixation and in the 128 to 160 ms period of fixation. Thus, even when measured in absolute value, disconjugacy was minimal except during saccade and to a less extent during the first 48 ms of the fixation following the saccade.

To summarize, the alignment of the eyes was quite stable just before the saccade. During the saccade, the eyes often diverged at the beginning and converged at the

end of the saccade. After the saccade, during the fixation, the disconjugacy evolved mainly during the first 48 ms of the fixation and was mostly convergent. Subsequently, the disconjugacy became much smaller during the next 80 ms. Note that the criteria used to determine the beginning and the end of the saccade could influence the value of the measured disparity and disconjugacy. In the present study, the disconjugacy was low before the onset of the saccade and very low after 58 ms of fixation. After 128 ms, the disconjugacy remains very low, either divergent or convergent as the individual means were not statistically different from 0. Thus, the rest of the analysis covers the period when the disconjugacy occurred. The choice of 160 ms of fixation was validated *a posteriori*. Finally, the significant disconjugacy at the end of the saccade and at the beginning of fixation highlights the necessity to examine the disconjugacy both during the saccade and during the fixation, to fully determine how the binocular motor system is behaving during reading.

Is disconjugate post-saccadic drift correcting saccade disconjugacy?

A Spearman correlation analysis showed that for 4 subjects (s1, s2, s3, s7), the disconjugate post-saccadic drift was negatively correlated with the saccade disconjugacy ($R = \{-0.49; -0.36; -0.34; -0.53\}$; $p < 1.10^{-4}$): when the saccade disconjugacy became more divergent, the drift disconjugacy became more convergent. Thus, post-saccadic drift reduced the misalignment of the eyes remaining at the end of the saccade. For the other subjects, no correlation was found. The disconjugacy could be moderate (s4, s5 and s9, means below 0.24°) or minimal (subject s6 and s8, means below 0.12°). Examples are shown in Figure 5B (subject s1, significant correlation; subject s4, non-significant correlation, moderate saccade disconjugacy; subject s6, non-significant correlation, minimal saccade disconjugacy).

To summarize, for 4 of the 9 subjects, the drift disconjugacy was correlated with the saccade disconjugacy, reducing the misalignment left at the end of the saccade. No significant correlation was found for the 5 other subjects; however, two of them had minimal saccade disconjugacy.

Is the drift equally distributed between the eyes?

Two subjects (s6 and s7) had a drift which was equally distributed between the eyes, i.e. an ocular index ($(|LE| - |RE|) / (|LE| + |RE|)$) between -0.01 and 0 . The drift of subject s6 is shown in Figure 5C (right panel): it was mainly a version drift, either onward (in the top-right hemi-part of the graph) or backward (in the bottom-left

hemi-part of the graph). Three subjects (s2, s3 and s8) had ocular index between 0.01 and 0.15 , i.e. almost equally distributed between the eyes with a very slightly larger movement for the left eye. Three subjects (s4, s5 and s9) had ocular index between -0.50 and -0.15 , i.e. almost equally distributed between the eyes with a slightly larger movement for the right eye. The drift of subject s4 is shown in Figure 5C (center panel): it was often a combination of an onward drift and a divergence, causing the right eye to move slightly more than the left eye. Only one subject (s1) had a mainly monocular drift, with an ocular index of 0.54 (larger movement for the left eye than for the right eye). The drift of subject s1 is seen in Figure 5C (left panel): it can be described as a combination of an onward drift (top-right hemi-part) and a convergence (bottom-right hemi-part), causing the left eye to move more than the right eye. Note that the eye with a larger drift could be either the dominant or the non-dominant eye.

To summarize, for 8 of the 9 subjects, the drift was rather equally distributed between the eyes. This drift could be almost purely conjugate (onward or backward) or purely disconjugate (convergent or divergent). Only one subject had a drift that could be qualified as monocular, i.e. with the left eye moving approximately 3 times more than the right eye. A drift equally distributed between the eyes can be explained by a binocular command (either version or vergence) sent to the two eyes. The drift of subject s1 could be due to distinct commands for the left and the right eye, the left eye receiving about 3 times the input of the right eye. Alternatively, the drift of this subject could be caused by a command of version combined with a command of vergence of similar amount. The conjugate drift was quite important and almost always onward. The disconjugate drift was also substantial and was almost always convergent (see Figure 5C, left). Note that for this subject the disconjugate drift was well reducing substantial saccade disconjugacy (see Figure 5B, left).

Discussion

Summary of the results

The present study was designed to obtain saccades of similar amplitude during a reading task and during a single target task from young adults with perfect binocular vision and no vergence deficit. The main results are the following: (i) saccade disconjugacy was small (mean 0.16°), often divergent (non significant trend) and similar in both tasks; (ii) disconjugate post-saccadic drift was also small (mean 0.13°), often convergent (non significant trend) and similar in both tasks; (iii) the main changes of disconjugacy occurred during the saccade and at the beginning (first 48 ms) of the fixation; (iv) for almost

half of the subjects, during reading, disconjugate post-saccadic drift was correlated with saccade disconjugacy, i.e. divergent saccade disconjugacy was partially reduced by convergent drift; (v) for all subjects but one, the drift was equally distributed between the eyes, i.e. both eyes had a similar amount of drift. The significance of the results will be discussed below.

Excellent binocular motor coordination during reading

During reading, the magnitude of saccade disconjugacy, either divergent or convergent, was on average $0.16^\circ \pm 0.07^\circ$ and the magnitude of drift disconjugacy was on average $0.13^\circ \pm 0.07^\circ$. The saccade disconjugacy was often divergent (58%, non-significant trend) while the drift disconjugacy was often convergent (58%, non-significant trend). This predominant pattern of divergent-convergent disconjugacy was initially described by Collewijn et al. (1988a), who recorded human horizontal saccades with the high accuracy magnetic field-sensor coil technique (noise level below 40 seconds of arc). They found 0.3° of divergent disconjugacy at the end of saccades larger than 5° . This pattern of divergent disconjugacy was confirmed to be predominant both in humans and monkeys, but at lower rate, saccade disconjugacy could be convergent (Busetini & Mays, 2005a; Collewijn et al., 1988a, 1988b; Maxwell & King, 1992; Sylvestre, Galiana, & Cullen, 2002; Yang & Kapoula, 2003). Relative to these studies, the present study shows that this disconjugacy still exists for small reading saccades, but its magnitude is very small and its sign is more variable.

Our data complement those of Blythe et al. (2006), Liversedge, Rayner et al. (2006) and Liversedge, White et al. (2006). They reported that disparity measured at two distinct time points (end of saccade and end of fixation) is high during reading, up to 0.32° . We showed here that the value of saccade disconjugacy is half their value of disparity, and that such disconjugacy is often reduced substantially and rapidly by the post-saccadic drift at the beginning of fixation. As mentioned in the introduction, the time constant of physiological drift related to saccade control is below 160 ms (Leigh & Zee, 2006). The time analysis of disconjugacy presented here showed that the time constant of the disconjugate part of the drift may even be lower. Disconjugate drift is high at the beginning of fixation (see Figure 5A) and negligible after 48 ms of fixation. Thus, measures at the beginning of fixation would give the fixation disparity when the oculomotor system is overcoming asymmetric pulse-step mismatches, whereas measures after 48 ms (at least up to 160 ms) would give the fixation disparity when such mismatches are resolved and the eyes reach a stable vergence angle. Recall that in the present study we did not measure

absolute fixation disparity (which would have required monocular calibration) but change in disparity, resulting from disconjugacy during saccades and fixations. It has been shown that such measures of disconjugacy are almost similar after monocular or binocular calibration, even in children with strabismus (Bucci, Kapoula, Yang, Roussat, & Bremond-Gignac, 2002).

Evidence suggesting a link between fixation disparity and disconjugacy was found in patients with trochlear nerve palsy (Lewis, Zee, Repka, Guyton, & Miller, 1995), in patients with convergent strabismus (Kapoula, Bucci, Eggert, & Garraud, 1997) and in patients with cerebellar lesions (Versino, Hurko, & Zee, 1996). To our knowledge, in healthy subjects, showing disparity and disconjugacy within normal ranges, the existence of a correlation between fixation disparity and disconjugacy remains to be explored. Based on what is known about separate examination of disparity and disconjugacy, we suggest that during reading, an important issue is to maintain stable fixation disparity, within normal range. Indeed, null fixation disparity rarely occurs. For instance Jaschinski (1997) measured fixation disparity beyond 0.1° with nonius lines, at particular viewing distances, even in healthy subjects. Thus, the high quality of motor coordination reported here would allow readers to maintain stable fixation disparity, regardless of its value.

Note that our study is not directly comparable to the previous ones because of multiple methodological differences. First, we used a different eye-tracker; however, both types of apparatus are reliable since our values of disconjugacy are in the same range of those measured with other recording techniques (including magnetic search coil and Dr Bouis oculometer, see e.g. Bucci et al., 2001; Kapoula, Ganem et al., 2008; van der Steen & Bruno, 1995). Moreover, in the present study, reading distance was 40 cm, whereas in previous studies reading distances were 85 or 100 cm. In the single saccade task, the disconjugacy can slightly decrease with increasing viewing distance (Yang & Kapoula, 2003), while in the simple fixation task, uncrossed fixation disparity becomes crossed with increasing viewing distance (Jaschinski, 1997). Further studies are needed to investigate, in reading, the role of distance on both fixation disparity and disconjugacy. Finally, physical characteristics such as size of the characters, brightness, contrast and spatial frequency, may influence text visibility, saccade size, fixation disparity and disconjugacy. Those effects need to be further investigated.

Implications for reading over the life span

Binocular motor coordination improves with age during childhood (Yang & Kapoula, 2003). Moreover, aging or some functional disorders may affect optic and vergence systems, and mild deficits of vergence can be reflected in poor binocular oculomotor control (Kapoula, Vernet et al.,

2008). In the present study, only young healthy adults with excellent binocular vision (stereoacuity better than 40 seconds of arc) were examined. Thus, values reflect an optimal level of binocular motor coordination. High quality of binocular motor control, during reading saccades and fixations, can be achieved in young adults with excellent binocular vision. The optimal physiological performance shown here may be restricted to the early adult life. Thus, many adults and elderly as well as children may have to read with looser binocular motor control and consequently to experience important and variable disparities. We believe that poor binocular vision in such cases is compensated, at least to some extent, by sensory fusional effort and cognition; however, this might cause more visual fatigue. Further studies with experimentally induced disparities combined with time analysis of fixation durations and their variability are necessary to estimate the eventual cost of such effort. Moreover adaptation studies would be also of interest as the readers may adapt rapidly.

Robustness of binocular coordination over different tasks

The present study also shows great stability of binocular motor control over tasks: similar coordination was obtained during reading and during a task involving saccading to a single lighted target. Reading saccades being part of a motor sequence of high complexity, one could have expected looser coordination than for saccades to single target. But the opposite rationale could be also valid: coordination could have been better for reading saccades, as they belong to pre-learned automated motor sequences. None of these predictions are verified. Our observations rather show that the quality of binocular coordination is independent of the task. This is another important contribution of this study, reconciling the two fields of research on eye movements (visually guided saccades and reading saccades).

These findings of high quality binocular motor coordination are also important if claims about poor binocular coordination in dyslexics are to be taken into account. Indeed, Kirkby et al. (2008) reviewed studies showing eye dominance deficit in relation to age and reading difficulty. Stein, Riddell, and Fowler (1987) and Kapoula et al. (2007) reported poor vergence control in dyslexics. Bucci, Bremond-Gignac, and Kapoula (2007) reported poor binocular coordination in dyslexic children compared to aged-matched group of normal children both for saccades to LEDs and for reading single words. Kapoula, Ganem et al. (2008) extended these observations for saccades during free exploration of paintings. In addition to higher values of disconjugacy, there is no correlation between saccade disconjugacy and post-saccadic drift disconjugacy, i.e. disconjugate drift does not reduce the disconjugacy

caused by the saccade (Bucci et al., 2007). Moreover, poor binocular coordination of saccades and disconjugate drift associated with vergence deficits, were also found in children with vertigo (Bucci, Kapoula, Bremond-Gignac, & Wiener-Vacher, 2006; Bucci, Kapoula, Yang, Bremond-Gignac, & Wiener-Vacher, 2004; Bucci, Kapoula, Yang, Wiener-Vacher, & Bremond-Gignac, 2004).

To summarize, high quality binocular coordination is found during the single target and the reading tasks, in young healthy adults without vergence problems. Poor binocular coordination was previously found during various tasks in dyslexic children and in children with vertigo, both groups showing poor vergence control. Although reading studies are still missing in such populations, one can expect that problems of binocular coordination would exist in any situation. Conversely, problems of binocular coordination during reading are probably independent of the reading process and linked to a general deficit in the vergence system itself (see the review of Kapoula, Vernet et al., 2008 and the magnocellular theory of Stein & Walsh, 1997).

How is binocular coordination optimized?

The small transient disconjugacy during saccades could be due to differences in visco-elastic properties of the muscles co-activated during a saccade, for instance the lateral rectus of the right eye and the medial rectus of the left eye are co-activated during rightward saccades (Collewyn et al., 1988a; Zee, Fitzgibbon, & Optican, 1992). Another asymmetry concerns the delay of innervations between the two muscles, given that the pathway is longer for the adducting eye than the abducting eye (Zee et al., 1992). However, our driving hypothesis is that the observed transient saccade disconjugacy does not only reflect the peripheral asymmetries but also reflects a learning mechanism involving the vergence subsystem and the natural and permanent saccade-vergence interaction. Studies of combined movements in direction and depth revealed that during the saccade, the vergence is accelerated (Enright, 1984). Models have been designed to explain this phenomenon, leading to unequal saccadic trajectories for each eye (Busetini & Mays, 2005b; Zee et al., 1992) but they can be applied to explain the role of vergence in binocular coordination, for instance during reading.

Reading involves a succession of saccades and fixations. Different processes are elaborated during each fixation; among them are the visual analysis and the preparation of the saccade to the next word (occurring at least partially in parallel). A small vergence signal could be sent to the oculomotor plant, together with the saccade command, in order to correct partially the peripheral asymmetries (muscular, innervation). This command would result in a “3D saccade”. The existence of the

hypothetical pre-programmed vergence associated with each saccade is compatible with the learning of binocular coordination during childhood (Blythe et al., 2006; Fioravanti et al., 1995; Yang & Kapoula, 2003) and its adaptation throughout the life span (Bucci, Paris, & Kapoula, 2003; Eggert & Kapoula, 1995; Kapoula, Eggert, & Bucci, 1995; van der Steen & Bruno, 1995). The traditional modular approach in oculomotor research has led to isolate the question of binocular coordination of saccades from the question of saccade-vergence interaction. A more global conception of the oculomotor behavior leads us to consider saccades at a fronto-parallel plane, e.g. during reading, as 3D eye movements. The entire system of saccade and vergence, i.e. of rapid movements in three-dimensional space would be used instead of the saccade subsystem alone. Every natural movement would in fact use the 3D system in its integrity. This hypothesis has to be confirmed, e.g. with physiological cell recordings. Midbrain neurons recorded by Mays (1984) had a firing rate proportional to the vergence angle, with no change in activity associated with pure saccades. However, he observed that a convergence cell displayed a slight decrease in rate that was associated with the transient decrease in vergence angle during a saccade. A far smaller number of divergence neurons (9) were recorded. Mays, Porter, Gamlin, and Tello (1986) recorded convergent and divergent burst cells in which the profile of the burst is correlated with instantaneous vergence velocity. Those cells were silent during saccades. Once again, a far smaller number of divergence burst cells was encountered. Thus further recording of both divergence and convergence tonic and burst neurons are needed to quantify small divergence and convergence signals during saccades. As such pre-programmed small vergence signal hypothesized here is elaborated in absence of visual vergence error, mechanisms and dynamics of vergence may be different from that for natural gaze shift in direction and in depth. However, we suggest that the circuitry activated would be partially the same. Note that activation of saccade-vergence interaction should not interfere with the baseline static vergence already involved before the saccade. It is plausible to suggest the existence of dynamic and sustained vergence control mechanisms acting in parallel and in a complementary way.

Many processes may then contribute to maintain or re-establish eye alignment during fixation. If the learned vergence was well tailored (e.g. subject s6, Figure 5B), the saccade disconjugacy is minimal and so is the drift disconjugacy. In this case, the vergence command was properly calibrated to mask the peripheral asymmetries at the end of the saccade, and the only mechanism activated should be the one maintaining eye alignment. On the contrary, if the learned vergence was not well tailored (e.g. subject s1, Figure 5B), a disconjugate drift may be desirable. Two mechanisms may stimulate such disconjugate post-saccadic drift: detection of residual disparities at

the end of the saccade, and pre-programmed vergence drift coupled with the end of the saccade. The latter is supported by observation of slow vergence movement occurring even in monocular condition (for a review see Kirkby et al., 2008). Evidence for the existence of distinct vergence mechanisms controlling binocular coordination of saccade and fixation exists. For instance, Bucci et al. (2002) reported improvement of saccade disconjugacy after strabismus surgery but no improvement of fixation drift disconjugacy, indicating separated mechanisms activated with different time course. In the present study, the observation of a drift equally distributed to the eyes is another aspect in favor of a vergence mechanism. The time constant of this mechanism would be between 48 and 128 ms. Long term learning allows, from repetitive exposure to different depth and different disparity at the end of reading saccades, to elaborate learned vergence signals of short time constant.

The posterior parietal cortex and the cerebellum can be associated to calibrate pre-programmed vergence associated with saccades and slow vergence movements during fixation. It will allow both long-term and online adaptation (Vernet et al., 2008; Versino et al., 1996). We emphasize the idea that this learning involves the vergence system; however we cannot exclude some long term monocular saccadic recalibration. To explore further this adaptation hypothesis, several research projects are of interest, for example testing the quality of binocular coordination of left to right versus right to left reading.

Conclusion

Young adults with perfect binocular vision and no vergence dysfunction read with a high quality of binocular motor coordination during the saccade and during the first 160 ms of fixation. The small disconjugacy occurs mainly during the saccade and during the early fixation period (first 48 ms). We suggest that such high degree of binocular motor control could result from long-term learning processes. A small vergence signal may be elaborated with every saccade, hypothetically using similar circuits as those for saccade-vergence interaction activated for gaze shift in direction and depth. On the other hand, the disconjugate drift often reduces the saccade disconjugacy and is almost always equally distributed to the eyes, suggesting the implication of the vergence system also during fixation. Thus, from the oculomotor point of view, reading is a complex motor task involving 3D control: horizontal, vertical and in depth. Stability over task is indicative of robust physiological mechanisms.

Although it is physiologically possible to achieve such optimal binocular coordination, this may not last throughout life, as the vergence system is particularly fragile with fatigue, age and other functional problems. With lower

quality of binocular motor coordination, disparities during fixation may increase in magnitude or become more variable. Reading in such cases may become less comfortable, requiring more sensory fusional effort. The interplay with adaptive oculomotor abilities and possible cognitive facilitation needs further examination. Comparison with specific populations showing poor coordination, such as dyslexics, would also be of interest.

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