Pergamon

0042-6989(95)00157-3

Vision Res. Vol. 35, No. 23/24, pp. 3473–3492, 1995

0042-6989/95 $9.50 + 0.00

Unequal Saccades Produced by Aniseikonic Patterns: a Model Approach

P. BRUNO,*†‡ P. INCHINGOLO,* J. VAN DER STEEN†

Received 22 December 1994; in revised form 3 May 1995

This study addresses a possible mechanism for fast disconjugate adaptation of binocular horizontal saccades. Disconjugacy of binocular saccades was elicited by two dichoptically presented, identical but aniseikonic, random checkerboard patterns. Adaptation was achieved with the patterns at far distance (144 cm). In this condition, which requires a relatively small (8%) size difference of the saccades, a short learning period was mandatory for the binocular saccades to become disconjugate. The saccadic modifications were superimposed on an idiosyncratic pattern of intra-saccadic yoking. A model of saccadic signal generation is described, that has been used to separate the contributions on saccadic disconjugacy provided by modification of visual inputs processing, which alters the motor-system inputs, and by modification of the control system: the adaptation. We identified three major components of the saccadic command (two phasic and one tonic) that contribute and in a specific way to the saccadic yoking and disconjugacy. The model analysis proposes that separate control mechanisms exist operating on these phasic and tonic signals. We show that the saccadic system can generate the vergence component shown by our aniseikonic saccades. We discuss a distributed-parallel implementation of the saccadic system able to provide both the conjugate and disconjugate components of control.

Human Saccades Aniseikonia Adaptation Model

INTRODUCTION

Disconjugate ocular motor adaptation has been recently investigated by several authors in both humans and monkeys. Prisms (Henson & North, 1980; Oohira & Zee, 1992), anisometropic spectacles (Henson & Dharamshi, 1982; Erkelens, Collewijn & Steinman, 1989; Lemij & Collewijn, 1991a,b, 1992; Oohira, Zee & Guyton, 1991) and muscular weakening (Snow, Hore & Vilis, 1985; Viirre, Cadera & Vilis, 1988; Inchingolo, Optican, Fitzgibbon & Goldberg, 1991) have been extensively used to address this issue. More recently, both post-saccadic drift adaptation (Kapoula, Optican & Robinson, 1990; Kapoula, Eggert & Bucci, 1994) and fast disconjugate saccadic adaptation induced by aniseikonia (Van der Steen, 1992, 1993; Bush, Van der Steen & Miles, 1994; Eggert & Kapoula, 1992; Eggert, Kapoula & Bucci, 1995) has been studied with dichoptically presented images.

Despite that the variety of experimental methods applied so far did not result in an unitary theory that can explain the mechanisms of disconjugate ocular motor performance, it has been shown that: (1) adjustments of the relative innervation to the two eyes are possible; (2) these changes can be faster than the conjugate changes; and (3) many signals, e.g. monocular visual input, retinal disparity, extra-ocular proprioception, binocularity, can influence and modify the binocular coordination. Understanding the mechanisms of binocular disconjugate adaptation is further complicated by the fact that under certain conditions unequal sized saccades are made instantaneously. For example, when saccades are made between two targets differing in direction and distance, the gaze shifts involve a combination of version and vergence. Some authors have attributed this to a non-linear saccade vergence interaction (Zee, Fitzgibbon & Optican, 1992), others state that the oculomotor system is intrinsically able to produce disconjugate saccades (Enright, 1984, 1986, 1992; Maxwell & King, 1992). The involvement of adaptive processes in the generation of disconjugate, as well as conjugate (Deubel, 1995), saccades appears to be strongly dependent on stimulus conditions, context specificity and, possibly, cognitive factors.

A further complexity in the understanding of the mechanisms involved in the generation of disconjugate saccades is formed by the presence of an idiosyncratic pattern of binocular coordination that interacts with the fast adaptive disconjugate modifications.

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*Dipartimento di Elettrotecnica, Elettronica ed Informatica, University of Trieste, V. Valerio 10, 34100 Trieste, Italy.

†Department of Physiology I, Faculty of Medicine, Erasmus University Rotterdam, P.O. Box 1738, 3000 DR Rotterdam, The Netherlands.

‡To whom all correspondence should be addresssed at: Department of Physiology, Erasmus University Rotterdam [*Fax* 31 10 436 7594; *Email* bruno@.gnbts.univ.trieste.it.

In the accompanying paper (Van der Steen & Bruno, 1995) the effects of viewing distance on disconjugate saccades elicited by manipulation of the visual input (aniseikonia) are demonstrated: (1) in near vision, a condition that naturally calls for disconjugate movements; and (2) in far vision, a situation in which mainly conjugate control of the two eyes is required. The behavioural data as described in that paper show that the performance of the saccadic system is related to the tonic state of vergence. The capability of the system to immediately produce disconjugate saccades, observed when the projection screen was close to the subject, disappeared as the distance was increased. In this condition unequal size saccades were made only after a learning period.

This paper mainly focuses on the adaptive modification of horizontal binocular saccades observed during the experiments at far viewing. Using a model approach we extracted a common strategy for the saccadic modification despite the idiosyncratic differences of the saccadic binocular coordination of our subjects, and also verified that this modification was adaptive with a short time course.

The analysis of the parametrical setting of the model during the simulation of the experiment supports a distributed-parallel model implementation. This formalization of the system allows both adaptation and immediate responses according to the tonic state of vergence, and offers a possible explanation for the differences between the disconjugacy of saccades under far and near viewing.

METHODS

Experimental Procedures

Eye movements were recorded with the search coil technique.

Aniseikonic images were presented with a computer system (Silicon Graphics) that generated separate images for the two eyes. The dichoptic images were projected on a screen positioned in the frontal plane, located at 144 cm (far distance, FD) and at 37 cm (close distance, CD). We summarise only the protocol concerning binocularly driven horizontal saccades as this is the type of movements we discuss in this paper. Further details about subjects, stimulus presentation and recording procedures are discussed in the accompanying paper (Van der Steen & Bruno, 1995). Initially, for each subject two equally-sized images (random squares) were presented to each eye. The subject was instructed to make a sequence of saccades between two symmetric self-selected targets at about 10 deg right and left from the centre of the screen. With this arrangement we obtained a data set of iso-vergence binocular horizontal saccades that served as our baseline. We collected 4–5 saccades for each direction and built the baseline by taking the average of each direction.

The image for the right eye was then compressed horizontally by a factor of 8% and the subjects were instructed to repeat the same sequence of saccades. We recorded 10–12 measurements (sequences) with a total of 40–60 rightward and leftward saccades in the presence of aniseikonia. Each horizontal measurement was alternated with a test of the diagonal meridian (45 deg); the time between the first and the last aniseikonic measurement was about 12 min. The aniseikonic arrangement required the right eye to make smaller movements than the left eye. This resulted in a combination of version and divergence for movements towards the left and of version and convergence towards the right. Finally, as a check for plastic modifications, we recorded a sequence of saccades while the images to the two eyes were again equal.

Because the aniseikonic images provide only disparity cues, without taking into account other sources of distance information, we created a situation where version and vergence could cooperate to change fixations between target at different angle and/or distance without conflict of sensory information (e.g. between accomodation and disparity). So, in addition to the experiments with the computer-generated images, we performed a test with a real pattern (tilted plane, TP, at 144 cm). We used the same protocol as in the FD experiment, except that we substituted the screen with a cardboard panel on which a large picture of the pattern of random squares was suspended. This panel was positioned at an angle of 45 deg with respect to the frontal plane and covered 60 deg of visual angle in both horizontal and vertical directions. The distance gradient was close to the disparity gradient that was created across the pattern during the dichoptically presented aniseikonic patterns in the FD experiment. With this we could assess any differences between disconjugate saccades as a result of the aniseikonic stimulation and of the more "natural" distance cues conditions.

In another experiment we tested one subject using the FD protocol, but substituting the aniseikonic patterns with two equal-sized images (NO experiment). With this experiment we could asses possible modifications (improvements) of binocular coordination due to the repetition of the same movements.

Data Analysis

After sampling at 500 Hz, (12-bit precision, noise < 1.5 min arc, antialiasing filter at 125 Hz), the data were analysed by computer programs. After the off-line calibration, we digitally filtered the data with a symmetric low-pass FIR filter (100 Hz cut-off) (Inchingolo & Spanio, 1985), we evaluated the velocity and the acceleration by a digital two-points anti-symmetric derivative filter and computed the difference (left − right) of the eye position (vergence) and velocity (vergence velocity). We identified the saccades by means of the following "binocular" criteria: the velocity of both eyes had to be higher than a threshold (adjustable among 5 and 50 deg/sec), the duration should be at least 50 msec and the displacement of both eyes had to be > 15 deg. We analysed each single movement starting from 50 msec before the saccade onset up to 1 sec after the saccade had been completed. The velocity threshold of 50 deg/sec was used to divide the motion into an initial fast part (velocity higher than the 50 deg/sec threshold) and a slow part that appeared later. In this manner we achieved a good synchronization of the saccades. Because the presence of a disjunctive component within the saccade can introduce a long tail, with relatively high values of ocular velocity, the high threshold appears as a conservative criterion for the comparison of conjugate and disconjugate components of saccades (Collewijn, Erkelens & Steinman, 1995). It separates the fast phase, within which the ratio (*vr*/*vg*) between version velocity (*vr*) and vergence velocity (*vg*) is very high, from the slow phase, characterized by lower values of this ratio.

The unequal movements of the eyes were described with a number of parameters to which will be referred to in the result section. From the vergence signals we computed the post-saccadic vergence error and the intra-saccadic and post-saccadic change of the vergence signal.

The results reported in this paper generally show the signals that are separated for direction, and are averages of up to 5 saccades. For each movement the vergence is reset to zero by subtracting from the actual value its value before the saccade. So, we studied the change of vergence associated with saccades and not the absolute vergence signal.

In addition, we used the displacement ratio (DR). This value is defined as the ratio between the displacement of the abducting vs the displacement of the adducting eye. We analysed the time course of the DR signal from the moment the ocular velocity crossed downward the threshold (50 deg/sec for this analysis) up to 1 sec after the saccade stopped.

We compared the time course of the change of vergence and of the DR between the following different epochs of the experiment: (1) the baseline; (2) the first and the last aniseikonic saccades; and (3) the post-aniseikonic test (performed at the end of the experiment with equally-sized images).

The change of vergence was more sensitive to the early changes in saccadic flight time, but, due to the variability in saccadic amplitude, it provided little qualitative information about the final differences in amplitude of the two eyes. In combination with the aniseikonic arrangement the DR offered a more reliable estimation of the disconjugacy of the final position of the eyes. The DR function associated with the saccades appears as a positive impulse followed by a multi-exponential decay (as depicted in Fig. 4) reaching an asymptotical value. The impulse reflects the transient lack of conjugacy that characterises the saccades. The asymptotic value of the DR for equal size movements of the two eyes has a theoretical value of one. The compression of 8% of the image viewed by the right eye results in a value of 1.08 for leftward, and 0.92 for rightward saccades. The multi-exponential decay describes how this final value is reached.

To facilitate comparison of the DR during the different phases of the experiments a graphical time normalization was used. The normalization consisted of a compression–expansion of the time axis to standardize the duration of the fast part of the motion (the time interval between the two 50 deg/sec threshold crossings of the velocity traces) at the arbitrary value of 100 msec. The DR function provides evidence to separate the contribution of visual feedback from the programmed intra-saccadic misalignment. If the visual feedback is responsible for disconjugacy, then one expects that the DR is close to 1 during the saccadic flight when vision has not yet been restored. In our time-normalized graphical representation this corresponds to 0.1 sec, which is where saccadic velocity is 50 deg/sec. The appearance of a visually-driven correction would also show up as a late alteration of the time course of the DR. However, if the disconjugacy is programmed within the saccade, then differences should arise when we compare the intra-saccadic DR of conjugate with those of disconjugate movements. Again, the value at 0.1 sec (normalized) provides a reference value. In addition, the DR curve should, from that time on, follow a regular progression toward its asymptotic value.

To quantify the modifications of the DR during the experiments, we evaluated the following parameters: (1) the asymptotic value (AV) of the DR, computed as the mean of the DR between 0.9 and 1 sec after the saccadic onset; and (2) TIDR, which is the area subtended by the DR curve and its AV between 0.1 and 1 sec after the saccadic onset (as graphically defined in Fig. 5). This parameter (TIDR), because it is an integral parameter, clearly discriminates between two categories of errors: (i) large rapidly-corrected errors and persisting small errors; and (ii) large persistent errors.

The zero value of TIDR is reached when the ocular motion does not require disconjugate drift. The extremes for the parameter TIDR can be set to ± 0.036, that are the limiting values obtained by supposing a linear course of the DR, from 1 to the (theoretical) asymptotic AV (1.08 or 0.92). A linear DR models a strictly conjugate fast phase ($DR = 1$) followed by an almost linear disconjugate drift.

The speed of the saccadic modification was evaluated from the post-saccadic vergence error, i.e. the difference between the change of the alignment of the eyes required by the aniseikonia and the actual change of vergence (post-saccadic minus pre-saccadic vergence). The pre-saccadic vergence values were computed 10 msec before the saccadic onset; the post-saccadic vergence values were taken 50 msec after the end of the saccade. The onset of the saccades was defined on the basis of the 5 deg/sec velocity threshold.

RESULTS

General Findings

We tested six subjects at a distance of 1.44 m (FD paradigm) and four of them also at a distance of 0.37 m (CD paradigm). Only one subject has been tested with the slanted panel (TP paradigm), and without the aniseikonia (NO paradigm).

From the comparison of the results of the FD and CD experiments, it became clear that there was a systematic directional difference and modulation of the ocular response as a function of distance. At FD all subjects compensated at the end of the saccade only partially for the required misalignment (Fig. 1, cf. FD with TP panel). At CD the compensation was virtually complete for both directions. Modification of the saccadic yoking was always associated with a reduction of the post-saccadic vergence error: these modifications were adaptive only for the FD paradigm, as confirmed by the post-learning tests.

The TP test showed that, even for distant targets, the oculo-motor system was able to generate the changes of ocular alignment immediately within the saccade (see Fig. 1, TP panels). Moreover, the intra-saccadic vergence profile of the **TP** test differs (e.g. the amplitude of divergent peak associated with version + convergence) from the profiles recorded with the aniseikonic stimulation (Fig. 1, panels TP, FD and CD).

The NO test revealed no significant changes in the saccadic yoking of the eyes due to the repetition of the same conjugate movement (see Fig. 1, lower right panel).

In conclusion, for the CD, TP and NO experiments the changes in binocular alignment were close to the demand, regardless of whether they were executed at the beginning or at the end of the experiment (Fig. 1). Consequently the post-saccadic vergence error was small. In contrast to this, in the FD experiment the changes of the post-saccadic vergence error were less complete and only gradually reduced over time.

FD Experiments

Post-saccadic vergence error

For all six subjects the repetition of the movements in presence of aniseikonia induced a clear reduction (on average 0.6 deg) of the post-saccadic vergence error for left directed movements (see an example in Fig. 2). When, after 12 min of learning, the error had been largely reduced [almost zero for subjects **PB** (0.17 deg), **HS** (0.15 deg) and **HL** (0.17 deg)], it reappeared with opposite sign when the aniseikonic images were replaced with the equally-sized images [see the vertical shift of the squares corresponding to errors in the trials numbered 16–18 (post-aniseikonic tests) in relation to the position of the squares of trials 1–3 (baseline) in Fig. 2]. For saccades to the right, a similar time course of post-saccadic error reduction (described by the interpolating

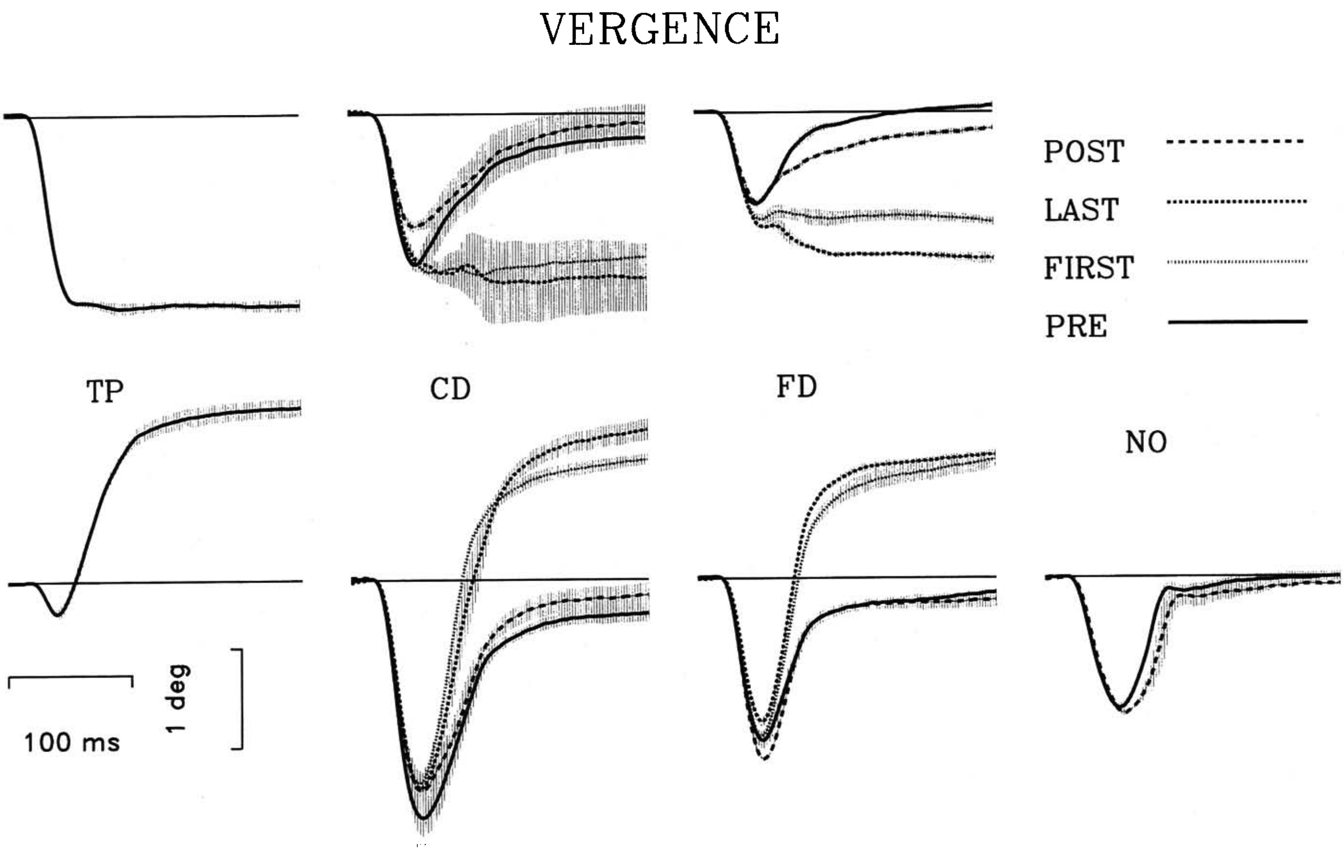


FIGURE 1. Examples of the vergence signal associated with saccades in four different paradigms (same subject). From left to right: TP—tilted plane; CD—close distance; FD—far distance; NO—no aniseikonia (for details about the paradigms see the text). The thin horizontal straight line in each panel identifies the pre-saccadic value of the vergence; values above this line indicate relative convergence, the values below divergence; the thicker lines are the mean vergence position; the standard error is indicated by the shading. All the signals are aligned on saccade onset. In the NO panel shows the vergence at the beginning of the experiment (—) and after 20 min (- - -). For the other three paradigms the upper panels refer to movements requiring divergence and the lower panels refer to movements requiring convergence. The two TP sections show the vergence during the first saccades. The legend in the upper right-hand corner refers to the two aniseikonic paradigms (CD and FD): PRE = baseline; FIRST = initial aniseikonic saccades; LAST = aniseikonic saccades after about 12 min; POST = binocular test post-aniseikonia.

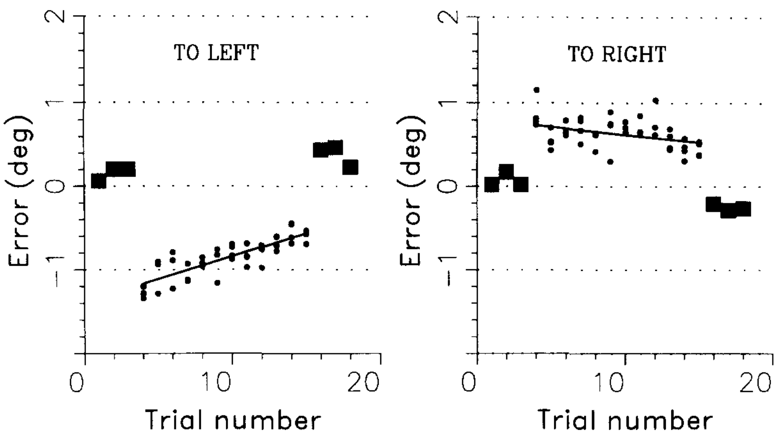


FIGURE 2. Example of the time course of post-saccadic vergence error reduction during the FD experiment (subject G1). The left panel shows leftward saccades, associated with divergence. The right panel shows rightward saccades in combination with convergence. ● Indicate the vergence error of individual saccades during the aniseikonic presentation (trials 4–15). For each trial 4–5 saccades were made in each direction (leftward saccades in left panel, rightward saccades in right panel). The course of the reduction of the vergence error over time is indicated by the linear interpolation (—). Trials 1–3 are the baseline (1 binocular viewing, 2 and 3 open-loop responses), trials 16–18 are the post-aniseikonia tests (18 binocular viewing, 16 and 17 open-loop responses). These are indicated by ■.

lines in Fig. 2) was observed only in two out of six subjects (subjects G1 and G2).

Time course of change of vergence

Rightward saccades (convergence)

Baseline. The intra-saccadic vergence of all six subjects had a transient divergent–convergent time course, with a peak amplitude of relative divergence that varied between 0.3 and 1.8 deg. In addition, one subject (G2) had a double "transient" pattern [Fig. 3(A),—].

Aniseikonia. A small reduction of the amplitude of the peak of divergence (0.2 deg on average) was observed in all subjects at the first aniseikonic presentation; a further reduction (as much as 0.4 deg from the baseline) was observed at the last aniseikonic presentation. Four subjects (HV, HL, PB and ST) immediately exhibited a relative convergence of about 1 deg. For the other two subjects (G1 and G2) the convergence was <0.5 deg. This change in vergence profile reduced the negative peak of vergence velocity and modified the peak and profile of the positive velocity phase (see Fig. 3). In addition to the intra-saccadic changes, the convergence drift, necessary to complete the convergence, was reduced in amplitude over the course of the aniseikonia trials, modifying the profile of the vergence velocity after the peak of negative velocity. Only G1 showed a tonic change (0.5 deg) associated with this dynamic modification.

Test. In four subjects (HV, HL, PB and ST) the intra-saccadic vergence profiles of binocular saccades in test trials performed after the aniseikonia did not change in comparison to the baseline. The other two subjects (G1 and G2) showed an excess of convergence near the end of the saccade and a change of ocular alignment of 0.2 deg (on average) after the saccade. G2 did not show the double peak found in the baseline [see Fig. 3(A)].

Leftward saccades (divergence)

Baseline. The intra-saccadic vergence of five (G1, HV, HL, PB and ST) out of the six subjects had an initial divergent–convergent time course with a peak of relative divergence of amplitude between 0.4 deg (subject G1) and 1.2 deg (subject ST), an example is given in Fig. 3(C) (—). Subject G2 showed a rare sequence of divergence (appreciable only in the velocity trace), convergence (peak of 0.1 deg), divergence (peak of 0.6 deg) and final convergence, resembling an oscillation in terms of vergence velocity [Fig. 3(B),—].

Aniseikonia. The required divergence was reached with a movement starting within the saccade in opposite direction to the motion that normally followed the peak of divergence: the larger the peak, the clearer this effect. Only PB and ST initially reached the theoretical misalignment of the eyes within 1 sec from the saccadic onset. The velocity vergence curves showed small idiosyncratic modifications of the negative peak combined with a progressive reduction of the area subtended by the positive part of the curve. The area reduction was achieved by a change of both the peak and the profile of the vergence velocity curve [see Fig. 3(B, C)]. In terms of position, the curves showed a higher divergence within the saccade combined with an increase of the divergent peak [as much as 0.6 deg, see Fig. 3(C)]. Also was evident a reduction, or sometimes even a complete suppression, of the disconjugate post-saccadic drift.

Test. All the vergence profiles of binocular saccades after removal of aniseikonia exhibited qualitative modifications in comparison to the baseline. The changes consisted of a smaller convergence (almost absent in subject G2) after the peak of divergence [see Fig. 3(B, C)]. The open-loop tests displayed a residual misalignment persisting 1 sec after the saccade.

Displacement ratio

From the data of Table 1 we can observe that the AVs of the DR (the first value in each column refers to saccades to the left, the second one to those to the right) is close to the theoretical value imposed by visual stimulation already at the first aniseikonic presentation. The AV under binocular test condition matches the baseline.

During the aniseikonic stimulation, the value of the DR at the time the eye velocity fell below the threshold of 50 deg/sec (the value at 0.1 sec in Fig. 4) was always lower than the AV; the sequences of the initial aniseikonic saccades had DR values between 1.02 and 1.06, increasing to 1.06–1.08 during the experiment. A curve approximately composed by a combination of exponential functions connected the initial and the AVs of the DR. The amplitude of these exponential decreased with the exposure time of aniseikonia [see Fig. 4(C)]. The curves of Fig. 4(C) show modulation of the DR at 0.1 sec. The curves of Fig. 4(A) smoothly approach the AV. The examples of DR associated with rightward-directed saccades [Fig. 4(B, D)] show that very little modification of the post-saccadic yoking occurs during the aniseikonic presentation. The persistent modification in the post-aniseikonic test was equally small. The DR modifications of the other four subjects were qualitatively similar to

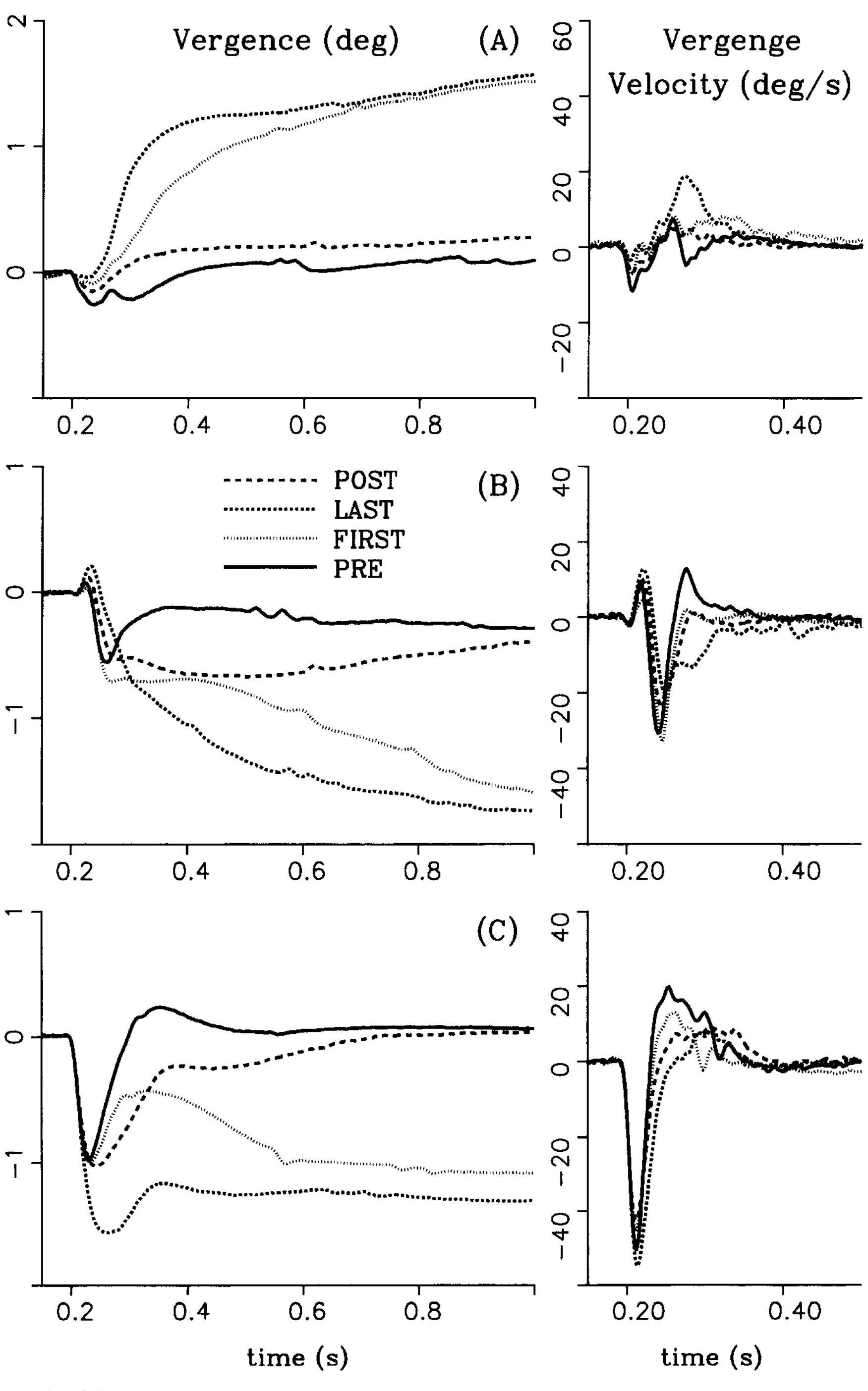


FIGURE 3. Example of the modifications of the vergence during the FD experiments. Vergence is compared during different epochs: left panels—position; right panels—velocity. From top to bottom the panels show: (A) saccades to the right (subject G2); (B) saccades to the left (subject G2); and (C) subject HV, also saccades to the left. Vergence has been set to zero before the saccades, therefore it coincides with the change of the vergence associated with the saccades. Convergence positive, divergence negative. The curves are temporally aligned at saccadic onset (at time 0.2 sec). The meaning of the different traces is indicated at the centre of the figure, abbreviations as in Fig. 1.

TABLE 1. FD experiment—AV of the DR

Subject	Baseline	First aniseikonic saccades	Last aniseikonic saccades	Binocular test
G1	1.003; 0.998	1.075; 0.942	1.086; 0.928	1.010; 0.991
G2	1.011; 0.996	1.065; 0.937	1.074; 0.944	1.016; 0.992
HL	1.003; 0.998	1.080; 0.928	1.090; 0.927	1.003; 1.007
HV	0.999; 1.003	1.064; 0.936	1.082; 0.931	0.999; 1.000
PB	1.004; 1.002	1.084; 0.932	1.089; 0.932	1.001; 1.006
ST	0.999; 1.001	1.067; 0.938	1.066; 0.929	0.989; 1.010

the example of Fig. 4(C, D) for leftward- and rightward-directed movements, respectively. No contribution of visual feedback could be noticed.

This suggests that the evolution of the DR is more consistent with the hypothesis of intra-saccadic programming of disconjugacy then with a contribution from visual feedback (see Methods).

A comparison of the DR curves evaluated at the last and at the first aniseikonic presentation reveals that the saccadic yoking has been altered due to the aniseikonia. By repeating this comparison between post-aniseikonic test and baseline a persistence of that modification was observed. The clearest modification of the DR is seen in subject G2. The aniseikonia altered the initial profile of the DR; such alteration appears also by comparing the binocular test after the aniseikonia with the baseline [see Fig. 4(A)]. Because of the masking effect of the transient divergence associated with saccades, the changes in the DR for the other subjects were more difficult to interpret [an example is given in Fig. 4(C)].

The modification of the DR function for leftward-and rightward-directed movements is quantified in Figs 6 and 7, respectively, using the TIDR parameter (the shaded area indicated by the arrow in Fig. 5). The height of the bars, clustered by experiment, of Figs 6 and 7 represents the value of the TIDR. The modification appears as a reduction of the height of the fifth bar in comparison with that of the fourth bar (the actual difference is represented by the height of the sixth bar).

For leftward saccades (Fig. 6) the binocular (post) tests of all subjects show at least a partial persistence of the dynamic modifications due to the aniseikonia (> 50% for

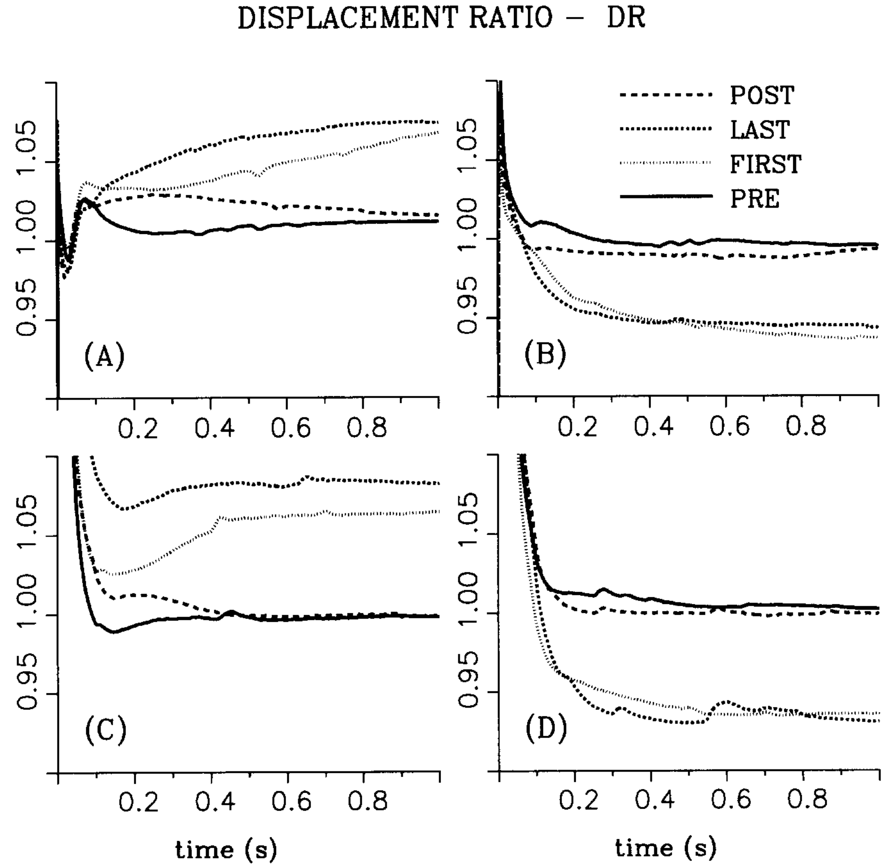


FIGURE 4. Examples of the time course of the DR. The data are collected with the FD paradigm. Each panel summarizes the time course of the DR for iso-vergence saccades (—), the modification of the DR during the aniseikonic experiment and the DR during the post-aniseikonia test. The panels show the DR during four different tests, as indicated in the key: (A) leftward saccades (subject G2); (B) rightward saccades (subject G2); (C) leftward and (D) rightward saccades (subject HV). To facilitate comparison of the curves the horizontal axes are normalized by a time compression or expansion that made the eye velocities cross (upward and downward) the 50 deg/sec threshold at 0 and 0.1 sec, respectively.

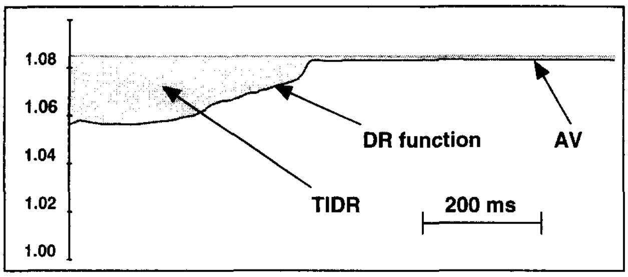


FIGURE 5. Graphical illustration of the TIDR evaluation. The TIDR, defined as the time integral of the difference between the DR and the AV of the DR, is represented by the shaded area.

G2, HL, HV and PB), as it emerges from the comparison between the difference of the TIDR value from the first to the last aniseikonic saccades, and the difference of the TIDR value from post test to baseline saccades [third and sixth bar of each cluster (subject) of Fig. 6]. The TIDR for rightward saccades (Fig. 7) indicates improvement and persistence of saccadic disconjugacy only for the subjects G1 and G2.

Model of the intra-saccadic vergence

Even for iso-vergence saccades we observed a transient loss of yoking of the two eyes, as has been previously observed by others (Collewijn, Erkelens & Steinman, 1988; Zee *et al.*, 1992). The origin for the transient lack of vergence is still unclear. Several hypotheses have been formulated until now, from a temporary disconnection of the tonic vergence (Kapoula, Hain, Zee & Robinson, 1987), to unknown central factors (Zee *et al.*, 1992), to peripheral asymmetries of the saccadic system: either mechanical (Collewijn *et al.*, 1988; Zee *et al.*, 1992) or temporal (Zee *et al.*, 1992). Our baseline data, which should mimic iso-vergence jumps, showed a number of idiosyncratic patterns for the intra-saccadic vergence ranging from the common bell-shaped divergent–convergent pattern to a number of small oscillations between convergence and divergence. The saccadic modifications were superimposed on these signals. In order to extrapolate such modifications from this composite signal we synthesised a minimal model able to qualitatively reproduce the different behaviours.

We started looking for a simple solution such as the 1-pole hypothesis, successfully implemented by Zee and colleagues in 1992, that considers that the models of the two plants differing from each other just for the position of one pole with time constants between 10–20 msec. We tested the 1-pole hypothesis on the basis of the theoretical scheme detailed in the Appendix A. This scheme suggests how it is possible to: (1) identify the two time constants associated with the pole of each eye; (2) remove the transient divergence from conjugate saccades; and (3) extract the disconjugate control signal component added to the common-mode signal during disconjugate saccades. We evaluated the two time constants, then we filtered the data to remove the transient divergence associated with the baseline and to extract the disjunctive component associated to disconjugate movements. The data processed following the scheme of the Appendix A disclose that: (1) the final curvature of the function $B(t)$ appears to be related to the disconjugacy of the saccade

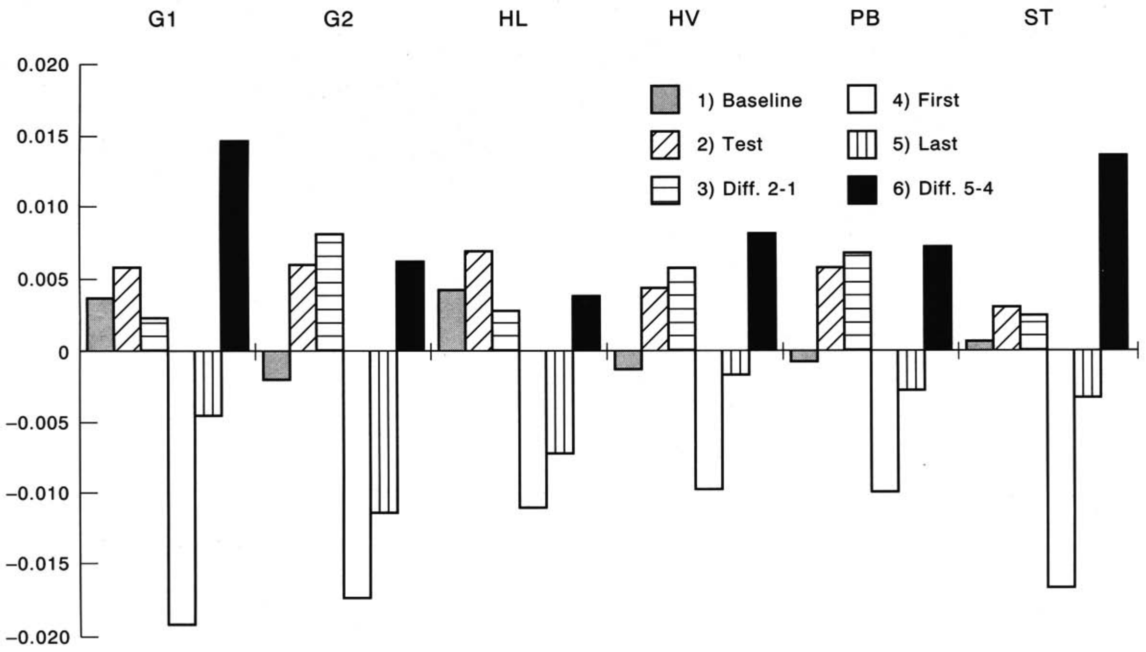


FIGURE 6. Summary of the TIDR parameter (see also Fig. 5), for leftward saccades associated with divergence. The bar graph shows the values of the TIDR at different experimental epochs and the TIDR variation recorded by the FD paradigm for all six subjects. In this and in the next figure the following conventions are applied: category axis—subjects; vertical axis—TIDR. Each cluster of 6 bars refers to one subject (code on top of graph). Numbers appearing in the legend indicate the order of the bars within each cluster. For each cluster: the height of the third bar shows the difference between the TIDR evaluated from the binocular test after the presentation of aniseikonia (second bar, labelled "test"), and the TIDR of the baseline (first bar, labelled "baseline"). The difference between the TIDR of saccades made after 12 min of aniseikonia (fifth bar, labelled "last") and the TIDR of the initial aniseikonic saccades (fourth bar, labelled "baseline") is indicated by the sixth bar of each cluster.

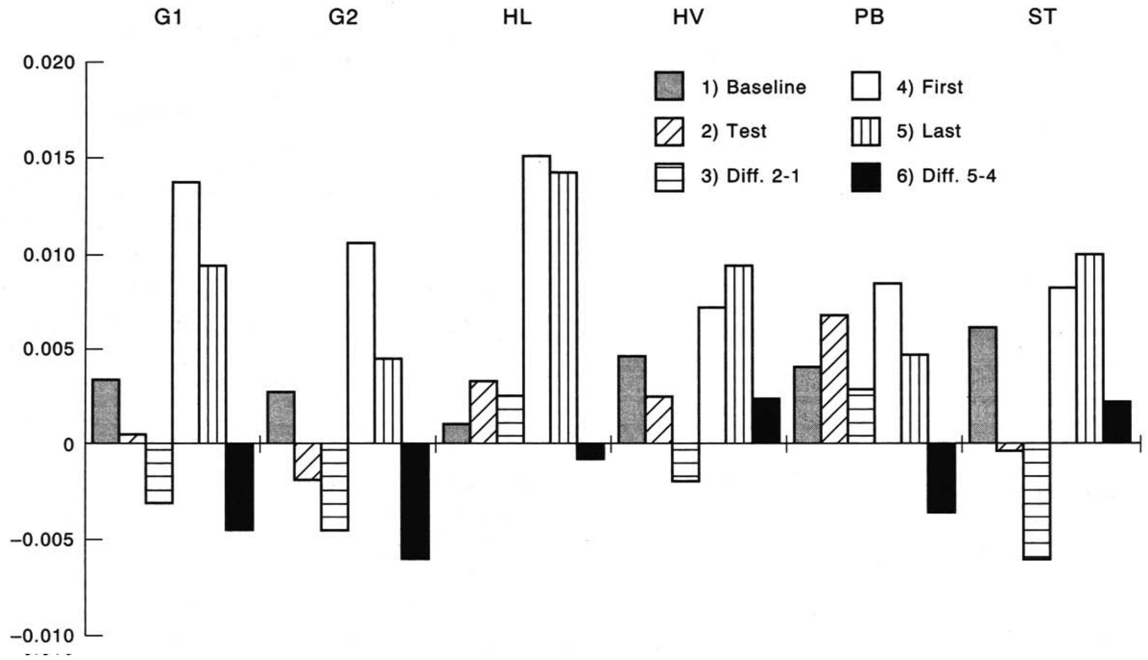


FIGURE 7. Summary of the TIDR parameter, for rightward saccades associated with convergence. The bar graph shows the value of the TIDR at different experimental epochs and the TIDR variation recorded by the FD paradigm. For explanation of the legends and labels, see Fig. 6.

[Fig. 8(C)]; and (2) the residual vergence differs from conjugate to disconjugate saccades only during the last part of the motion [Fig. 8(B)]. This suggested that the signal driving the disjunctive ocular motion appears late into the saccadic flight. An example of the results that can be achieved by this procedure is represented in Fig. 8. The intra-saccadic vergence associated with the conjugate and disconjugate (version + convergence) saccades [Fig. 8(A)] is compared with the residual vergence after filtering [Fig. 8(B)]. The bottom panel [Fig. 8(C)] represents the values of the time constant [$B(t)$] associated with the left eye plant: for iso-vergence saccades its value should be a constant. However, a large deviation of this function from the 1-pole scheme prediction appears during the ocular deacceleration. In addition, the fact that the post-saccadic drift is usually unequal in the two eyes (Collewijn *et al.*, 1988) and lasts for more than 100 msec, proves that it cannot be due to dynamic elements which have already extinguished the transient (the 1-pole scheme led actually to values of the time constants between 10–20 msec).

We concluded that the 1-pole scheme is inadequate for describing the intra-saccadic vergence and, therefore, we extended the difference between the two plants to a second dynamic element of the models (2-pole scheme). Possible candidates for this additional asymmetry, that we describe here as a low-pass filter with a time constant of about 200 msec, are the muscles (in particular the antagonist), the orbital tissues and the neuronal structures conveying tonic and phasic signals to the motoneurons.

This 2-pole scheme allowed us to fit most of the data, but, in order to reproduce also the unusual behaviour of subject G2 [Fig. 3(B)], we hypothesized a combined action of mechanical differences between the two ocular plants with small structural differences between the pre-motor circuits conveying neural signals to the motoneurons, as suggested by Zee *et al.* (1992). Consequently, we interposed two blocks (interfaces) between controller(s) and controlled system(s) (Fig. 9). The two interfaces are structurally identical, combining first order low-pass filters (time constant of 1–3 msec) and delays (1–2 msec), but parametrically different for each eye. The difference between the interfaces models the different routing for the neural signal to the couples of agonist and antagonist muscles. The parametrical setting of the interfaces varied from subject to subject in order to fit the individual pattern of intra-saccadic vergence shown by each subject. We postulated that only the plants, and not the interfaces, dynamic was compensated by the saccadic controller.

Model results. We reproduced the baseline data, collected with the screen placed at the FD, combining a conjugate saccadic signal with peripheral asymmetries. So, we assumed two different plants and two different interface blocks. Figure 11 shows (—) the model prediction in terms of DR, vergence and vergence velocity for the baseline data reported in Fig. 3(B, C) and Fig. 4(A, C).

An important feature of such a 2-pole scheme is that it conceptualizes the existence of short-term transients that extinguish within the fast part of the movement (mainly responsible for the initial loss of vergence during the saccade) and long-term transients that last during the later slow motion and that, in order to maintain the binocular alignment, have to be controlled (not necessarily in the same way) by the saccadic system. The different role of these transients in the saccadic binocular yoking is qualitatively illustrated in Fig. 10 by means of model simulations of dynamic disconjugate controls of the two plants. Figure 10(A) shows the "baseline" conjugate-control situation. Figure 10(I, L) shows the effect on the intra-saccadic vergence and on the post-saccadic drift associated with the disconjugate control of the larger time constants (about 200 msec in these examples). Figure 10(M, N) shows the effect of the disconjugate control of the short time constants (close to 20 msec). Further details about the simulations of Fig. 10 are illustrated in the next section.

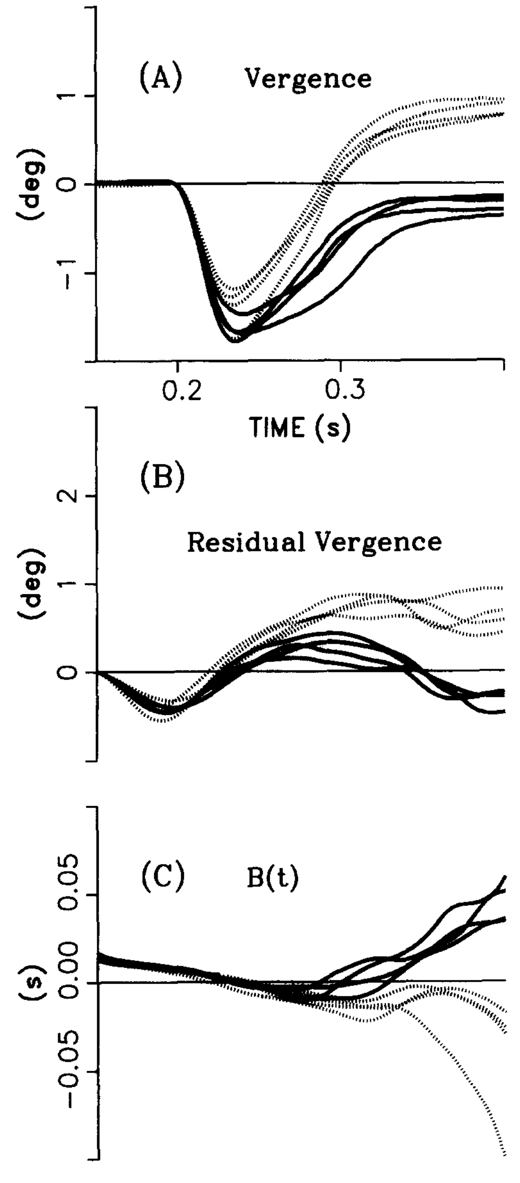


FIGURE 8. The 1-pole scheme test. (A) The vergence of individual saccades on which the 1-pole scheme has been tested. The curves are aligned on the saccadic onset (0.2 sec) and offset to zero before the saccade. In all the sections of this figure the continuous lines identify the curves associated to iso-vergence saccades and the dotted lines are the curves derived from aniseikonic saccades (version + convergence). (C) The function $B(t)$ during the fast phase of the motion (versional velocity > 50 deg/sec). Following the 1-pole prediction, detailed in the Appendix A, the $B(t)$ function should be a constant (one-model parameter) for iso-vergence saccades, and, for the aniseikonic movements, the same constant plus a function of the disjunctive control signal and of the vergence velocity. (B) The results (the residual vergence) of the filtering (see the Appendix A) that should, in the 1-pole hypothesis, remove the transient intra-saccadic vergence from iso-vergence movements and extract the disjunctive control signal from the aniseikonic saccades. Although the residual vergence does not match the model prediction, the curves show a modulation of the residual vergence due to the presence of a disjunctive control.

Model of the controllers

From the point of view of the controller a saccade is generated sending a weighted combination of tonic and phasic signals, built from a "velocity like" code of the desired displacement to the controlled system (the plant). The phasic signals are needed to compensate for the inherently poor dynamics of the plants. Therefore a model of the controller, even if only conceptual, has to generate and combine many correlated signals, the number of which depends on the complexity of the controlled system. We synthesised a "saccadic like" controller (Fig. 9) able to drive the plants described with the minimal model of the previous section. Having assumed a 2-pole model for the plant, the controller has to generate one tonic signal for the final position and two phasic signals to compensate the two poles of the plant.

The scheme we are proposing here is a model for signal generation and it is not intended as a description of the saccadic system. This tool allows us to identify constraints on signal generations that will sketch the system model (see also the Discussion).

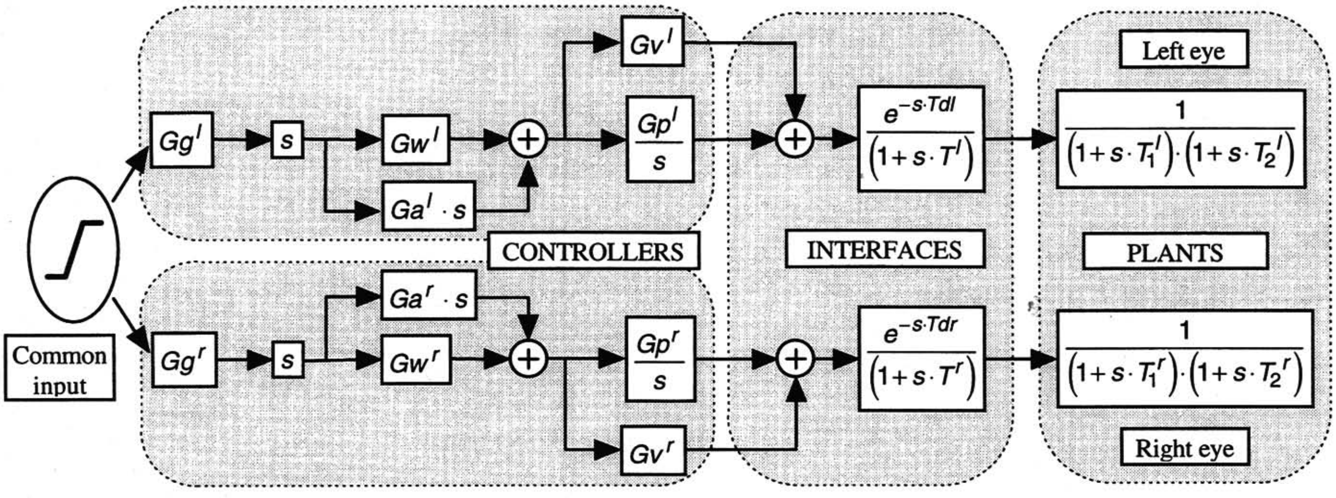
The scheme is linear because the restricted range of movements we analysed allows us to use local linearization of a non-linear system. Moreover, for methodological reasons, we made the scheme redundant with many degrees of freedom. Two of the five modifiable gains of each controller are redundant [G^j_w and G^j_p, see equation (1) and Fig. 9]. They can be fixed to a value of 1 without deteriorating the model performance (e.g. the combined modification of G^r_g and G^r_a can substitute the action of G^r_w). However, the model data can be more simply interpreted with a redundant number of modifiable gains, which can be altered once a time, than with a minimal number of gain elements that require combined modifications. So, modifications of all the blocks of each of the controllers were considered as "possible", allowing the fit of the data to define constraints on the parametrical setting of the model. We interpreted these constraints as an indication for the final structure and the disconjugate capability of the "real" system model.

The structural arrangement of our model allows independent as well as dependent control of each of the signals but imposes the correct balance between tonic and phasic signals for the compensation of the plant.

Each controller of Fig. 9 realizes the following transfer function:

$$W^j(s) = G^j_g \cdot G^j_p \cdot G^j_w \cdot \left(1 + s \cdot \frac{G^j_a}{G^j_w}\right) \cdot \left(1 + s \cdot \frac{G^j_v}{G^j_p}\right), \quad (1)$$

where $j = \mathrm{l, r}$ refers to the left and the right controllers, respectively. The metric compensation is realized by setting the product $GT^j = G^j_g \cdot G^j_p \cdot G^j_w = 1$. By neglecting the dynamic effects of the interfaces, the dynamics compensation is achieved by setting $Z^j_1 = G^j_a / G^j_w = T^j_1$ and $Z^j_2 = G^j_v / G^j_p = T^j_2$, where T^j_1 and T^j_2 are the time constants of the plant. A conjugate control of the two eyes could be



EYE	G_g^j	G_w^j	G_a^j	G_p^j	G_v^j	T^j	T^{dj}	T_1^j	T_2^j
left : j = l	1.000	1.000	0.018	1.000	0.201	0.003	0.001	0.200	0.020
right : j = r	1.000	1.000	0.018	1.000	0.201	0.003	0.001	0.202	0.016

FIGURE 9. Block diagram of the conceptual model applied for the data analysis. The apex j = l, r of each parameter identifies the corresponding eye that is controlled. The default values of the model parameters for rightward saccades are reported in the table. The model works as follows: a "common input" excites two "controllers", one for each eye. The input to each controller can be independently scaled modifying the gain G_g^j and is differentiated (block s) to give a velocity command. A second differentiator with gain G_a^j (block $G_a^j \cdot s$) generates an acceleration command which is mixed to the velocity command reaching the summing junction (+) with gain G_w^j. This composite signal is integrated with gain G_p^j (block G_p^j/s). The output of the integrator is formed by a tonic signal (final position) and a (phasic) signal proportional to eye velocity. It is one of the two outputs of the controller. The second one carries two phasic components, of which one is proportional to eye velocity and the other to eye acceleration. It is derived with gain G_v^j from the input of the integrator. Each controller sends this combination of signals to its eye plant through an "interface", that operates a low-pass filtering with time constant T^j (block $1 + s \cdot T^j$) and a delay T_d^j [block $\exp(-s \cdot T_d^j)$]. Each plant is described by a second-order linear system, with time constants T_1^j and T_2^j. During the data analysis the parametrical setting of the interfaces and of the plants has been varied according to the saccade direction and to the peculiarities of the baseline saccade of each subject. In order to reproduce the adaptation each of the five gains of the controllers has been suitably modified. For further explanations see Results.

simulated simply by setting $GT^l = GT^r$, $Z_1^l = Z_1^r$ and $Z_2^l = Z_2^r$. However, in order to simulate a basically cyclopean controller for the baseline fitting, we started considering all the parameters of the left controller equal to those of the right one, respectively: $G_g^l = G_g^r$, $G_p^l = G_p^r$, $G_w^l = G_w^r$, $G_v^l = G_v^r$, $G_a^l = G_a^r$. An example of the resulting simulation is represented in Fig. 10(A). Unequal movements can be generated by independently altering this "conjugate setting", in one or both of the controllers. Disconjugate control of the dynamics compensation can be simulated modifying the gains G_v^j or G_a^j. The examples of symmetric ($G_v^l \cdot G_v^r = 1$) unsettlement reported in Fig. 10(I, L) show that the alteration of the larger time constants T_2^j compensation can modify both the intra-saccadic vergence and the post-saccadic drift. Alternatively, the examples of symmetric ($G_a^l \cdot G_a^r = 1$) unsettlement of the neural zeros Z_1^j reported in Fig. 10(M, N) show only short-term modifications of the yoking of the eyes. The model can produce unequal saccades by means of several combinations of phasic and tonic signals. Figure 10 depicts a set of these possibilities in terms of ocular position, vergence and vergence velocity. Disconjugate final position (metrics) can be achieved by modifying either the couples G_g^j, or the couples G_p^j, or the couples G_w^j, independently in the two controllers. The movements resulting from modifications of only one couple at a time, as reported in Fig. 10 for symmetric modifications of G_g^j [Fig. 10(B, C)], G_p^j [Fig. 10(D, E)] and G_w^j [Fig. 10(F, G)], are quite dissimilar. A qualitative analysis of these simulations shows that: (1) long drifts are required only in association with the modulation of G_p^j that combines the metric modification with an altered dynamic compensation of T_2^j; (2) the modifications of G_g^j or G_w^j can be distinguished from the shape of the vergence or from that of the related velocity: in fact, the gains G_g^j do not alter the dynamics while the gains G_w^j modify also Z_1^j. An example of the combined effect of symmetric alterations of G_p^j and G_w^j is reported in Fig. 10(H). The parametrical setting of the model for these simulations is summarized in Table 2.

Our data show quite idiosyncratic patterns of the vergence signal and, to a lesser extent, of the DR associated with adaptive modifications induced by the aniseikonia (see Figs 3 and 4). In order to extrapolate the mechanisms of the adaptation from the data, we simulated our FD experiments by reproducing the disconjugate features of the baselines, of the learning phases and of the post-aniseikonia tests. We focused our attention on movements to the left (version + relative divergence), which showed the most clear, fast but not immediate, alterations. Thereafter, we report the results of the model replica of the responses of the two subjects

HV and G2 [Figs 3(B, C) and 4(A, C)], which showed the most dissimilar vergence and DR signals. Being the extreme cases, they can be considered as a crucial test for the procedure that we implemented. Subject HS showed a large intra-saccadic vergence on the baseline, the fastest post-saccadic vergence error reduction and a transfer of 75% to the final control of the changes occurred during the aniseikonia; subject G2 had the smallest and more unusual intra-saccadic vergence associated with an apparently null error reduction, but the higher dynamic transfer to the control in terms of TIDR.

Simulations. We started by fitting the baseline data with two independent controllers, each one dedicated to one eye, driven by the same input (a filtered step) and with exactly the same structure and the same parametrical setting. So, we simulated an initial cyclopean drive for the saccades. Then we modified each controller in order to match the unequal "aniseikonic" saccades and the final test; next we looked for the existence of common strategies of the modifications we had to impose on the controllers, in order to reproduce the different stages of adaptation among the different experiments. The sensitivity analysis summarized in Fig. 10 drove our attempts to match the experimental data, providing a qualitative link between the modifications of the parameters of the experimental signals (e.g. modification of the divergent peak of intra-saccadic vergence) and the setting of the controllers.

Figure 11 shows the simulation of G2 and HV experiments in terms of DR, intra-saccadic vergence and vergence velocity. Each experiment is summarised by means of four saccades: (1) the baseline; (2) the first aniseikonic saccade; (3) the last aniseikonic saccade; and (4) the post-aniseikonia test. The qualitative matching between experimental and model data has been achieved implementing in both cases the following strategy. Any conjugate alteration of the saccades has been translated into a modification of the input of the controllers (e.g. velocity reduction). The transition from the baseline to the first pre-adaptive aniseikonic saccades (1 to 2) has been simulated with a disconjugate symmetric modulation of the gain G^j_p of the integrators and with a partial or absent (G2) modification of the gains G^j_v. Adapted saccades (3) have been matched by an unequal

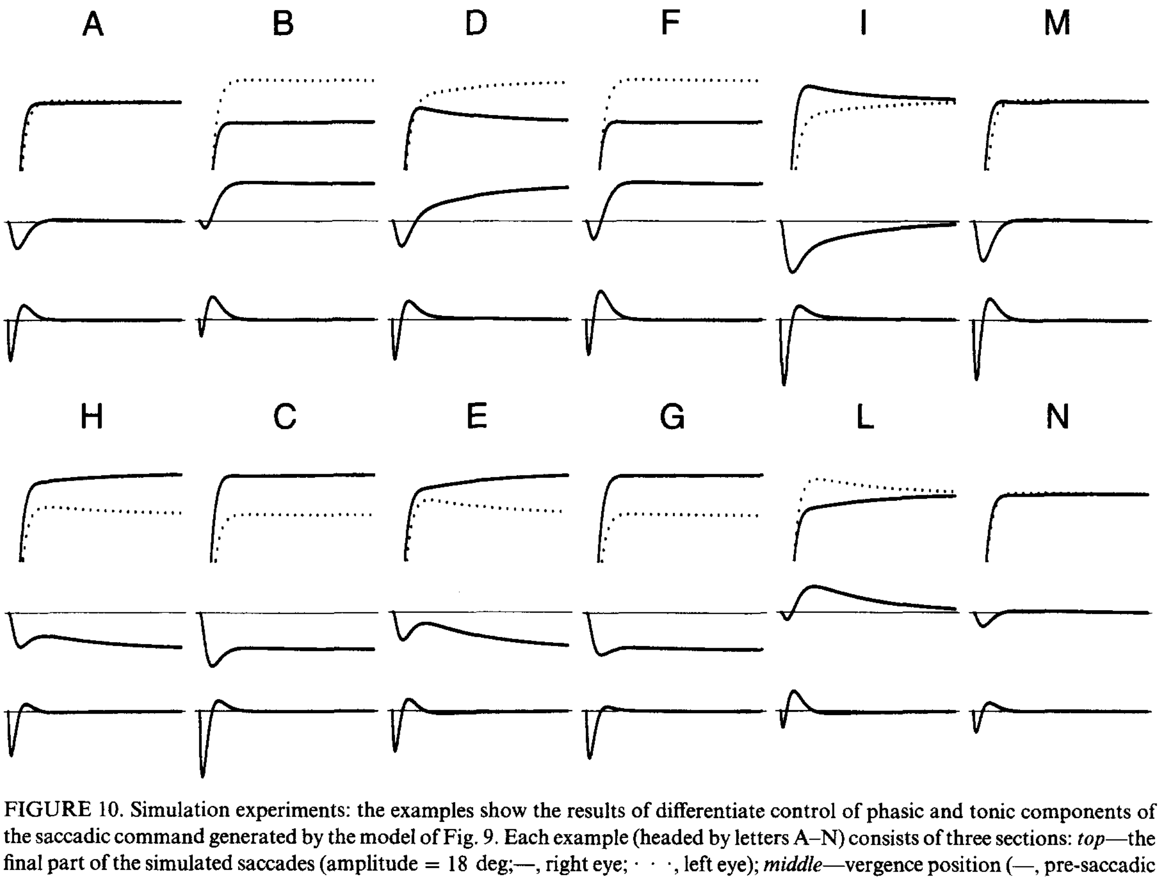


FIGURE 10. Simulation experiments: the examples show the results of differentiate control of phasic and tonic components of the saccadic command generated by the model of Fig. 9. Each example (headed by letters A–N) consists of three sections: *top*—the final part of the simulated saccades (amplitude = 18 deg;—, right eye; · · ·, left eye); *middle*—vergence position (—, pre-saccadic value of the vergence); *bottom*—vergence velocity (—, zero velocity). The observation time is 1 sec; and the saccadic onset is at 0 sec. Panels A, I, L, M and N represent the simulations of equally-sized saccades but with different disconjugate dynamic compensation. Panels B–H represent the simulations of unequally-sized saccades with various disconjugate dynamic compensation. Panels B, D and F show the results of simulations of disconjugate saccades (version + convergence). Panels C, E, G and H show movements of version + divergence. Panel A shows the "baseline". All the other panels represent simulations with different parametrical settings, taking the model setting generating the movement depicted in panel A as a starting point and modifying one couple of model parameters at a time (except for panel H, see below). The parametrical setting of the model for these simulations is reported in Table 2. The scheme of the modification of the parameters can be summarized as follows: (1) panels B and C modification of the model gains G^j_g; (2) panels D and E modification of G^j_p; (3) panels F and G modification of G^j_w; (4) panels I and L modification of G^j_v; (5) panels M and N modification of G^j_a. The simulations reported in panel H required the contemporary modification of the model gains G^j_p and G^j_w.

TABLE 2. Parametrical setting of the model of Fig. 9: simulations of Fig. 10 ($T^l = 0.003$, $T^l_d = 0.001$, $T^l_1 = 0.200$, $T^l_2 = 0.020$, $T^r = 0.003$, $T^r_d = 0.001$, $T^r_1 = 0.202$, $T^r_2 = 0.016$)

Panel	Eye	G^j_g	G^j_p	G^j_w	G^j_t	G^j_a
A	Left: $j = l$	1.000	1.000	1.000	0.201	0.018
A	Right: $j = r$	1.000	1.000	1.000	0.201	0.018
B	Left: $j = l$	1.050	1.000	1.000	0.201	0.018
B	Right: $j = r$	0.950	1.000	1.000	0.201	0.018
C	Left: $j = l$	0.950	1.000	1.000	0.201	0.018
C	Right: $j = r$	1.050	1.000	1.000	0.201	0.018
D	Left: $j = l$	1.000	1.050	1.000	0.201	0.018
D	Right: $j = r$	1.000	0.950	1.000	0.201	0.018
E	Left: $j = l$	1.000	0.950	1.000	0.201	0.018
E	Right: $j = r$	1.000	1.050	1.000	0.201	0.018
F	Left: $j = l$	1.000	1.000	1.050	0.201	0.018
F	Right: $j = r$	1.000	1.000	0.950	0.201	0.018
G	Left: $j = l$	1.000	1.000	0.950	0.201	0.018
G	Right: $j = r$	1.000	1.000	1.050	0.201	0.018
H	Left: $j = l$	1.000	0.975	0.975	0.201	0.018
H	Right: $j = r$	1.000	1.025	1.025	0.201	0.018
I	Left: $j = l$	1.000	1.000	1.000	0.192	0.018
I	Right: $j = r$	1.000	1.000	1.000	0.212	0.018
L	Left: $j = l$	1.000	1.000	1.000	0.212	0.018
L	Right: $j = r$	1.000	1.000	1.000	0.192	0.018
M	Left: $j = l$	1.000	1.000	1.000	0.201	0.017
M	Right: $j = r$	1.000	1.000	1.000	0.201	0.019
N	Left: $j = l$	1.000	1.000	1.000	0.201	0.019
N	Right: $j = r$	1.000	1.000	1.000	0.201	0.017

modification of the gains G^j_t associated with modifications of G^j_a. Next, the post-aniseikonia traces (4) have been predicted applying the same kind of modifications required by the transition 1 to 2, but with opposite increments, starting from the parametric setting reached by the model at the end of the adaptation (stage 3). The parametrical setting of the model for these simulations is summarized in Table 3. The modifications of the gains G^j_a occurring at stage 3 were not systematic; they could be conjugate modifications (simulation of HV) as well as disconjugate modifications (simulation of G2). Hence, looking for the unifying features of the adaptations, we did not consider those variations of the model setting as part of the general mechanism of the adaptation.

To summarize, for the range of saccadic amplitude we tested the common features of the unequal saccades are: (a) on-line correction of the final position; (b) adaptive modification of at least part of the dynamics; and (c) persistence of these modifications under binocular viewing of equally-sized images.

DISCUSSION

The goal of this study was to investigate the mechanisms involved in the generation of the unequal horizontal saccades induced by dichoptical presentation of aniseikonic images at the FD. The main finding of the present investigation is that we have been able to extract small but coherent modifications of the saccades in the two eyes. By using a model description of the problem we propose a unitary theory for disconjugate adaptation induced by aniseikonia.

Several years ago Van der Steen studied the earliest stages of differential motor programming for the two eyes by means of dichoptical presentation of unequal sized images to the two eyes (Van der Steen, 1992); this author found that a disconjugate adaptive modification of the saccadic size can be elicited in a very short period of time (several minutes). Similar results have been reported by others (Eggert & Kapoula, 1992). Later, it has also been found that the adaptation is dependent on stimulus characteristics and driven by monocular depth cues (Eggert *et al.*, 1995). In contrast to these studies it has also been shown that the saccadic system did not need to adapt, to modify itself, because it is "intrinsically" able to generate the required saccades of different size (Bush *et al.*, 1994). These authors claimed the ocular disparity as the signal responsible for saccadic inequality. In the accompanying paper (Van der Steen & Bruno, 1995) it is demonstrated that this apparent controversy between adaptation and non-adaptation is dependent on the tonic level of vergence. Saccadic adaptation takes place only when the aniseikonic images are projected on a distant screen, a condition that "naturally" implies to keep the eyes almost parallel (low level of tonic vergence), but not in near vision, where just a simple "un-aniseikonic" target foveation requires a large vergence (about 10 deg of convergence in those experiments).

Vergence vs Saccadic Disconjugacy

So far, it is still a matter of debate how the disconjugacy of saccades takes place. We addressed this issue in the present work by means of a model approach.

For this, we designed a model to test the hyphothesis that with aniseikonia unequal saccades are generated by the saccadic system alone. The role for the vergence system in refixations between targets differing in direction and depth is not discussed.

Unequal size rotations of the two eyes can mathematically be described by means of the decomposition into a common mode "version" (the mean of the eye positions of the two eyes) and a differential signal "vergence" (the difference). We assumed that in the aniseikonic experiments the differential signal originates mainly from the saccadic system and not from a separate "vergence subsystem". The reasons for our choice are the following:

(1) The separate generation of version and vergence signals imply a "symmetry" into the unequal saccades. This "symmetry" [implemented for example by Zee *et al.* (1992) and Cova & Galiana (1995)] cannot account for the changes in the saccadic profile (e.g. peak velocity) of each eye as has been observed during refixations that also involve changes in depth (Collewijn *et al.*, 1995). One solution is that the saccadic system actively participates with monocular components to the generation of the disjunctive ocular motion [as proposed by Enright (1992)].

(2) The vergence system should interact with the saccadic system in other to boost the vergence signal.

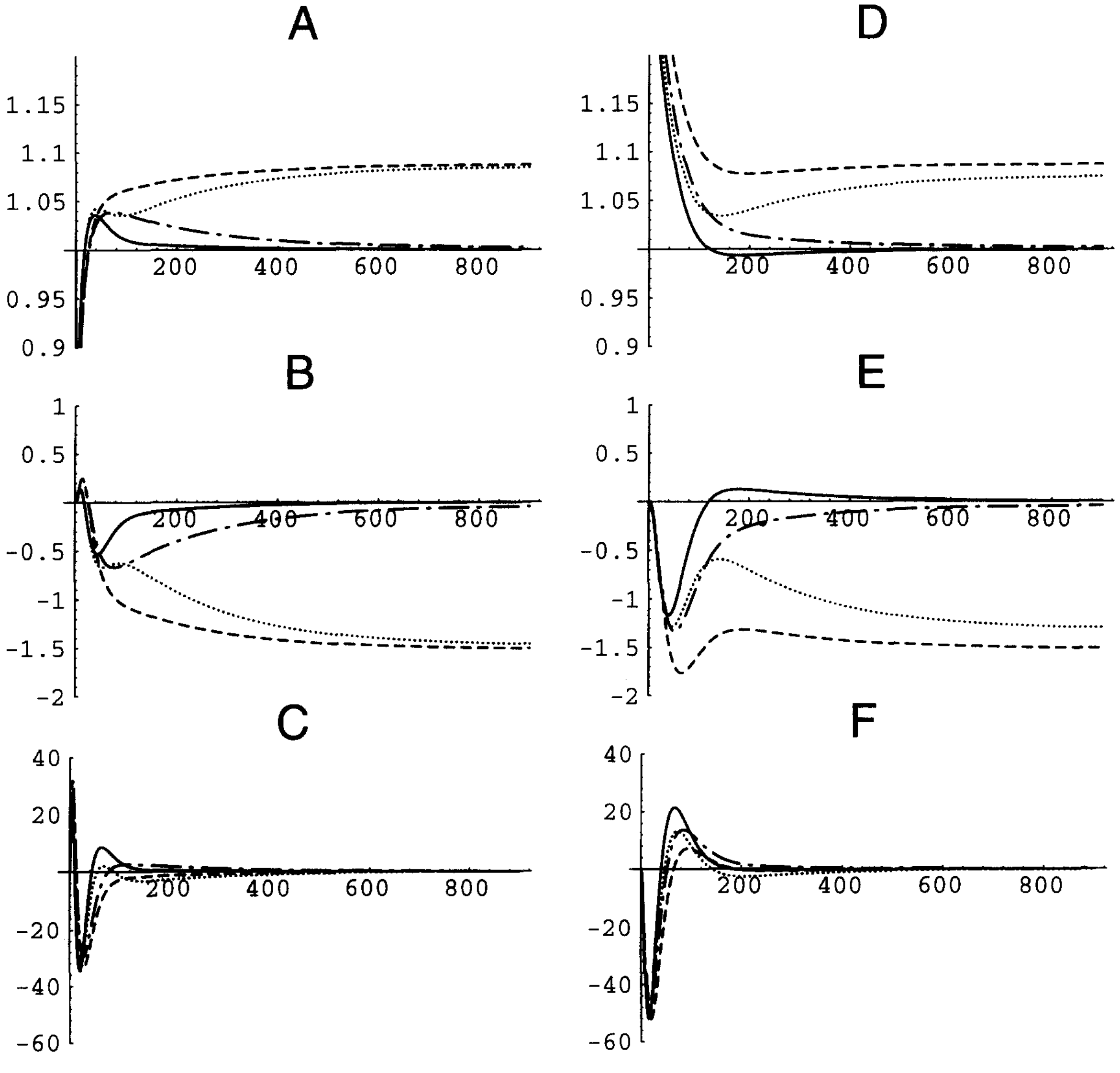


FIGURE 11. Simulation of the aniseikonic experiments. The figure shows two examples of the model replica of the aniseikonic experiment. The three panels on the left (A–C) refer to subject G2, the three panels on the right (D–F) refer to subject HV. The template movements are leftward saccades obtained with the FD paradigm, which are shown in Figs 3(B, C) and 4(A, C). The curves are aligned at the saccadic onset (0 sec). The horizontal axes of all the graphs represent the time (msec). The upper panels (A and D) show the DR, the central panels (B and E) the vergence (offset to zero) and the lower panels (C and F) the vergence velocity. Each panel is composed of four superimposed traces, describing saccadic disconjugacy during different epochs:—, iso-vergence saccades (baseline); · · ·, initial aniseikonic saccades; - - -, response after several minutes of aniseikonic stimulation;– · –, binocular test after the presentation of aniseikonia. The parametrical setting of the model for these simulations is reported in Table 3.

TABLE 3. Parametrical setting of the model of Fig. 9: simulations of Fig. 11

Trial	Eye	G_g^j	G_p^j	G_w^j	G_r^j	G_a^j
Subject G2 ($T^l = 0.003$, $T^r = 0.002$, $T_d^l = 0.001$, $T_d^r = 0.001$, $T_1^l = 0.200$, $T_1^r = 0.202$, $T_2^l = 0.018$, $T_2^r = 0.020$)						
Baseline	Left: $j = l$	1.000	1.000	1.000	0.201	0.020
Baseline	Right: $j = r$	1.000	1.000	1.000	0.201	0.020
First	Left: $j = l$	1.000	1.041	1.000	0.201	0.020
First	Right: $j = r$	1.000	0.959	1.000	0.201	0.020
Last	Left: $j = l$	1.000	1.042	1.000	0.203	0.018
Last	Right: $j = r$	1.000	0.958	1.000	0.195	0.020
Test	Left: $j = l$	1.000	1.001	1.000	0.203	0.018
Test	Right: $j = r$	1.000	0.999	1.000	0.195	0.020
Subject HV ($T^l = 0.003$, $T^r = 0.003$, $T_d^l = 0.001$, $T_d^r = 0.001$, $T_1^l = 0.203$, $T_1^r = 0.200$, $T_2^l = 0.015$, $T_2^r = 0.020$)						
Baseline	Left: $j = l$	1.000	1.000	1.000	0.201	0.018
Baseline	Right: $j = r$	1.000	1.000	1.000	0.201	0.018
First	Left: $j = l$	1.000	1.036	1.000	0.203	0.018
First	Right: $j = r$	1.000	0.963	1.000	0.203	0.018
Last	Left: $j = l$	1.000	1.042	1.000	0.205	0.016
Last	Right: $j = r$	1.000	0.958	1.000	0.190	0.016
Test	Left: $j = l$	1.000	1.001	1.000	0.203	0.018
Test	Right: $j = r$	1.000	0.999	1.000	0.195	0.018

We observed such efficient vergence control during the experiment with the TP (see Fig. 1) but not with the aniseikonic paradigm in FD viewing. Others modelled the vergence system in a saccadic like fashion (Zee *et al.*, 1992), that is to say that it provides the proper combination of tonic and phasic signals. Our FD data indicate an inadequate phasic contribution into the disconjugate control signal during saccades (see Figs 1, 3 and 4) that is exactly the opposite to what expected from saccadic facilitation.

(3) The disjunctive motion starts within the fast phase of the saccades and does not exhibit large modification (over time) during the following drift. This suggests that the saccadic disconjugacy can not be due to a late slow corrective disjunctive motion induced by visual feedback.

We investigated the possibility of having the vergence system shut down and the disconjugacy provided by the saccadic system. Nevertheless, we cannot exclude minor contributions from either the vergence signals or visual feedback that could account for the variability in some parameters of the model analysis.

Mechanisms of Disconjugate Adaptation

Saccadic modifications do not automatically involve adaptation, this can be caused by either a change of the input(s) or an internal modification of the system. The modification can be gradual and progressive, or immediate; in the former case a learning process can be assumed. Adaptation is mediated by learning, but learning alone does not imply plastic modification of the system. An example can clarify this point: a gradual improvement of the estimation of target position could imply a progressive better motion (e.g. drift reduction) but it would not involve (as a variation inside the control system does) persistence of this modification by changing the target, because only the inputs to the system are concerned and not the system itself. Hence, plastic modifications can be identified on the basis of their persistence after the removal of what caused these modifications. For this reason we assessed the adaptive nature of binocular modification induced by aniseikonia by comparing saccadic yoking during different epochs.

The mechanisms for the generation of the unequal binocular horizontal saccades made during the FD experiments (the paradigm that induced fast disconjugate adaptation) have been deducted from the model analysis.

Unadapted saccades. At the beginning of the presentation of the aniseikonic images, an immediate (on-line) monocular correction of the programmed final position for the movement takes place, superimposed on the transient loss of yoking of the conjugate movements. The tonic modification is not associated with a corresponding phasic one: these features characterize the unadapted saccades. This means, in model terms, that the gains of the tonic components of the saccadic command are monocularly controlled in a non-adaptive fashion. Enright (1992), claimed the existence of largely independent systems for the generation of pulse and step components of the saccades to explain the large modification of the final position ("the missing step") evoked by its paradigm. His proposal is that the pulses originate from weighted combinations of the two retinal inputs while the steps needed by each eye are evaluated from monocular inputs: a challenge to the validity of most of the current models of the saccadic system based on the idea (Robinson, 1975) that the step is generated by temporal integration of the pulse. Zee *et al.* (1992) proposed three possible schemes to explain the saccadic facilitation of the vergence. One of these models, although this was not their favoured one, was based on the existence of two saccadic systems, each one dedicated to one eye. More recently, differentiated control for each muscle has been suggested (Inchingolo & Bruno, 1994) or even a set of dedicated systems to each muscle (Dell'Osso, 1994). In principle any scheme involving independent generation of the tonic component for each eye (muscle) can explain the variation of the programmed final position observed during our experiments. However, the 8% size difference of the 20 deg saccades studied by us is also, and more simply, compatible with the idea of independent control of the gains of the tonic signals sent to the two eyes. The concept of independent control involves neither a generation of independent steps nor a build-up of the steps different from the temporal integration of the phasic components. Instead, it implies the existence of a mechanism to differentiate the output of the neural integrator to the motoneurons controlling the two eyes. Because in our experiments the retinal disparity was <2 deg, and therefore detectable (Bishop & Pettigrew, 1986), the differentiating mechanism could originate from the retinal disparity detection, as suggested by Bush *et al.* (1994) for the generation of unequally sized saccades. The resulting uncompensated movements (characterized by phasic signals that do not match to the disconjugate steps) may be due to a persisting cyclopean phasic programming based on averaging (Findlay & Harris, 1993).

Finally, we found that the alteration of the dynamic compensation was, for the unadapted saccades, restricted to the long-term disconjugate phasic components. This suggests a scheme of partially monocular and partially binocular dynamics control. In our paradigm only the latter was used for the compensation of short-term dynamic elements. In terms of anatomo-functional structures (and therefore of model topology), this points to either two partially overlapping systems or a parallel-distributed system with some areas prevalently monocular (outputs mainly to one eye) and some other areas prevalently binocular (balanced outputs to the two eyes).

Adapted saccades. The prediction of the conceptual model for the adapted saccades is achieved by restoring the dynamic compensation in presence of unequal tonic components. This process, even when it does not appear complete within the observation time, is still largely effective in improving saccadic disconjugacy. It involves mainly the uncompensated long-term disconjugate phasic components, previously discussed. In the presence of tonic and these phasic disconjugate modifications, the compensation of the small time constant of the controlled system (short-term effect) does not show systematic changes. From these observations it follows that the control system can be regarded as formed by two parts: the first part dedicated to the generation of these short-term signals and not subjected to fast disconjugate adaptive control, and a second part producing the long-term components that is under this adaptive control.

Post-aniseikonia tests. Learning took place in the FD experiment and, to a lesser extent, in the CD paradigm, but adaptation was found only in the FD condition, as demonstrated by the persistence of the learned disconjugate dynamic compensation on the binocularly driven saccades of the post-aniseikonia tests, observed only with the FD paradigm. Our model study points out the following scheme of signal modification, which is able to predict the generation of unequal saccades in the presence of aniseikonia: as the target changes, an immediate tonic correction and a phasic correction progressing over time emerge. So, if adaptation has taken place, the ocular motion will appear altered in its phasic disconjugate features after removing the aniseikonia. Nevertheless, the final position will appear correct, even if previously modified, because it is subjected to on-line control. The model prediction of the post-aniseikonia saccades successfully implemented this adaptive mechanism.

Implications for the saccadic system

Considering a peripheral source for the idiosyncratic pattern of binocular saccadic coordination and conceptualizing the existence of short- and long-term disconjugate transients due to an imperfect matching between the plants and their "neural inverse models", our analysis points out that the system acts functionally differentiating the controls for the many signals required to accomplish saccadic eye movements. An appropriate model representation of the saccadic controller must be able to exhibit, within a limited range, (1) an on-line independent control of final positions with associated modified dynamic compensation and (2) a fast disconjugate adaptation requiring the matching of the phasic with the tonic component.

On-line generation of the disconjugate tonic signal and of the long-term phasic unbalancing. So far several bilateral and distributed structures have been proposed for the neural integration (Cannon, Shamma & Robinson, 1983; Cannon & Robinson, 1985; Galiana & Outerbridge, 1984; Galiana, Flohr & Jones, 1984; Inchingolo, 1985; Inchingolo, Spanio & Bianchi, 1987; Arnold & Robinson, 1991; Galiana, 1993; Cova & Galiana, 1995). One important aspect of these conceptualizations is that the integration is achieved by the bilateral differential couples of excitatory and inhibitory inputs (Van Gisbergen, Robinson & Gielen, 1981). For the generation of the saccadic tonic commands these inputs originate from the excitatory burst neurons (EBNs) at the ipsilateral side (McCrea, Baker & Delgado-Garcia, 1979; Strassman, Highstein & McCrea, 1986a) and from the inhibitory burst neurons (IBNs) at the contralateral side (Strassman, Highstein & McCrea, 1986b). The inhibitory inputs to the bilateral integrator are mandatory for the saccadic signals, to allow (Inchingolo, 1985) a balanced output of the tonic pair even though the input is not balanced (the EBNs of the contralateral side with respect to the direction of the movement are silent during saccades). The EBN and IBN phasic commands are also sent to motoneurons and interneurons of the VI nuclei (Strassman *et al.*, 1986a,b). The IBN projections to the VI nuclei have mainly a gating effect: to switch off (interdict) motoneurons and interneurons of the contralateral side, controlling the antagonist muscles. Therefore, an asymmetric modulation of the IBNs can produce a modification of the outputs of the integrator and in turn a differential co-relaxation of the antagonist muscles, without a corresponding direct modification of the phasic discharge of motoneurons. In addition, during our FD experiments the eyes behaved as if short-and long-term disconjugate transients were differently affected by the presence of the disconjugate steps. These findings are compatible with the following two mechanisms: (1) the monocular setting of the tonic component acts late into the saccadic flight, after the short transient has already extinguished; and (2) the short-term compensation is generated differently from the long-term component. The first hypothesis is compatible with a late activation of the IBNs (Scudder, Fuchs & Langer, 1988; Strassman *et al.*, 1986b) and can be related to cerebellar control (Fuchs, Robinson & Straube, 1993). For the immediate on-line response to a new demand of eye coordination the second hypothesis implies in addition to a tonic-only contribution from the IBNs, that: (a) a conjugate control exists for the elements that affect the intra-saccadic yoking with little residual misalignment when vision is restored; and (b) a mainly monocular tuning of the compensation for long-term components takes place, resulting in large post-saccadic effects. All these behaviours can be explained in terms of a distributed-parallel integrator, which is characterized by a large flexibility (e.g. Arnold & Robinson, 1991). A shared premotor network, providing for both vergence and conjugate integrators in a single bilateral controller, has been proposed also by Cova and Galiana (1995). The multiple outputs of the system could provide the following adjustments as an immediate response to a novel disconjugate stimulus: (a) the binocular (essentially conjugate) set of output could, in combination with phasic signals, compensate for the short transients; and (b) the monocular sets could provide the tonic components needed for the long-transient compensation, although it would lack to supply the additional phasic components necessary for this compensation.

Generation of the adaptive compensation of the long-term phasic unbalancing. An important additional feature of a distributed structure is that it can tolerate internal modifications without changing its global output. This feature permits that the adaptive process, working during the learning phase, alters the compensation of the previously unbalanced phasic components with only minor changes on the other phasic outputs of the controller. The system can obtain this by a simple redistribution of its internal phasic activation towards more monocular areas. This idea is supported by Arnold and Robinson (1991), who proved that a learning network can perform tasks more complex than just integration, by readjusting its internal weights.

This interpretation, that takes advantage from the inherent redundant distributed structure of all the neural circuits, offers "for free" a possible link with the effect that the distance has onto the disconjugate performances of the saccadic system [see Van der Steen and Bruno (1995) for details]. The distribution of activity within the system could be controlled by the tonic vergence level by combining the efferent copies, automatically keeping the system conjugate when the eyes are almost parallel (far viewing) and spreading the activity to more independent areas (areas which project mainly monocularly) as convergence increases.

The adaptive mechanisms of the phasic components here described, have compensating features because they involve an improvement, mediated by learning, of the matching of the phasic signals to the tonic ones and because such modification persists afterwards. Conversely, Optican and Robinson (1980) suggested that the suppression of the conjugate pulse–step mismatch is obtained by adaptation of the gain of the step component to motoneurons, in order to freeze the eye at the position reached at the end of the pulse. As an alternative, compatible with our results, Inchingolo (1986) proposed that the step control is not involved in the suppression of the post-saccadic drift, and that small mismatches can be cancelled by controlling the gain of the pulse components to motoneurons while large mismatches require the modification of the gain of the integrator inside the saccadic local loop. More recently, a much more complex mechanism has been proposed (Inchingolo *et al.*, 1991), involving all these three gain controls, aimed to make the non-linear saccadic system working properly with the different demands of conjugate and may be disconjugate drift suppression (see also Inchingolo, 1994). The discrepancy among these various proposals could be explained with a more general consideration. Some changes (in particular the conjugate ones) may imply a complete change of the network setting and others just a redistribution of the activities inside the net. We suggest that the latter is responsible for disconjugate adaptation, at least as far as small and fast modifications are concerned. These processes are likely to be fast, because they probably are required continuously during daily life to recalibrate the oculomotor system after changes (e.g. due to fatigue, aging etc.) that are mainly not equal in the two eyes.

Adaptive transition from on-line to adaptive generation of the disconjugate tonic signal. One question emerges from the results till now discussed. Because a required tonic change of disconjugate control to the two eyes is done on-line while the corresponding phasic change requires learning and therefore adaptation before to be accomplished, what happens when the new condition persists over time, as usually occurs in our life? Does the tonic change continue to be mediated on-line? As a first reaction one could argue there is no sense to fail to memorize globally the new condition. Actually, open-loop measurements made at the end of the aniseikonic adaptation showed (Van der Steen & Bruno, 1995) that on average 25% of the tonic disconjugate change (the final steady-state vergence), initially acquired on-line, persisted (see Fig. 2, trials 16 and 17). However, we have seen that at the presentation of a normal couple of images of the same size this tonic change disappeared immediately. These conjoined results demonstrate that the tonic disconjugate signal, generated on-line at the first presentation of the aniseikonic images, was substituted, as learning progressed, with an adaptive mechanism. After removing the aniseikonia, both the tonic (step) and the phasic (pulse) components of disconjugate adaptation persisted, and decayed over time. However, only the effects of the phasic changes were observed in the saccadic responses, since those due to the tonic changes were probably cancelled by the on-line tonic mechanism, working this time in the opposite direction.

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Acknowledgements—This work was supported by the European Community, Contract No. SCI-CT91-0747 (TSTS) and the Human Frontiers Science Programme.

APPENDIX A

The ocular positions can be regarded as the output of two complex systems (R and L) that differ for the position of one pole. The two systems are excited by a conjugate signal—U. The two outputs can be described in terms of Laplace transformation (as far as a linear model is concerned), in the following way:

$$R(s) = \frac{U(s) \cdot CY(s)}{1 + s \cdot T^r}$$

and

$$L(s) = \frac{U(s) \cdot CY(s)}{1 + s \cdot T^l};$$

where T^r and T^l are the time constants associated with the poles and $CY(s)$ is the transfer function of the common part of the two complex systems [see Fig. A1(A)]. We can rearrange these two equations and get the following relation:

$$R(s) \cdot (1 + s \cdot T^r) = L(s) \cdot (1 + s \cdot T^l). \tag{A1}$$

Defining then $\Delta T = T^r - \mathrm{T}^l$ and $VE(t) = L(t) - R(t)$, and transforming the relation in the time domain we get:

$$VE(t) + T^l \cdot VE'(t) = \Delta T \cdot R'(t). \tag{A2}$$

The apex indicates the signal velocity.

Equation (A2) tells us that, at the time the ($t = \tau$) velocity of the signal VE is zero, the difference ΔT can be evaluated by the ratio between VE and the velocity of the signal R at that time:

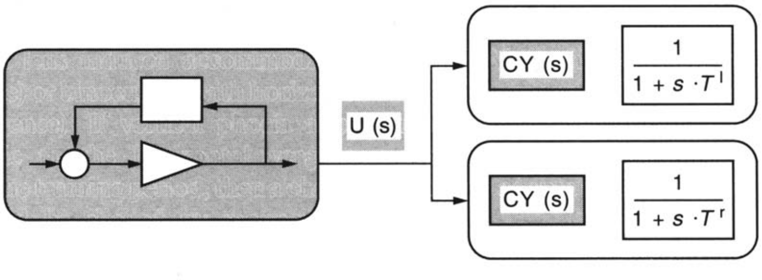
$$\Delta T = \frac{VE(\tau)}{R'(\tau)}.$$

Dealing with ocular rotations, the problem appears to be quite well-conditioned because at $t = \tau$ both the signals [$VE(t)$ and $R'(t)$] are close to their maximum and therefore affected by a small relative error. Next, the time constant of the L system can be evaluated with:

$$T^l = \frac{\Delta T \cdot R'(t) - VE(t)}{VE'(t)}. \tag{A3}$$

This procedure is independent of any elaboration (e.g. filtering) performed on both $R(t)$ and $L(t)$, because it can be regarded as an extra element forming the common part CY of the systems (see Fig. A1). We

(A) 1-pole scheme



(B) 1-pole scheme with disjunctive control signal

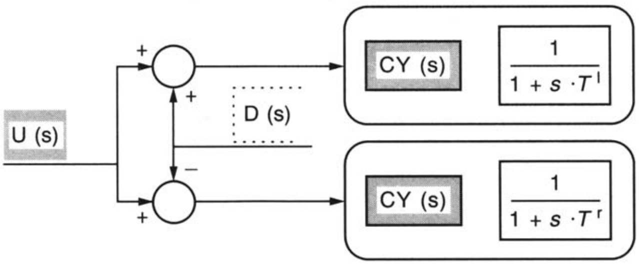


FIGURE A1. Block diagram of the 1-pole scheme used for the explanation of the transient divergence during iso-vergence saccades. (A) In this panel the rounded block at the left represents a versional system that provides a signal U to both the left and right eye plants (the two blocks on the right-hand side: top—left plant model; bottom—right plant model). Each plant model is divided into two sections, consisting of a part CY that is equal for the two models, and a low-pass filter that differs. All the elements that are common in both plants are shaded. (B) A variation of the model of (A), on which the common block generating U is omitted and a disjunctive control signal D is added (for explanation of the symbols see the text).

evaluated the parameter A and the function $B(t)$ from the data as follows:

$$A = \frac{VE(\tau)}{R'(\tau)}; \tag{A4}$$

and

$$B(t) = \frac{\Delta T \cdot R'(t) - VE(t)}{VE'(t)}. \tag{A5}$$

If the function $B(t)$ remains constant (and equal to T^{l}) during the saccades, we can assume that the model is correct; otherwise, we will need to consider other additional sources of disconjugacy. If, in addition to the conjugate input U, the two plants are excited by a differential input D [see Fig. A1(B)] the parameter A and the function $B(t)$, which we can evaluate from the recorded data, have the following meaning:

$$A = \Delta T - \frac{2 \cdot DM(\tau)}{R'(\tau)} \tag{A6}$$

and

$$B(t) = T^{l} - \frac{\dfrac{DM(\tau)}{VE'(\tau)} + 2 \cdot DM(t)}{VE'(t)}; \tag{A7}$$

where $DM(s) = D(s) \cdot CY(s)$.

In the presence of a disjunctive control, the 1-pole scheme predicts that: (1) the residual vergence, if it is extracted with the filters defined from our baseline data, should be related to $DM(t)$; and (2) the function $B(t)$ evaluated from disconjugate data should be modulated by the differential input.

We tested the 1-pole scheme. For this we set the two time constants to $T^{l} = \mathrm{B}(0)$ and $T^{r} = \mathrm{B}(0) + \mathrm{A}$, respectively, and removed the transient vergence, for both conjugate and disconjugate movements, by filtering the signals with: $E^{l}(\mathrm{s}) = (1 + \mathrm{s} \cdot \mathrm{T}^{l})$ and $E^{r}(\mathrm{s}) = (1 + \mathrm{s} \cdot \mathrm{T}^{r})$, for the left and right eye, respectively.