Voluntary Binocular Gaze-shifts in the Plane of Regard: Dynamics of Version and Vergence

HAN COLLEWIJN,*†‡ CASPER J. ERKELENS,† ROBERT M. STEINMAN§

We studied the dynamics of voluntary, horizontal, binocular gaze-shifts between pairs of continuously visible, real three-dimensional targets. Subjects were stabilized on a biteboard to allow full control of target angles, which were made to differ only in distance (pure vergence), only in direction (pure version; conjugate saccades) or in both distance and direction (disjunctive saccades). A wide range of changes in vergence (0–25 deg) and version (0–65 deg) was recorded to study the dynamics of disjunctive saccades, described until now for limited ranges, throughout the horizontal oculomotor range within manual working space, and to study the velocity–duration–amplitude relations ("main sequence") of disjunctive vs conjugate saccades. Pure vergence was almost never observed; divergence, especially, was always associated with saccades. Likewise, horizontal saccades were never strictly conjugate, they always contained a transient divergence–convergence sequence. The amplitude and velocity of these transient components varied systematically with saccadic size. In combined version–vergence movements, vergence was, in general, accelerated and shortened as a function of increasing version. This effect was fairly uniform for divergence, which appeared to increase in velocity by about as much as the transient peak divergent velocity of the version saccade. The intrasaccadic fraction of divergence increased from about 50% to close to 100% as a function of increasing version. For convergence, saccades up to about 20 deg were also accelerating; in this case it appeared as if the transient peak convergent velocity of the version saccade was added to the basic convergence velocity. For larger saccades this effect was partly counteracted by the penetration of an initial divergence associated with the saccade. This initial divergence delayed and slowed down convergence. The intrasaccadic fraction of convergence varied between about 40% and 70%. In disjunctive saccades the individual eyes did not follow the main-sequence parameters of conjugate saccades of comparable sizes, except for the eye that moved with the combination "abduction and divergence". For all other combinations of vergence and version, disjunctive saccades had lower peak velocities and longer durations than conjugate saccades. As a consequence, disjunctive version was also slower than conjugate version. Thus, while version accelerates vergence, vergence slows down version: in the generalized case of three-dimensional gaze-shifts, peak velocities and durations are in between those of the limiting cases of pure version and pure vergence. We conclude that, within manual working space, binocular gaze-shifts are effected by the highly integrated action of conjugate and disjunctive mechanisms, both of which are expressed preferentially in fast, saccadic movements.

Saccade   Version   Vergence   Binocular   Oculomotor   Conjugate   Disjunctive   Hering's law

In traditional conceptualizations of human oculomotor behavior, control of direction and distance of the binocular fixation point is attributed to two essentially independent subsystems. Rapid shifts in direction (*version*), involving similar (conjugate) changes in the angles of the lines of sight of the two eyes, are attributed to a saccadic subsystem. On the other hand, shifts in distance, involving a change in the angle between the lines of sight, are considered to be controlled by a separate *vergence* subsystem. This dichotomy, originally conceived in a theoretical form by Hering (1868), has been experimentally supported by the finding of characteristic differences in the dynamic properties of saccadic and vergence movements when investigated separately. Classical investigations (Westheimer, 1954; Rashbass & Westheimer, 1961) indicated about an order of magnitude difference in typical velocities between the systems. While saccadic peak velocities were found to be on the order of hundreds of deg/sec, vergence velocities appeared to reach only tens of deg/sec. This difference strongly argued for separate neurophysiological mechanisms controlling binocular direction and distance, a view which was

*Department of Physiology, Faculty of Medicine, H-EE-1540, Erasmus University Rotterdam, P.O. Box 1738, 3000 DR Rotterdam, The Netherlands.
†Helmholtz Institute, Utrecht University, P.O. Box 80000, 3508 TA Utrecht, The Netherlands.
‡To whom reprint requests should be addressed.
§Department of Psychology, University of Maryland, College Park, MD 20742-4411, U.S.A.

probably most strongly expressed in Yarbus' (1967) well known schematic diagrams of the trajectory of binocular fixation in gaze-shifts involving both version and vergence. In this view, vergence and version have not only very different dynamic properties when evaluated separately, but these properties are maintained when both subsystems are operating simultaneously, and the combined motor output is equal to the summed outputs of the two subsystems. Neurophysiological support for a separate control of vergence originates from the discovery of a class of midbrain neurons in the monkey that appears to encode (changes in) vergence angle (Mays, 1984; Mays, Porter, Gamlin & Tello, 1986; Judge & Cumming, 1986).

From a functional perspective this dichotomy is puzzling because it would imply that the overall dynamics of natural binocular gaze-shifts, which most often involve changes in distance as well as direction, are limited by the slow vergence component, so that targets distributed in three-dimensional space would typically not be foveated with saccadic velocities. Several more recent observations have, however, suggested a more integrated view of version and vergence control, with a less rigid separation between these subsystems.

Firstly, the very low vergence velocities elicited under laboratory conditions by manipulations of the disparity of (otherwise constant) targets as the *only* input (Rashbass & Westheimer, 1961; confirmed recently by Erkelens, 1987) are not representative for vergence associated with *voluntary shifts* of gaze. Rather, they are probably typical for corrective vergence movements that serve to eliminate errors in binocular foveation that may occur in between gaze-shifts. Natural shifts of gaze between different targets, even when these differ in distance but not in direction, typically reach much higher vergence velocities. Erkelens, Steinman and Collewijn (1989b) measured an approximately linear relation between vergence velocity and vergence amplitude, with a slope of the order of 5 deg/sec per degree of vergence, in agreement with earlier reports (unfortunately not documented by published data) by Bahill, Clark and Stark (1975). Thus, vergence shifts of 20 deg between real targets typically have peak velocities on the order of 100 deg/sec.

Secondly, nonconjugate saccades that cannot be accounted for by a linear addition of conjugate saccades with ongoing, smooth vergence have been documented first as curious exceptions (Ono & Nakamizo, 1978; Ono, Nakamizo & Steinbach, 1978; Kenyon, Ciuffreda & Stark, 1978, 1980a,b) and later as the regular mode of operation in combined version–vergence shifts (Enright, 1984, 1986; Erkelens et al., 1989b; Zee, Fitzgibbon & Optican, 1992; Oohira, 1993). Similar version–vergence interactions have been reported for monkeys (Maxwell & King, 1992). The mechanism underlying these fast, nonconjugate gaze-shifts is still unclear, although various possibilities have been proposed. Erkelens et al. (1989b) advocated an inherent capability for the saccadic system to generate nonconjugate saccades, which is used in natural three-dimensional gaze-shifts. The inherent capability to generate nonconjugate saccades was independently supported by experiments on nonconju-

gate adaptation to anisometropic spectacles, which clearly demonstrated a facility to adapt the size ratio between the saccades executed by the two eyes to values different from the default setting of unity (Erkelens, Collewijn & Steinman, 1989a; Lemij & Collewijn, 1991a,b, 1992). Obviously, instantaneous, independent control of the size of the saccades of the two eyes would be a very efficient way to generate disjunctive eye movements, but such a mechanism will require strong experimental support in order to be accepted. A more conservative view is that vergence and saccades are neurophysiologically distinct but communicating subsystems, which show interaction, notably facilitation of vergence by saccades (Enright, 1986; Maxwell & King, 1992). Zee et al. (1992) have proposed a mechanism for such facilitation in which "vergence burst neurons" (Mays, Porter, Gamlin & Tello, 1986) are disinhibited during saccades by the inactivity of pause cells. Experimental support for such a mechanism was briefly reported by Mays and Gamlin (1992).

Whatever the mechanism of the interaction between version and vergence in three-dimensional gaze-shifts, further study of this integrated action, rather than of the limiting conditions (pure vergence and version) in isolation, seems of primary relevance to oculomotor behavior. As we have noted before (Erkelens et al., 1989b), this would also be in the spirit of Hering (1868), who emphasized the cooperative behavior of the two eyes, more than their control by several, dynamically distinct subsystems. Previous investigations of version–vergence interactions have been limited to a small range of combinations of changes in gaze angles. In the present experiments, we have collected data covering a large range of combinations of changes in vergence (0–20 deg) and version (0–65 deg); control of these angles necessitated the immobilization of the heads of our subjects on a biteboard. The present data suggests that the acceleration of vergence is not uniform throughout the range of version, that the interaction between version and vergence shows systematic asymmetries which largely derive from the transient vergence changes associated with "conjugate" horizontal saccades, and that version is generally slowed down by the simultaneous occurrence of vergence. A preliminary, partial analysis of these experiments was published before (Collewijn, Erkelens, Pizlo & Steinman, 1994). The present, more complete analysis also serves as a further baseline for the study of gaze control under free-head conditions, aspects of which are covered in Collewijn, Steinman, Erkelens, Pizlo and Van der Steen (1990), Steinman, Kowler and Collewijn (1990), Collewijn, Steinman, Erkelens, Pizlo, Kowler and Van der Steen (1992), and Epelboim, Steinman, Kowler, Edwards, Pizlo, Erkelens and Collewijn (1995).

METHODS

Real targets (LEDs) were positioned on isovergence circles, subtending vergence angles of 5–25 deg with intervals of 5 deg; the distances of such targets from the interocular baseline varied, in the midsagittal plane,

between 74.4 and 14.7 cm. Directions ranged between 35 deg left and 35 deg right, also with intervals of 5 deg. (These nominal isovergence angles were correct for an interocular distance of 65 mm; individual differences in this distance would slightly change the vergence angles subtended by each of the isovergence circles, but not the directions of the targets). Differences in direction were distributed symmetrically about the straight-ahead position, to avoid asymmetries between centripetal and centrifugal saccades (Collewijn, Erkelens & Steinman, 1988). In the experiments described here, all targets were generally in a horizontal plane at eye level, with a few exceptions in which a small vertical offset between near and far targets in the midsagittal plane were introduced (see Results). Two targets were lit at any time, and subjects were instructed to shift their gaze between these targets voluntarily and accurately, at a comfortable pace (about once every 1.5 sec). Pairs of targets were chosen such that they differed only in vergence angle, only in version angle, or in both angles.

Subjects who had no known deficiencies of binocular vision or oculomotor control were recruited, after informed consent, among the authors and their colleagues. Five subjects [two women (AP and ST) and three men (CE, ZP and RR); ages between 25 and 45 yr] provided the body of data for the present results. Four additional subjects participated, but their data showed anomalies that made them unsuitable for our present purposes. The reasons for their exclusion were, respectively, (i) presbyopia with blurred vision of, and poor vergence towards, near targets; (ii) anisometropic spectacle corrections with nonconjugate saccades as a baseline condition; (iii) latent phoria that became manifest during a session; (iv) habitual generation of fractionated instead of single, primary saccades. The results described in this report were obtained with the subject's head stabilized on a dental impression biteboard, to allow full control of the target viewing angles.

Horizontal and vertical motions of both eyes were measured with the scleral coil technique and digitized at a rate of 488/sec with a resolution of 1 min arc (least significant bit noise) during trials lasting 10–16 sec (for details of recording technique, see e.g. Collewijn et al., 1988). Analysis of the digitized signals started with detection of saccades fulfilling velocity and size criteria, and averaging of a number (3–16) of successive saccades in a same direction between the same targets. For the averaging, a 15 deg/sec criterion was used for synchronization of the start of the saccades, and only saccades with a size close to the angle between the targets were included. (Secondary, corrective saccades were not included in the analysis.) Standard deviations of such averaged saccades proved to be very small compared to the signals, indicating only slight variability among successive saccades. The averaged position signals were differentiated with a minimum of smoothing and no time shift, using the following formula:

$$V_n = (f/6)*([n + 1] + [n + 2] - [n - 1] - [n - 2])$$

in which V_n is velocity at sample n; $[n + 1]$ etc. are position samples; f is the sampling frequency (488/sec). These routines eliminated most of the bit noise (equivalent to 488 min arc/sec in the raw signals) without affecting the magnitude and timing of peak velocities. Version was calculated as the average of, and vergence as the difference between, the positions of the two eyes. Trials with a pure vergence stimulus were analyzed on the basis of the vergence response; in this case a 5 deg/sec criterion was used for the beginning of vergence. In all operations on the data, time relations between the two eyes were conserved. Peak velocities of monocular and binocular (vergence and version) components of gaze-shifts could be simply determined as the maximum value of the differentiated data. Duration of saccadic gaze-shift components (each eye apart and version) was defined as the period during which speed exceeded 50 deg/sec. The amplitude of the saccadic movements was calculated as the displacement in this same period. Moderate changes in this velocity criterion hardly affect the timing of the start of a saccade, due to the large initial acceleration, but they do substantially affect the timing of the end. The 50 deg/sec criterion was a conservative choice, intended to exclude all slow components that were not clearly of saccadic nature. The duration of vergence was defined differently. A 5 deg/sec velocity (in the appropriate direction) criterion was used to label the beginning (t_0) of a vergence movement. Then, the total amplitude of the following vergence movement, and the moment (t_{90}) at which 90% of this movement was completed, were determined. Vergence duration (D_{90}) was defined as ($t_{90} - t_0$). The different criteria for vergence and version movements were necessitated by their very different dynamics. These differences do not confound the analysis, because comparisons are made only between data defined by similar criteria. In most cases the period of analysis extended over 800 msec, the first 100 msec of which preceded the beginning of the gaze-shift.

RESULTS
Vergence and Version: the Basic Picture

"Pure" vergence

Gaze-shifts between targets that differ only in vergence and not in direction could, in principle, be achieved by "pure" vergence responses, i.e. symmetrical movements of each eye, without changes in version. As has been noted before (e.g. Erkelens et al., 1989b), such pure vergence is almost never encountered in practice. Our present data confirm that execution of vergence was least efficient, and subjectively experienced as most difficult, when vergence alone was called for, i.e. when the two targets were in the median plane, aligned exactly in the same horizontal and vertical directions, so that they were viewed at the same vertical level with the diplopic images of the non-fixated target positioned symmetrically about the fixated target. (As targets were in the median plane, they were not aligned for either of the eyes, nor did the near target occlude the far target.) When the differences in target

vergence were not very large (5 deg, sometimes also 10 deg), ocular vergence even tended to be ambiguous. In many cases, as illustrated in Fig. 1, vergence shifts had only half the required size: one eye shifted to the nearer or farther target while the other eye continued to fixate the same target; sometimes the required vergence change was eventually achieved by a second step of half the required change in vergence [Fig. 1(B), divergence]. Furthermore, these ambiguous vergence movements were always accompanied by saccades (see Fig. 1, eye and version traces). The subjects were often well aware that their motor performance was inadequate, but were unable to correct this.

Such ambiguous responses did not occur unless the targets were carefully aligned for the subject, and they were eliminated—subjectively as well as objectively—by introducing a small vertical offset between the near and far targets. As shown in Fig. 2(A), a vertical offset of 1 deg was sufficient to disambiguate the responses to a 5 deg vergence stimulus. Increasing the vertical offset to 2 or 5 deg did not further improve the vergence responses consistently. For pure vergence stimuli subtending larger angles (10 deg in most cases; 15 and 20 deg always),

(A) Targets differ in vergence by 5 deg (CE)
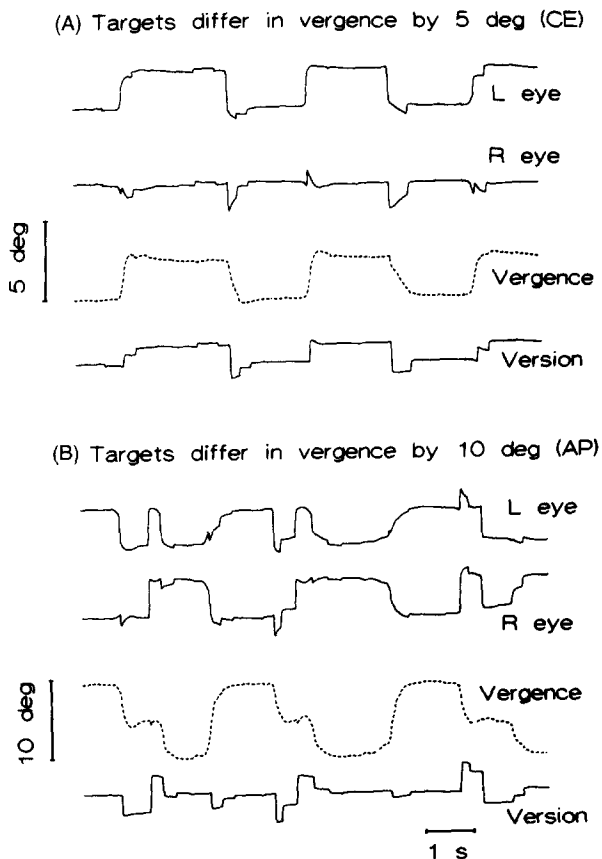

(B) Targets differ in vergence by 10 deg (AP)

FIGURE 1. Examples of 10 sec trials with voluntary gaze-shifts between carefully aligned stimuli differing only in vergence angle. (A) For 5 deg differences in target vergence, responses (here shown for subject CE) were usually inadequate and monocular (except for saccadic intrusions). Vergence shifts were only 2.5 deg. (B) Even for 10 deg differences in target vergence, responses were occasionally ambiguous, as shown here for subject AP. In this case, 10 deg divergence occurred in two successive steps of 5 deg divergence. Positions of the two eyes and the derived binocular signals are shown. Sign conventions, for this and all following figures: *rightward* and *convergence* are plotted upwards.

adequate vergence responses were generated even with perfectly aligned stimuli, and modest vertical offsets (1–5 deg) between such targets did not substantially alter such responses [Fig. 2(B)].

A set of typical velocity profiles of adequate convergent and divergent responses to midline, pure vergence stimuli of 5, 10, 15 and 20 deg (with the 5 deg vergence stimulus disambiguated by 1 deg vertical offset between the near and far targets) is shown in Fig. 3 (subject CE).

These graphs confirm the existence of a kind of "main sequence" for vergence, i.e. peak velocity and duration of vergence increase systematically with vergence amplitude, in agreement with earlier findings (Bahill *et al.*, 1975; Erkelens *et al.*, 1989b). Such plots of vergence alone, however, are somewhat misleading in as far as they suggest that the pure vergence stimuli elicited pure, symmetric vergence responses. In reality, this was the case only exceptionally. When vergence was plotted in combination with version, saccades were evident in virtually *all* cases. More saccades occurred during divergence than during convergence; we actually found *no* divergence responses that were unaccompanied by saccades in any of our present experiments. This tendency to generate small saccades in association with vergence, even though no net change in version is called for, has been noted before (Erkelens *et al.*, 1989b).

The combined plots of vergence and version in Figs 4–6 show typical three-dimensional gaze-shifts for three subjects (ZP, CE and RR); the other two subjects behaved similarly. These figures show changes in vergence by 10 deg, between far targets subtending 5 deg of convergence and near targets subtending 15 deg of convergence. These angles correspond to fixation distances of about 74 and 24 cm, which are representative of routine gaze behavior in the working space near the subject. Version changes were 20 or 30 deg symmetrical about the midposition; again, this appears representative of demands encountered during natural behavior. Panels (A) and (B) in Figs 4–6 show responses to pure vergence stimuli. They nearly always contained saccadic components; the saccades that accompanied divergence were often large enough to cause one [Fig. 6(B)] or several [Fig. 5(B)] marked peaks in the velocity of divergence.

Thus, pure vergence responses were elusive in the voluntary gaze changes of our normal subjects, even when stimuli were optimized for eliciting such behavior. This has a practical consequence for our comparison of "pure vergence" to "vergence with version". Because pure vergence was, for practical purposes, nonexistent, we had to settle instead for vergence with a small saccadic contribution, and the actual comparisons will be between gaze-shifts elicited by targets differing only in distance (iso-direction targets), only in direction (iso-vergence targets), or in both of these. In the evaluation of vergence velocities of gaze-shifts between iso-direction targets we avoided, as much as possible, peaks that were obviously related to the occurrence of saccades [e.g. such as in Fig. 6(F)].
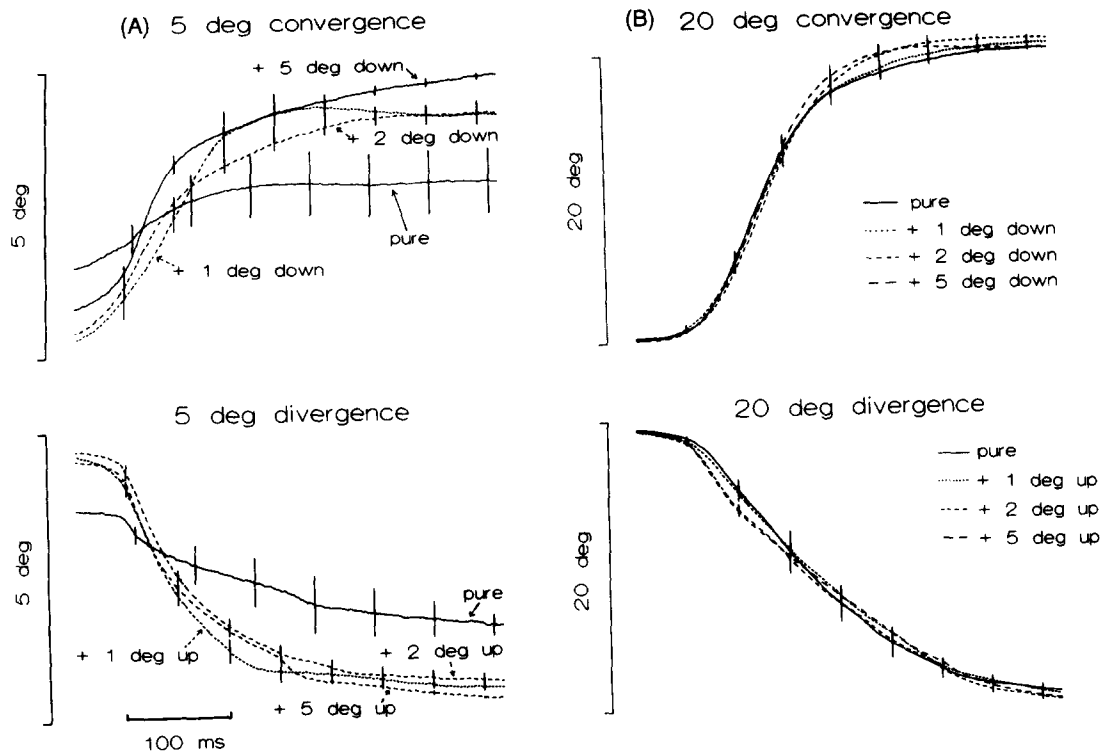
FIGURE 2. Inadequate vergence responses to carefully aligned stimuli subtending a 5 deg difference in vergence only (as in Fig. 1), and the abolishment of this problem by slight vertical offsets of the targets (A). Responses to a 20 deg pure vergence stimulus were adequate even with perfect alignment, and vertical offsets had no substantial effect. Only *vergence position* is plotted; subject CE.

"Pure" version

As has been described before (e.g. Collewijn *et al.*, 1988), saccadic gaze-shifts between iso-vergence targets always showed consistent, transient deviations from conjugacy during the saccade. Nearly all normal subjects show an initial divergence, followed by a convergence. (Outside our present sample we have encountered a few rare individuals who show an opposite sequence of transient vergence.) The abducting eye accelerates faster, reaches a higher peak velocity, and decelerates faster than the adducting eye. Thus, the abducting eye moves faster than the adducting eye in the accelerating phase of the saccade, and the reverse is the case during the decelerating phase. The velocity profiles of the two eyes and vergence during conjugate saccades, shown for three subjects in panels (C) and (D) of Figs 4–6, all demonstrate this typical pattern, despite idiosyncratic differences in the micro-structure of the profiles. These figures further show that time relations followed an equally typical pattern. The two eyes started to move synchronously (at least at the resolution of our sampling frequency, 488/sec), but the duration of the saccade made by the adducting eye was always longer than that of the abducting eye. The figures also corroborate that the 50 deg/sec speed criterion for the duration of the saccade was effective in separating saccadic from postsaccadic events. Postsaccadic movements carried each of the eyes to the target, so that final conjugacy was achieved. The way in which this end position (final zero velocity point) was reached was somewhat idiosyncratic. To illustrate: subject CE tended

to land on target always with his right eye first. This was straightforward when the right eye was abducting, i.e. for saccades to the right [Fig. 5(C)]. For leftward saccades [Fig. 5(D)], the left eye would arrive earlier on target, but instead of stopping there the left eye overshot the target so that the right, adducting eye yet landed on target first. Subject RR [Fig. 6(C, D)] landed on target with the abducting eye first, for rightward and leftward saccades. A third variant is shown by subject ZP [Fig. 4(C, D)], who overshot the target with the abducting eye and undershot it with the adducting eye in such a way that *version* (the average of the two eyes) landed on target first. Possibly, such differences in behavior are related to eye preferences, but we have not investigated this. Whatever pattern of terminal binocular foveation was used, convergence always continued during the last, "postsaccadic" phase of a gaze-shift between isovergent targets.

Combined vergence and version

Panels (E) and (F) of Figs 4–6 illustrate cases in which the same vergence and version movements shown in the upper and middle panels of these figures are integrated into a single, disjunctive movement. It is important to notice that, *in this comparison*, the sizes of vergence and version are similar, but that the sizes of the movements of each eye in the disjunctive gaze-shift are different from those in the conjugate case. For instance, in rightward + convergent movements, the size of the total left eye movement is increased by half the change in vergence angle, while the right eye movement is decreased by a

similar amount. Three general features emerge from an inspection of these figures. (i) The peak velocities and durations of the saccadic components of the movement of each eye changed when a disjunctive component was introduced. The general trend was for peak velocities to become lower, and for durations to become longer. (ii) Vergence as part of a combined version–vergence gaze-shift was faster than and had a shorter duration than vergence between iso-direction targets, as is clear from a comparison between the upper and lower panels of Figs 4–6 (notice the difference in the time scales). A direct, representative comparison is given in Fig. 7. (iii) The transient vergence changes associated with conjugate saccades were transformed during disjunctive gaze-shifts. When divergence was required the initial divergence was enlarged in speed and duration, and the transient convergence was abolished, so that the divergence became permanent instead of transient. When convergence was required the usual transient convergence was similarly enlarged, however, in most cases it was still preceded by a (reduced) transient divergence. As a result saccadic

enhancement was less effective for convergence than for divergence; a larger fraction of divergence than of convergence was achieved within the saccadic part of the gaze-shift.

A more detailed analysis of these three aspects follows.

Changes in V_{max} and Duration (Constant Version Amplitude)

We shall now examine in greater detail the changes in peak velocity and duration of the saccadic movements of each of the two eyes when a vergence demand is superimposed on a version demand. A casual inspection of Figs 4–6 (panels E and F) would seem to suggest a different strategy for convergence and divergence. In both cases the saccadic movements become disjunctive but, at first sight, the disconjugacy associated with convergence [Figs 4–6 (panels E)] appears to originate mainly from a difference in duration of the fast movements of each eye, whereas the disconjugacy associated with divergence [Figs 4–6 (panels F)] appears to derive from a difference in velocity. While this observation is basically correct, it cannot be concluded that convergence is achieved by increasing the difference in duration of the saccades of the two eyes, and divergence by increasing the difference in velocity, because of the inherent abduction–adduction asymmetry that is already present in conjugate saccades. This point is worked out in more detail in Fig. 8, which shows representative peak velocities and durations for each eye for the full range of conjugate shifts in version and during similar shifts in version, combined with 10 deg of convergence or divergence (subject CE).

Again, it should be emphasized that in this comparison version demands are equal, and that vergence demands are 0, 10 deg convergence or 10 deg divergence. As a baseline, peak velocities and durations for conjugate saccades are shown (solid lines) in a main sequence plot for version amplitudes from 5 to 65 deg. As expected, the abducting eye (crosses) consistently showed a higher peak velocity and a slightly shorter duration than the adducting eye (triangles). The interocular *differences* (abducting eye minus adducting eye) for the conjugate case are plotted as **▲**. The conjugate baseline graphs are slightly different for the comparisons with convergent and divergent disjunctive gaze-shifts, because in our experiments we usually linked rightward version with convergence and vice versa, and we make the appropriate comparisons with conjugate version in the corresponding direction: many individuals show idiosyncratic differences between main sequence properties of rightward and leftward saccades.

The interrupted lines show the corresponding relations for similar versions combined with 10 deg vergence. In this case the saccadic movement of each eye had a different amplitude (about 5 deg larger or smaller) and a different peak velocity and duration, compared to the conjugate case. The changes are somewhat complex, because there are changes in the absolute velocities and durations of each eye apart, as well as in the interocular differences. For convergence, *both* eyes were slowed down, despite the fact that the overall amplitudes of the movements of the adducting eye were larger than in the
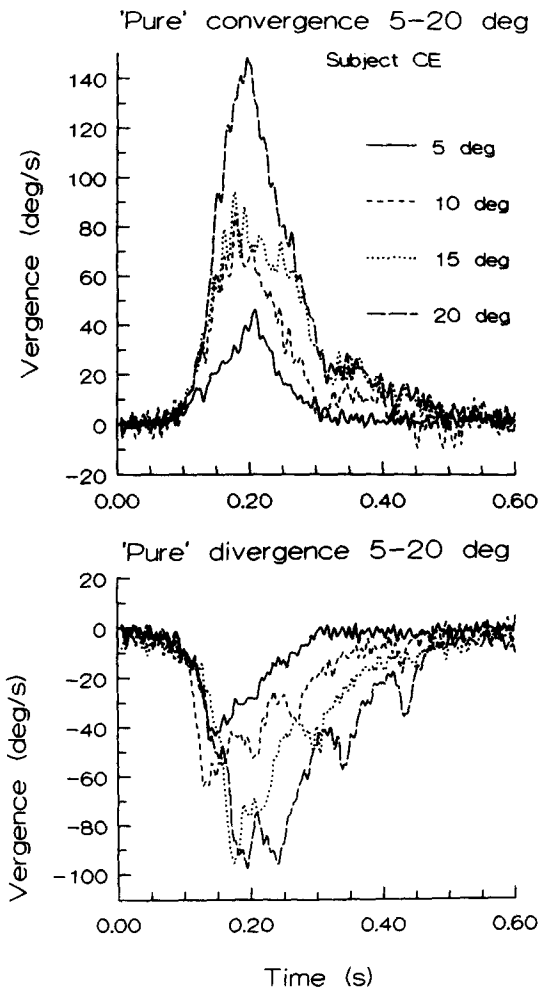

FIGURE 3. Typical profiles of *vergence velocity* during responses elicited by pure vergence stimuli of 5, 10, 15 and 20 deg. For the 5 deg vergence only, near and far stimuli were disambiguated by a vertical offset of 1 deg. Averages of 3–4 responses; vertical bars represent ±1 SD. Subject CE.
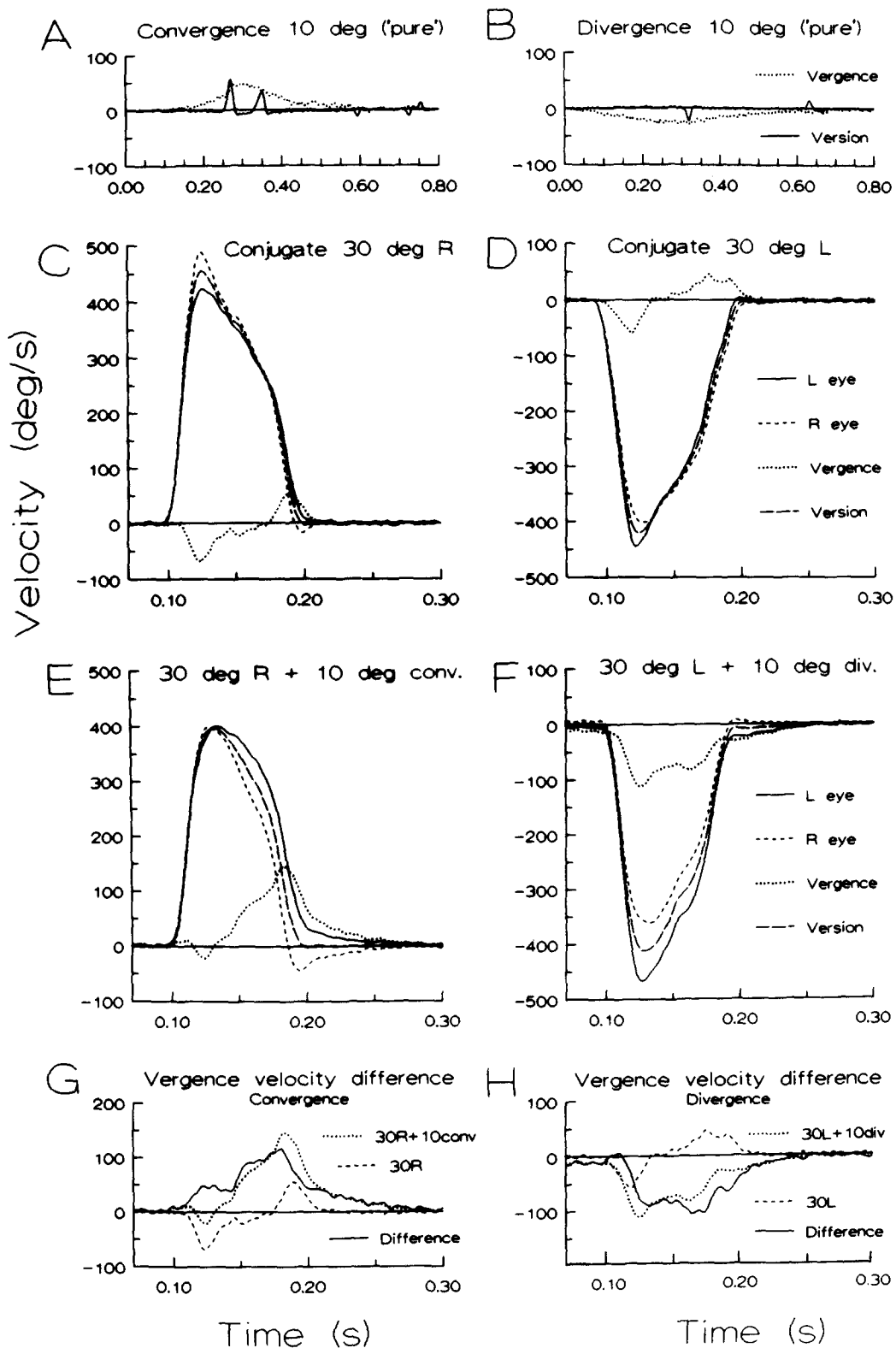
FIGURE 4. Examples of velocity profiles of pure vergence (10 deg; A, B), pure version (30 deg; C, D) and their combination (E, F). Subject ZP. Traces show velocities of right eye, left eye, vergence and version. Each panel shows the average of 3–4 subsequent movements; SDs are not plotted but are very small. (G) and (H) show vergence velocities from the conjugate and disjunctive gaze shifts plotted above, and their difference (disjunctive minus transient, conjugate vergence velocity); see text.

conjugate case. The peak velocities of the eye that converged and abducted were reduced very markedly, by 100 deg/sec or more [Fig. 8(A)]. The peak velocities of the eye that adducted and converged were also reduced, but by a much smaller amount (on the order of 50 deg/sec).

These tendencies existed over the whole range of version amplitudes, although they tended to become smaller for large version amplitudes. As a consequence, the abduction–adduction asymmetry in peak velocity was reversed, and in the convergent case the adducting eye

reached a higher peak velocity than the abducting eye. This reversed difference is plotted as ▼. The interocular differences contribute to disconjugacy; the *change* in this difference (convergent case minus conjugate case) represents the change in the interocular difference in peak velocity when eye movements change from conjugate to convergent. This change in difference in velocity is plotted in Fig. 8 as ◆; it reached values up to about −100 deg/sec.

Convergence also affected the durations of the saccades of each of the eyes [Fig. 8(C)]. For the abducting eye durations were elevated slightly, but consistently, in comparison to the conjugate case. Durations of the fast

movements of the adducting eye were increased more markedly (by as much as 50 msec) during convergence. Thus, while duration was increased for both eyes, the difference in duration that already existed for conjugate saccades (adduction lasting longer than abduction) was magnified (and unchanged in sign) during convergence. Differences in duration and their changes are plotted similarly as for peak velocity in Fig. 8.

For divergence the changes for each eye compared to conjugate gaze-shifts were different from the changes in convergence but, as will be shown, the overall *changes* in the interocular differences in velocity and duration were symmetrical for divergence and convergence. Figure 8(B)
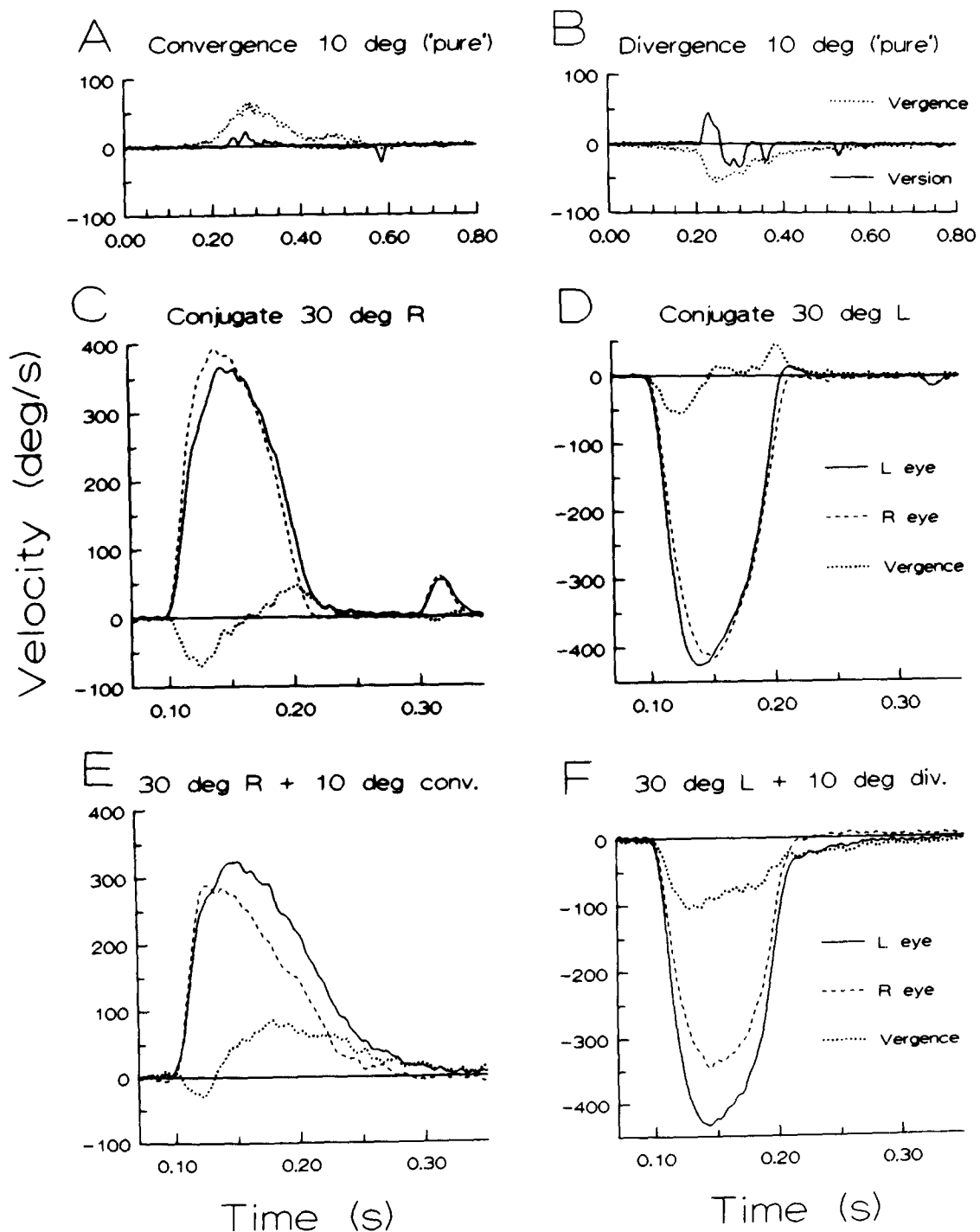

FIGURE 5. Examples of velocity profiles of subject CE. Conventions as in Fig. 4(A–F) (version not plotted).
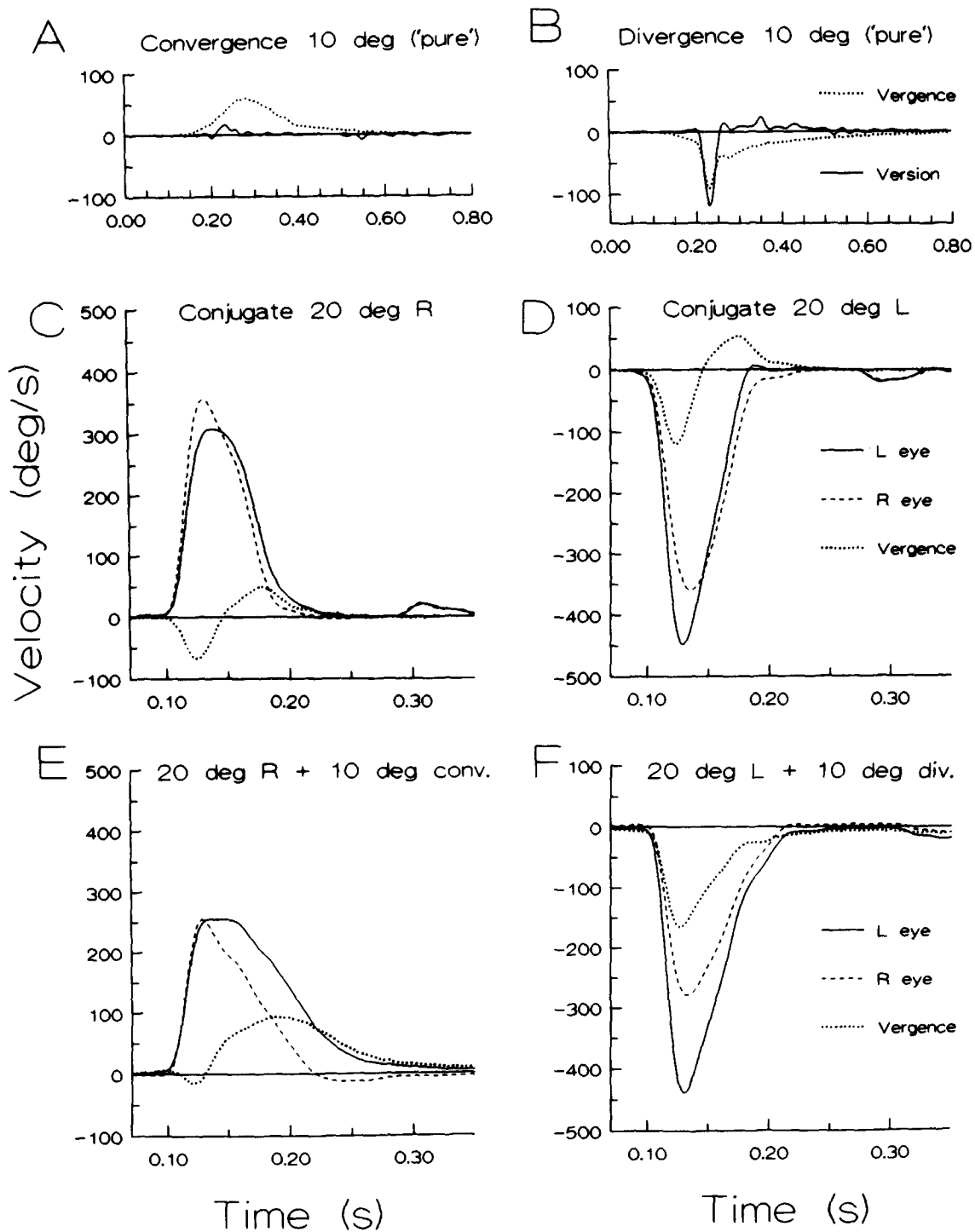
FIGURE 6. Examples of velocity profiles of subject RR. Conventions as in Fig. 4(A–F), except that version amplitude is 20 deg, plots are averages of about 16 subsequent saccades, and version is not plotted.

shows that the abducting eye moved as fast during a divergent disjunctive gaze-shift as during conjugate gaze-shifts. There are even hints (also in other subjects) that the abducting, diverging eye occasionally moved faster than during conjugate abduction. On the other hand, the adducting eye was slowed down considerably during divergence. Thus, the asymmetry in peak velocity existing for conjugate saccades was magnified (without change in sign) when divergence was added to version. The changes in the peak velocities of the individual eyes are different for convergence and divergence with, at the

average, more slowing down during convergence than during divergence. However, the changes in the interocular differences in peak velocity [Fig. 8(A, B) ◆] turned out to be symmetrical for convergence and divergence; in both cases the changes in the velocity difference were on the order of 100 deg/sec (starting from the inherently asymmetrical situation in conjugate saccades).

For duration a similar symmetry was found. The changes in duration of the saccadic components for divergent compared to conjugate gaze-shifts were small

for each eye [Fig. 8(D)]. For the adducting eye durations were slightly elevated during divergence, whereas for the abducting eye there was a stronger increase in duration. As a result, the abduction–adduction asymmetry for duration in conjugate saccades was reversed (without much change in magnitude) during divergent, disjunctive gaze-shifts. The changes in the interocular asymmetries in duration, starting from the conjugate condition, turned out to be symmetrical for convergence and divergence [Fig. 8(C, D) ◆].

These trends are confirmed by a cross-section through our five subjects, shown in Fig. 9. In this diagram we show means and SDs for the case of 30 deg version, conjugate or combined with 10 deg vergence; a combination which seems well within the range of daily routine behavior. The bars represent peak velocities and durations of each eye

and their differences (abducting minus adducting eye); the changes in these differences due to additional convergence and divergence are marked by the horizontal, interrupted lines. (Average values of rightward and leftward conjugate saccades are plotted in this diagram.) The following main conclusions are supported by Fig. 9: (i) In *conjugate* version the abducting eye has a higher peak velocity and a shorter duration than the adducting eye (Fig. 9, left group of bars). (ii) With additional *convergence* both eyes are slowed down, but the abducting eye much more so than the adducting eye. As a result, the interocular velocity asymmetry is inverted. The duration of the saccade increases only slightly for the abducting eye, but markedly for the adducting eye, and the duration asymmetry is enhanced (Fig. 9, middle group of bars). (iii) With additional *divergence* only the adducting eye is slowed down, and the conjugate asymmetry in velocity is enhanced. Duration increases for both eyes, but especially for the abducting eye, and the conjugate duration asymmetry is inverted (Fig. 9, right group of bars). (iv) The overall shifts in interocular asymmetry of peak velocity and duration are symmetrical for convergence and divergence but because these are superimposed on asymmetrical values in conjugate saccades, the overall result is that, in disjunctive gaze-shifts, convergence is predominantly achieved by a longer duration of the saccade of the adducting eye, while divergence is mainly achieved by a lower velocity of the adducting eye. As differences in peak velocity occur early in the saccade, while differences in duration (after a simultaneous beginning) occur at the end, one should expect that intrasaccadic divergence is effected early in the saccade, and intrasaccadic convergence late. This tendency is indeed evident in Figs 4–6 and will be elaborated upon later.

Changes in V_{max} and Duration (Constant Eye Amplitude)

The preceding comparisons of peak velocities and durations between conjugate and disjunctive gaze-shifts were made for comparable version amplitudes; the additional vergence, however, affected the sizes of the movements of the individual eyes, and a strict comparison of the dynamics of each eye requires that these changes are taken into account. This can be done by comparing velocity profiles in which the same eye makes a movement of the same actual size as part of a conjugate or disjunctive gaze-shift, or by plotting main sequence parameters as a function of the actual size of the movements. The first approach is exemplified in Fig. 10, in which movements of the same eye are superimposed that had the same amplitude, but were obtained in different trials, requiring either conjugate or disjunctive gaze-shifts *with actual amplitudes matching for the single eye shown*. All possible combinations of abduction or adduction (as part of version) and convergence or divergence are shown.

The grouping of the combinations was done after considering some hypothetical expectations for the interaction between version and vergence. For example, adduction together with convergence, as well as abduction together with divergence, would appear to
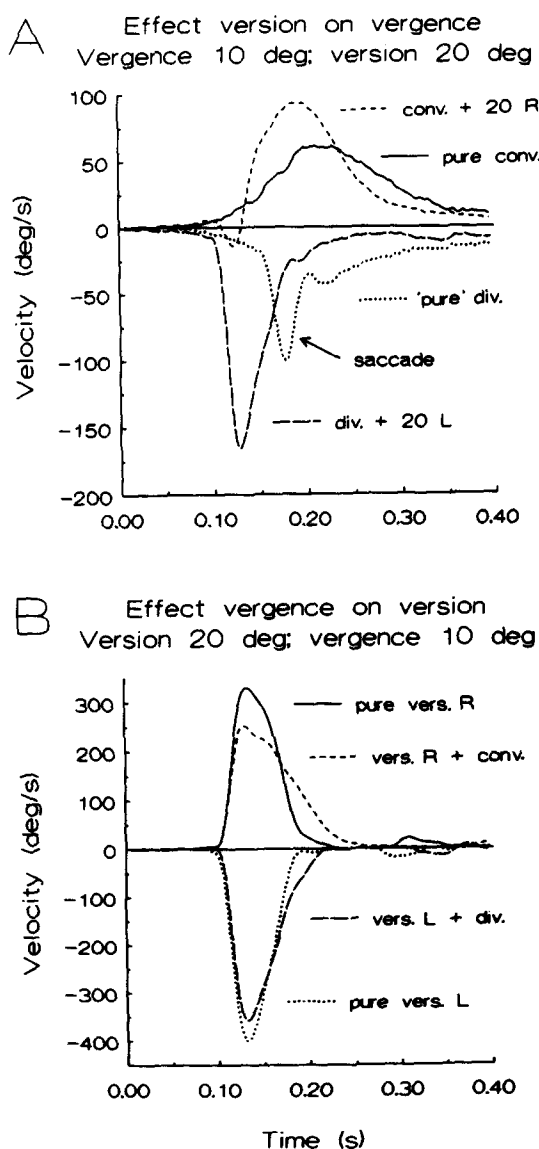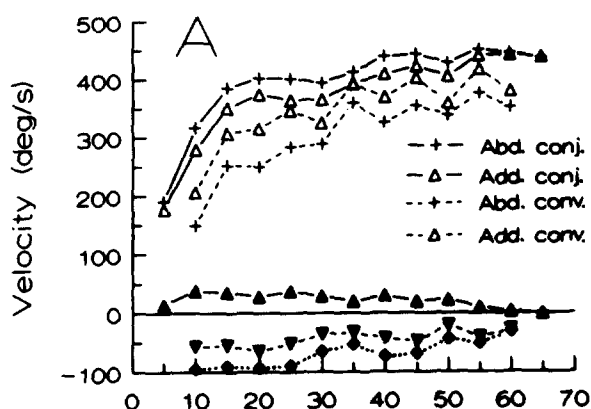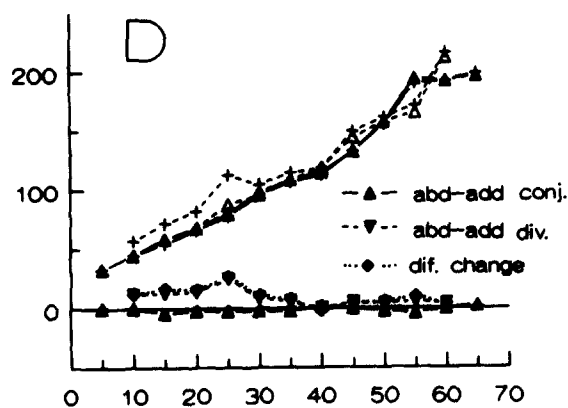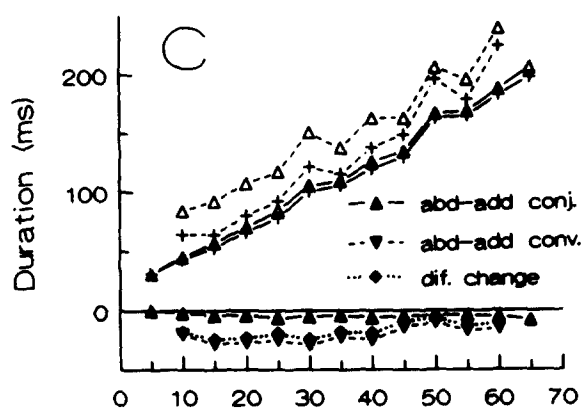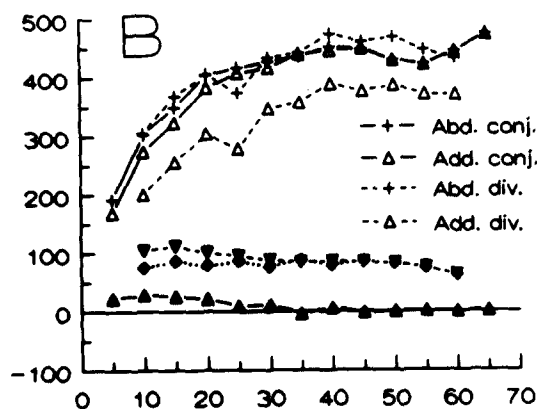
FIGURE 7. Representative plots showing the effects of (A) version on vergence velocity, and (B) vergence on version velocity. Subject RR. (A) Notice that pure divergence is accompanied by a saccade which speeds up divergence, but that a 20 deg version accelerates divergence much stronger. Convergence is also accelerated by the 20 deg version, but notice that initial divergence already intrudes at this version amplitude. (B) Version is slowed down by vergence, especially by convergence, compared to conjugate, pure version.

FIGURE 8. Peak velocity and duration of the saccadic movements of each eye during saccades that are conjugate (solid lines) or disjunctive (10 deg convergence or divergence; interrupted lines). The abducting eye is denoted by + symbols, the adducting eye by △. Various interocular differences are plotted as solid symbols; see text for explanation. All data in this comparison are plotted as a function of the version stimulus size, not as a function of the actual size of the individual eye movements.

require similarly directed motion of an eye. One might call these "synergistic" combinations, and one might expect that such movements would be relatively fast and short in duration. On the other hand, the combinations abduction + convergence, and adduction + divergence, might be considered "antagonistic" because each of the components by itself would require eye movements in opposite directions. One might expect such combinations to result in relatively slow movements with longer duration. Figure 10, which is representative for the results as a whole, shows that these expectations were only partially fulfilled. Figure 10(A) shows movements of a right eye (subject RR) all of which have an amplitude of 14 ± 1 deg. Such movements as part of conjugate saccades are compared with the theoretically, antagonistic combinations. (For the conjugate movements targets were separated by 15 deg; for the disjunctive movements, movement from the left to the right target required 20 deg of version and 10 deg convergence, and vice versa; the actual saccadic eye movements fell, as usually, slightly short of the targets.) In both combinations (abduction + convergence and adduction + divergence), the eye movement had a lower peak velocity and longer duration

than in the corresponding conjugate deviation with the same amplitude. Figure 10(B) shows movements of a left eye (subject RR), matched for amplitudes of 23 ± 1 deg in which conjugate movements are compared with, theoretically, synergistic disjunctive combinations. (For this comparison conjugate movements were made between targets separated by 25 deg; the disjunctive targets were the same as in the previous case.) The combination adduction + convergence turned out to be, like the previously discussed combinations, much slower and longer than the corresponding conjugate movement. Abduction + divergence proved to be the only combination that was consistently virtually equal in peak velocity and duration to a corresponding conjugate movement of the same eye with the same actual amplitude.

A more systematic demonstration of these effects is shown in the main sequences of Figs 11 and 12, for subject CE. Peak velocities and durations of one eye are shown as a function of the actual amplitudes (reached within the period in which speed exceeded 50 deg/sec). Conjugate movements are compared with disjunctive movements with vergence components of 5, 10 and 15 deg. Figure 11
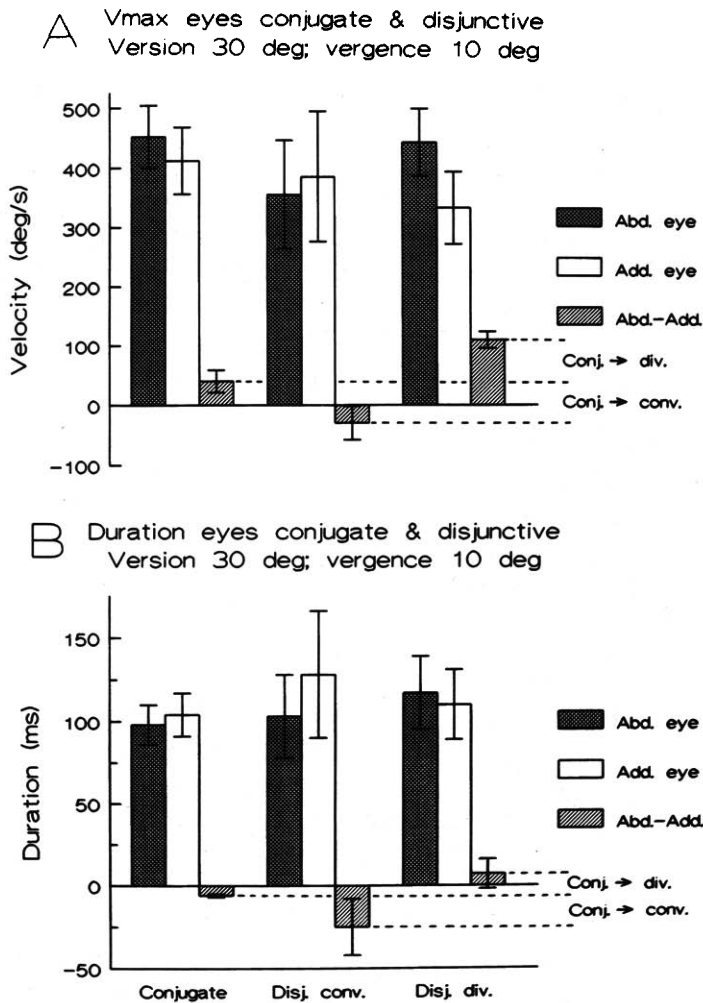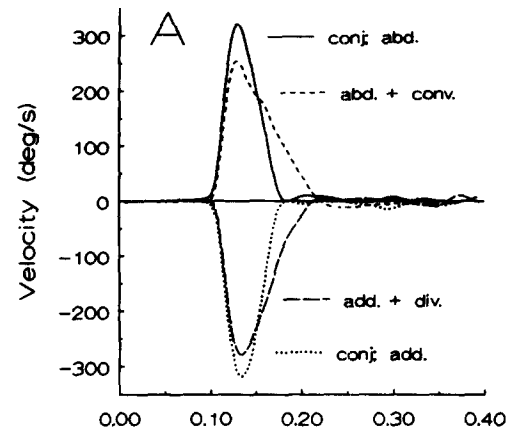
FIGURE 9. Peak velocities and durations for the abducting eye, the adducting eye, and their differences, for conjugate, convergent disjunctive and divergent disjunctive saccades of 30 deg. Means ± 1 SD for five subjects. The graph shows the basic asymmetries for conjugate saccades, and the changes in this asymmetry when the same version is combined with 10 deg convergence or divergence. The *changes* from the conjugate values for peak velocity and duration are symmetrical for convergence and divergence; because velocity and duration are already disjunctive in conjugate saccades, the disjunctive saccades contain a new asymmetry. During divergence the eyes differ mainly in velocity; during convergence the two eyes differ mainly in duration.
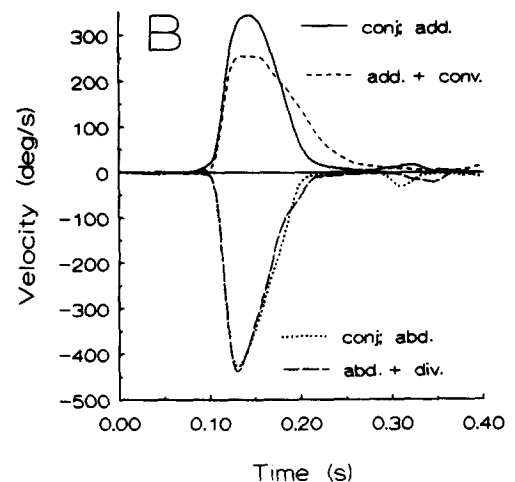

FIGURE 10. Pair-wise comparisons of velocity profiles movements of the same eye, matched for similar *actual* amplitudes, made as part of a conjugate or disjunctive movement. Subject RR. (A) Disjunctive combinations that would drive the eye in opposite directions (antagonistic; abduction + convergence; adduction + divergence). (B) Combinations driving the eye in similar, synergistic directions. The eye is slowed down in all disjunctive movements, compared to conjugate movements, with the exception of the combination abduction + divergence, which is as fast as (and occasionally even faster than) a similar conjugate movement.

shows the antagonistic combinations abduction + convergence and adduction + divergence; Fig. 12 shows the synergistic combinations adduction + convergence and abduction + divergence. These figures confirm the trends discussed above in Fig. 10: saccadic components (compared for equal actual amplitudes) were slowed down and prolonged in duration for all disjunctive combinations compared to conjugate saccades, except for the combination abduction + divergence [Fig. 12(B, D)], in which the disjunctive component did not slow down (and occasionally even slightly accelerated) the saccadic eye movement. The effect was progressive with vergence amplitude. The magnitudes of the reduction in peak velocity and extension of duration increased systematically when vergence amplitudes rose from 5 to 15 deg. These trends confirm those described previously with respect to Fig. 8, which were, however, uncorrected for *actual* eye amplitudes. Clearly, the effects of vergence on

saccadic dynamics are quite robust and not sensitive to moderate mismatches in saccadic size. That this should be the case is in fact apparent from Fig. 8 and Figs 11 and 12 because the velocity reductions extend throughout the amplitude range, affecting also the peak velocities in the right parts of the graphs, were peak velocities tend to saturate. Obviously, such differences in saturation levels cannot be compensated by shifting the "disjunctive" graphs along the amplitude axis, which is what amplitude correction amounts to. Clearly, the negative effects of simultaneous vergence on saccadic eye movement dynamics are not limited to saccades that are relatively small compared to the size of the vergence. Figs 11 and 12

show that even a 5 deg vergence movement (i.e. 2.5 deg for each eye) severely reduced peak eye velocities (except for the combination abduction + divergence) throughout the amplitude range, up to the largest saccades measured (around 60 deg). There is no trend for the various graphs to converge at higher amplitudes. On the contrary, any convergence appears to occur for *small* saccades; this trend is apparent for the antagonistic combinations in Fig. 12, for both peak velocities and durations. For the synergistic combinations (Fig. 12), the course of the several graphs appears to be more or less parallel. These trends are especially clear for the durations.

Effects of Vergence on Version

As we demonstrated above, the movements of each eye slow down when vergence is added to version (except for the combination abduction + divergence, for which the eye remains equally fast), it follows logically that version as a whole (the average movement of the two eyes) is slower for disjunctive than for conjugate gaze-shifts. A first example of this is shown in Fig. 7(B) (subject RR). While Fig. 7(A) shows clearly the acceleration of a 10 deg vergence by 20 deg version, Fig. 7(B) shows that for the same disjunctive combinations version has a substantially lower peak velocity and longer duration than is the case for a conjugate version of 20 deg. Especially convergence appears to result in a lower velocity of version.

Figure 13 shows similar examples from a different subject (CE) for a variety of version amplitudes (20, 40 and 60 deg) in combination with 10 deg convergence or divergence. These examples confirm that version is systematically slowed down by vergence, especially by convergence, and that this effect extends over the whole oculomotor range. The effects of a 10 deg vergence are equally evident for a 60 deg version as for a 20 deg version. This is further corroborated by the main sequence diagrams of Fig. 14 (subject CE), in which peak velocities and durations of conjugate vergence are compared with the corresponding values during 5, 10 and

FIGURE 11. Peak velocities and durations of individual eyes (abducting and adducting) as a function of actual amplitude of its movement, for conjugate and disjunctive movements (vergence 5, 10 or 15 deg). Antagonistic directions of vergence and version; see Fig. 10 and text. Subject CE.
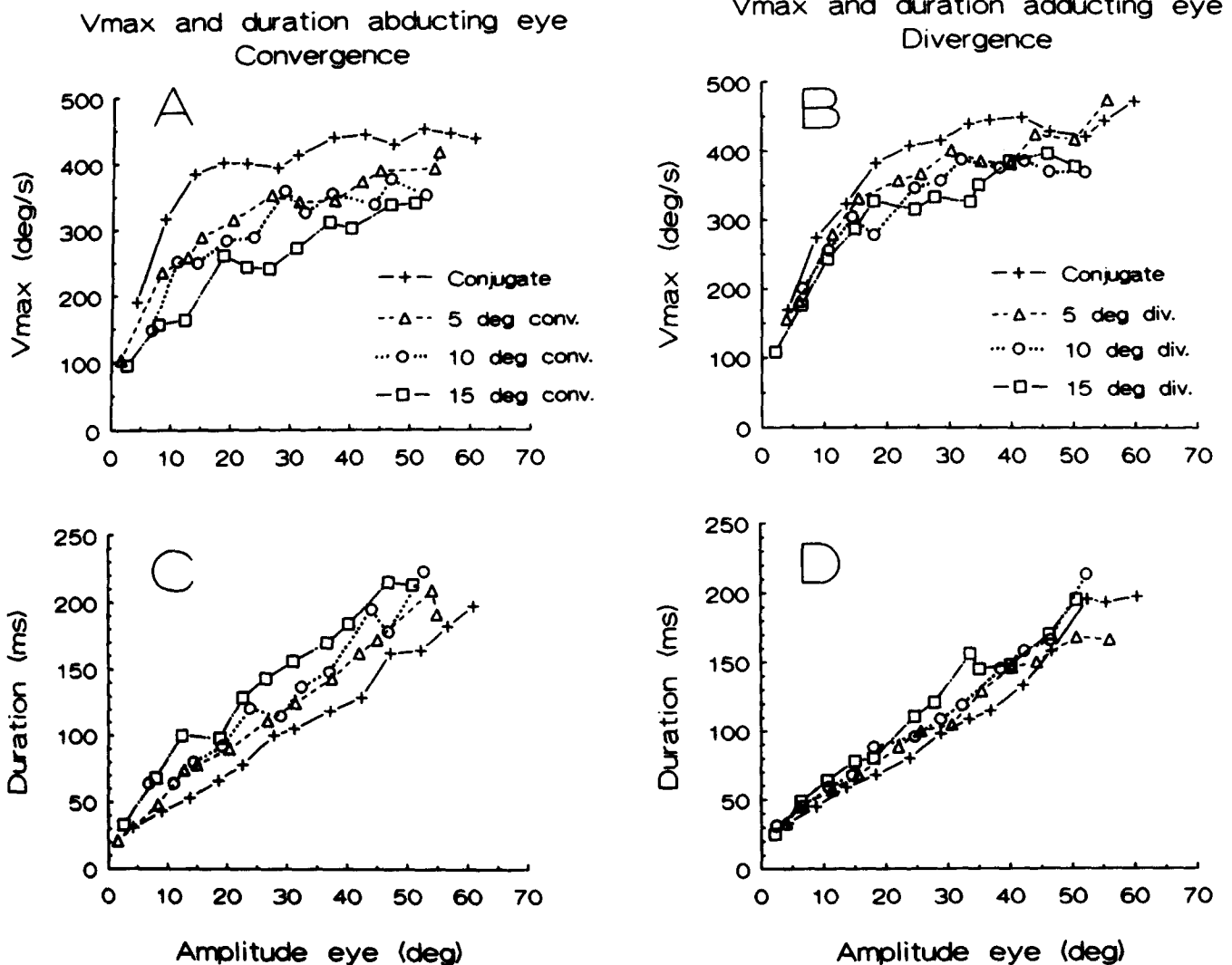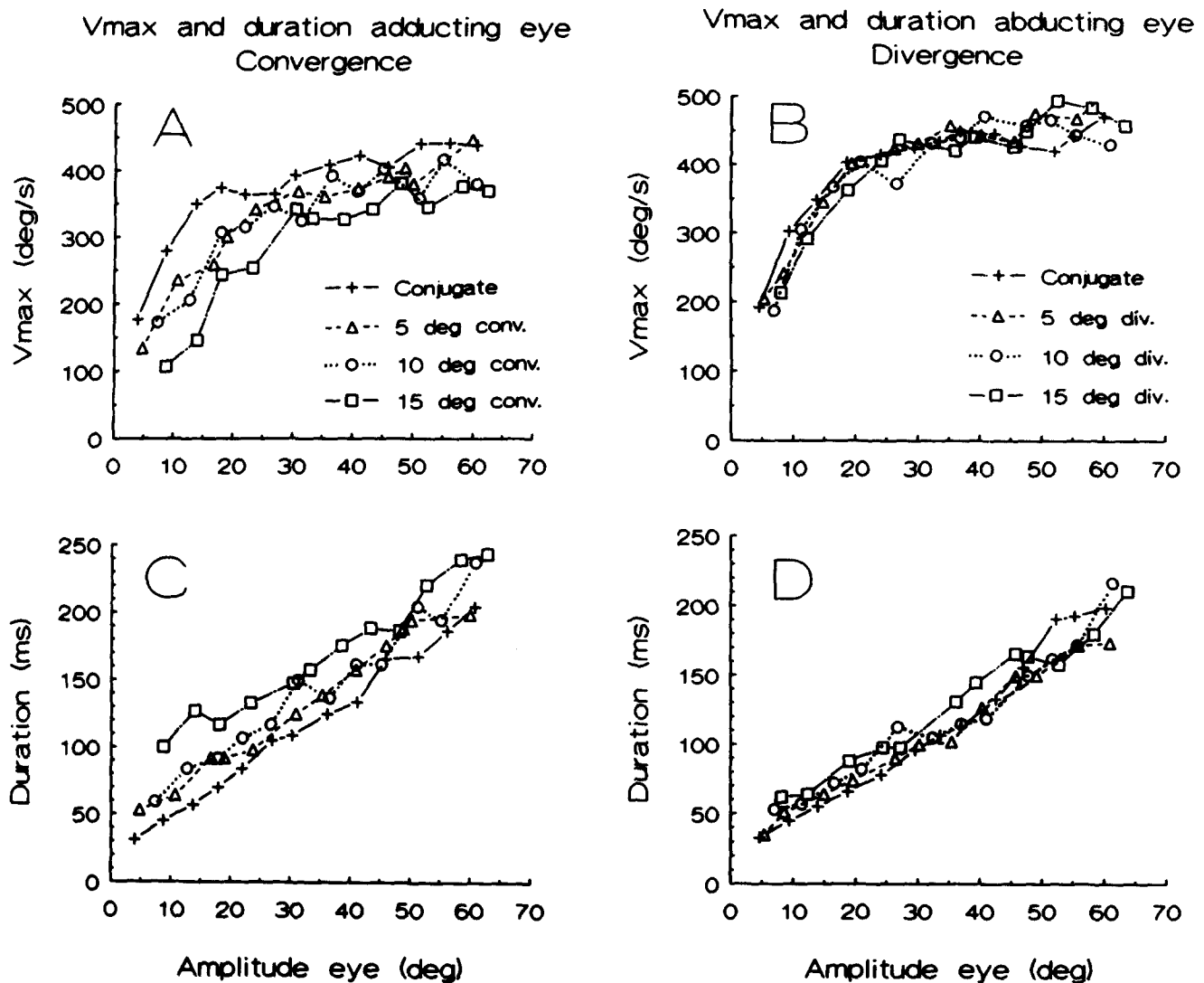
FIGURE 12. Peak velocities and durations of individual eyes (abducting and adducting) as a function of actual amplitude of its movement, for conjugate and disjunctive movements (vergence 5, 10 or 15 deg). Synergistic directions of vergence and version; see Fig. 10 and text. Subject CE.

15 deg of convergence [Fig. 14(A, C)] or divergence [Fig. 14(B, D)].

Figure 14 amounts to an "average" between the behavior of the individual eyes shown in Fig. 11 and Fig. 12. It shows that version is slower in the presence of vergence and that this effect extends over the whole range of version, and also that it becomes systematically stronger as the vergence angle increases. The effects of convergence are much stronger than those of divergence. These effects were confirmed for each of our five subjects.

The Effects of Version on Vergence

We shall now examine in greater detail how the dynamics of vergence are affected by concomitant version. In particular, we want to see how peak velocity and duration of vergence change as a function of the magnitude of version. We show the main effects in two figures. Figure 15 shows representative (subject CE) position and velocity plots of *vergence* for 10 deg convergence (A, D), 10 deg divergence (B, E) and for conjugate version (C, F). (All movements started at

$t = 0.1$ sec). Version amplitudes varied between 0 and 60 deg. Figure 16(A, C) shows the peak velocities of the convergent (A) and divergent (C) components of the transient vergence associated with conjugate saccades (+ symbols), as well as the peak vergence velocities of disjunctive gaze-shifts with 5, 10 and 15 deg convergence or divergence (same subject, CE).

Transient vergence in conjugate saccades

First, we shall examine the transient vergence associated with conjugate version. These transient vergence movements show a typical evolution as a function of increasing version amplitude. The initial divergence showed an increase in peak velocity when version amplitude increased from small to intermediate sizes. A maximum divergent velocity was reached for saccades of about 40 deg. For larger saccades, transient divergence peak velocity became smaller again [Figs 15(F) and 16(C), lower trace]. These changes in the magnitude of divergent peak velocity occurred without a substantial

shift in the timing of the divergence peak velocity [Fig. 15(F)]. The durations of the transient divergent (negative) velocity profiles varied about proportionally with the peak velocities. As a result, the amplitude of the transient divergence [Fig. 15(C)] increased for saccades up to about 40 deg but tended to decrease again for larger saccades. The evolution of the convergence movement, following the transient divergence, was different. For small saccades (up to 10–20 deg), the convergent velocity profiles were approximately symmetrical with those of the divergent movement. For increasingly large conjugate saccades, there was a downward trend in the peak velocity of convergence, so that for 40–60 deg saccades transient convergence was only about half as fast as transient divergence [Figs 15(F) and 16(A, C)]. Moreover, the velocity peaks of transient convergence occurred progressively later with the increase in saccadic size and, correspondingly, the duration of the transient vergence was progressively extended [Fig. 15(F)]. This pattern of transient divergence as a function of version amplitude, found—with some minor individual variations—in all subjects, is treated in some detail because it leaves clear

Effect of convergence on version

Effect of divergence on version

Time (s)

FIGURE 13. Representative examples of version velocity profiles in conjugate and disjunctive gaze-shifts, to show the systematic slowing of version by vergence. Subject CE.

fingerprints in the vergence movements in disjunctive gaze-shifts.

Effects of version on convergence

Typical convergence movements (amplitude 10 deg) with concomitant version movements of 0, 20, 40 and 60 deg are shown in Fig. 15(A, D). The beginnings are aligned at $t = 0.1$ in the figures. (The beginning of the pure vergence movements was defined as the time at which convergence velocity exceeded 5 deg/sec.) The pure convergence movement (continuous lines) was robust, free of saccades and had a peak velocity of about 80 deg/sec. In combination with a 20 deg version movement, convergence peak velocity was increased, and the end position of convergence was reached somewhat earlier. Thus, a 20 deg change in version made a 10 deg convergence faster and shorter than a pure convergence. For a 40 deg saccade this was, overall, still the case but we see that the convergence was preceded by a divergence. The latter was even more manifest for a 60 deg version, which induced an initial divergence of comparable size (about 1.5 deg) and duration (> 100 msec) as in a similar conjugate saccade before the required convergence movement starts. The peak velocity of this convergence was even lower than for pure vergence. A comparison of the vergence velocity profiles for disjunctive convergent and conjugate movements [Fig. 15(D, F)] shows a remarkable resemblance. The initial divergence peaks of conjugate saccades penetrated, although at a reduced size, into the convergent, disjunctive velocity profiles. Complete suppression or cancellation of initial divergence occurred only for the smaller shifts of version. The saccadic size at which divergence started to creep in depended on a trade-off between the divergence drive associated with the version shift and the convergence drive; large convergence stimuli (e.g. 20 deg) overcame the initial divergence for a larger range of version than smaller convergence drives (not illustrated). Also the distribution of velocity peaks during the convergent part of the gaze-shifts [Fig. 15(D)] bears a strong resemblance to those during conjugate saccades [Fig. 15(F)].

More specifically, comparison of these panels suggests that the increases in convergence velocity in disjunctive vs pure convergence were roughly equal to the magnitudes of the corresponding convergence velocity peaks in conjugate saccades. This point is further supported by Fig. 16(A), in which the shape of peak transient convergence velocity in conjugate saccades (+ symbols) as a function of version amplitude can be recognized in all the graphs of peak convergence velocity in disjunctive gaze-shifts. (Values for zero version represent responses to pure convergence stimuli). As a quantitative test, a fourth-order polynomial was fitted through the conjugate peak convergence velocity data [Fig. 16(A), solid line] and the corresponding conjugate values were subtracted from the disjunctive peak convergence velocities. The result is shown in Fig. 16(B). Subtraction of the inherent, transient peak convergence velocity associated with conjugate version abolished, in this subject (CE), any gain in peak
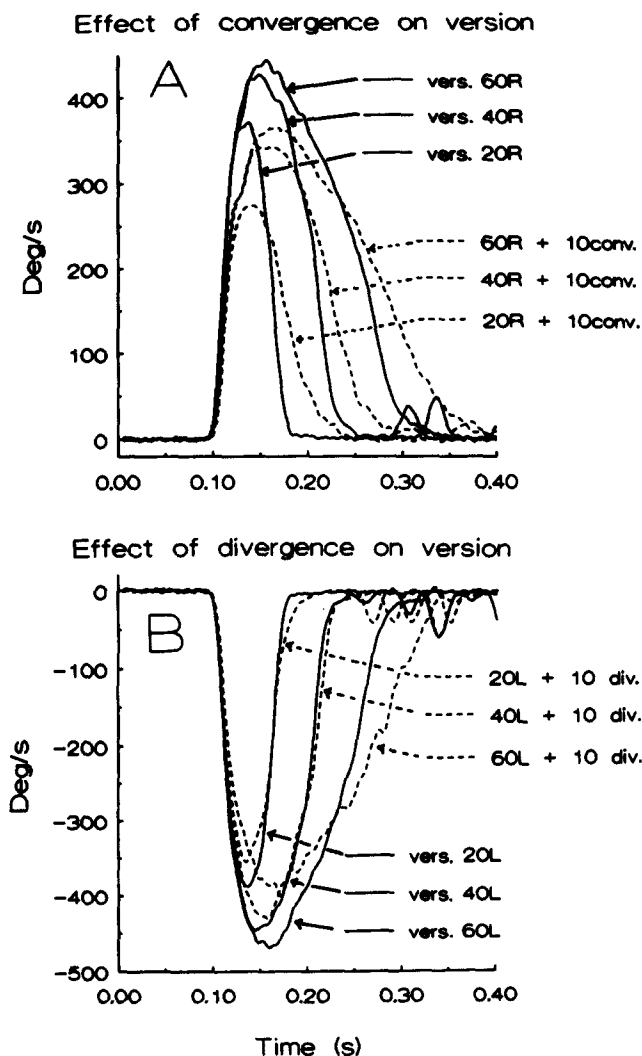
Vmax and duration version
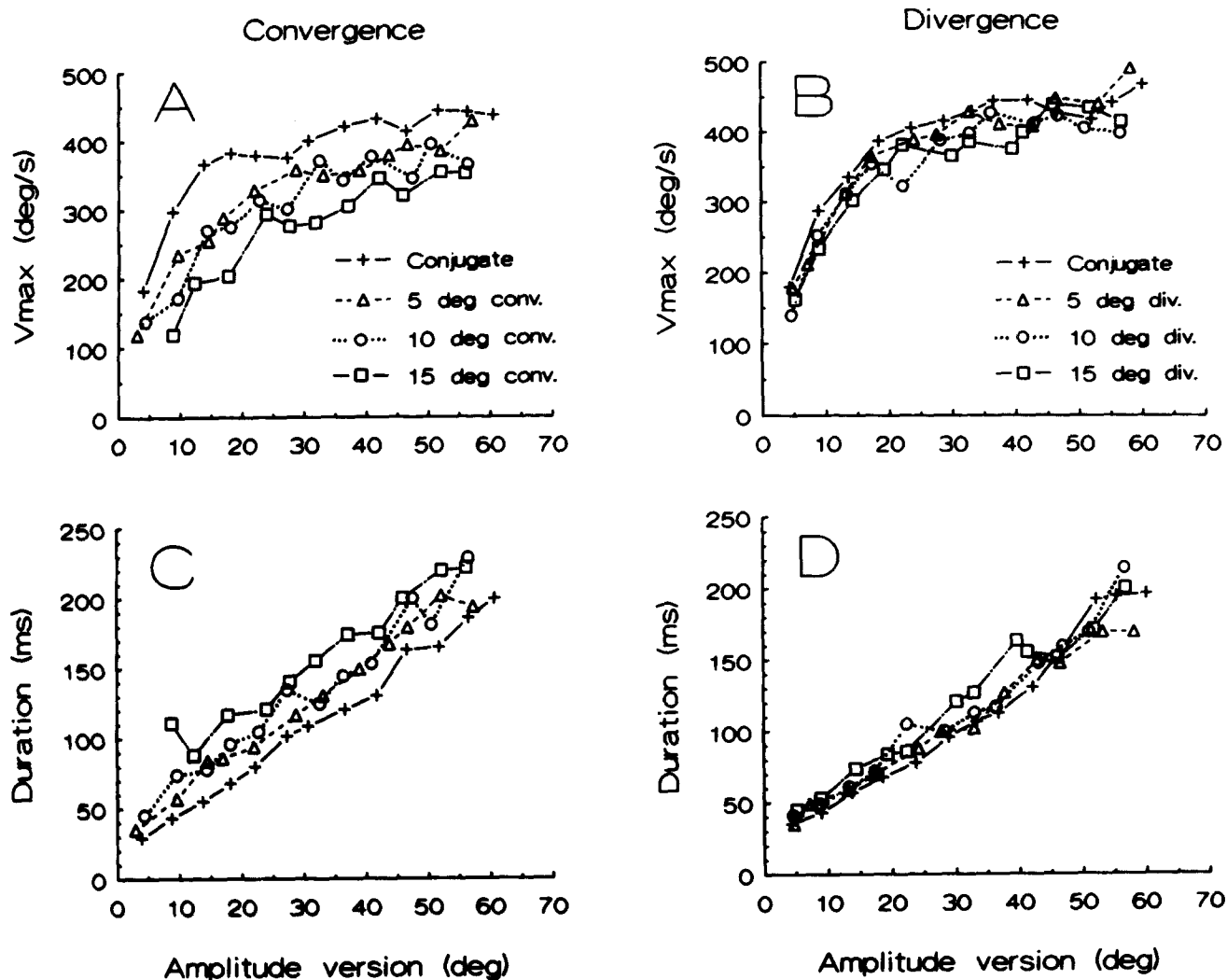
Convergence

Divergence

FIGURE 14. Peak velocities and durations of version (the averaged motion of the two eyes), during conjugate and disjunctive gaze-shifts (vergence 5, 10 or 15 deg). Peak velocities are lowered and durations are increased during disjunctive gaze-shifts, especially during convergence, compared to conjugate saccades. Subject CE.

convergence velocity in disjunctive gaze-shifts compared to pure vergence. Actually, the accelerating effect appeared to be even reversed in this subject: the difference velocity values tended to be lower than the velocities of pure vergence (version = 0).

A more complete evaluation of conjugate vs disjunctive peak convergence velocities is shown in Fig. 17, in which average values (and some representative SDs) are presented for the three subjects for whom all the required data were collected. Figure 17(A) is similar in form to Fig. 16(A), except that version *demands* are plotted instead of the actual version values to facilitate pooling of different subjects, and that version values > 40 deg have been disregarded because performance for very large gaze-shifts was somewhat variable. (Specifically, vergence was often inadequate in very eccentric gaze positions.) The peak velocities of responses to pure vergence stimuli (zero version) show a systematic increase as a function of vergence amplitude (5, 10, 15 or 20 deg), with relatively small SDs (for 5 deg convergence: smaller than the

symbol). The general trend for these peak velocities is to increase with increasing vergence, with some levelling between 20 and 40 deg version. Average transient convergence velocities for conjugate saccades are shown for comparison (+ symbols). Inspection of Fig. 17 corroborates that peak convergence velocities can be *approximately* accounted for by addition of the corresponding peak velocities of pure convergence and the peak velocities of the transient convergence of pure version. The most notable exception are the relatively low peak convergence velocities for 15 and 20 deg convergence with 10 deg version. In these cases version was of comparable size as the vergence component in one eye, and this could be a borderline situation in which the effects of version on vergence become marginal. Similar exceptions can be noticed in Fig. 16(A).

It should be emphasized that the comparisons of peak velocities in Figs 16 and 17 disregard time, and that the peak velocities that are compared do not necessarily occur at identical times after the start of the gaze
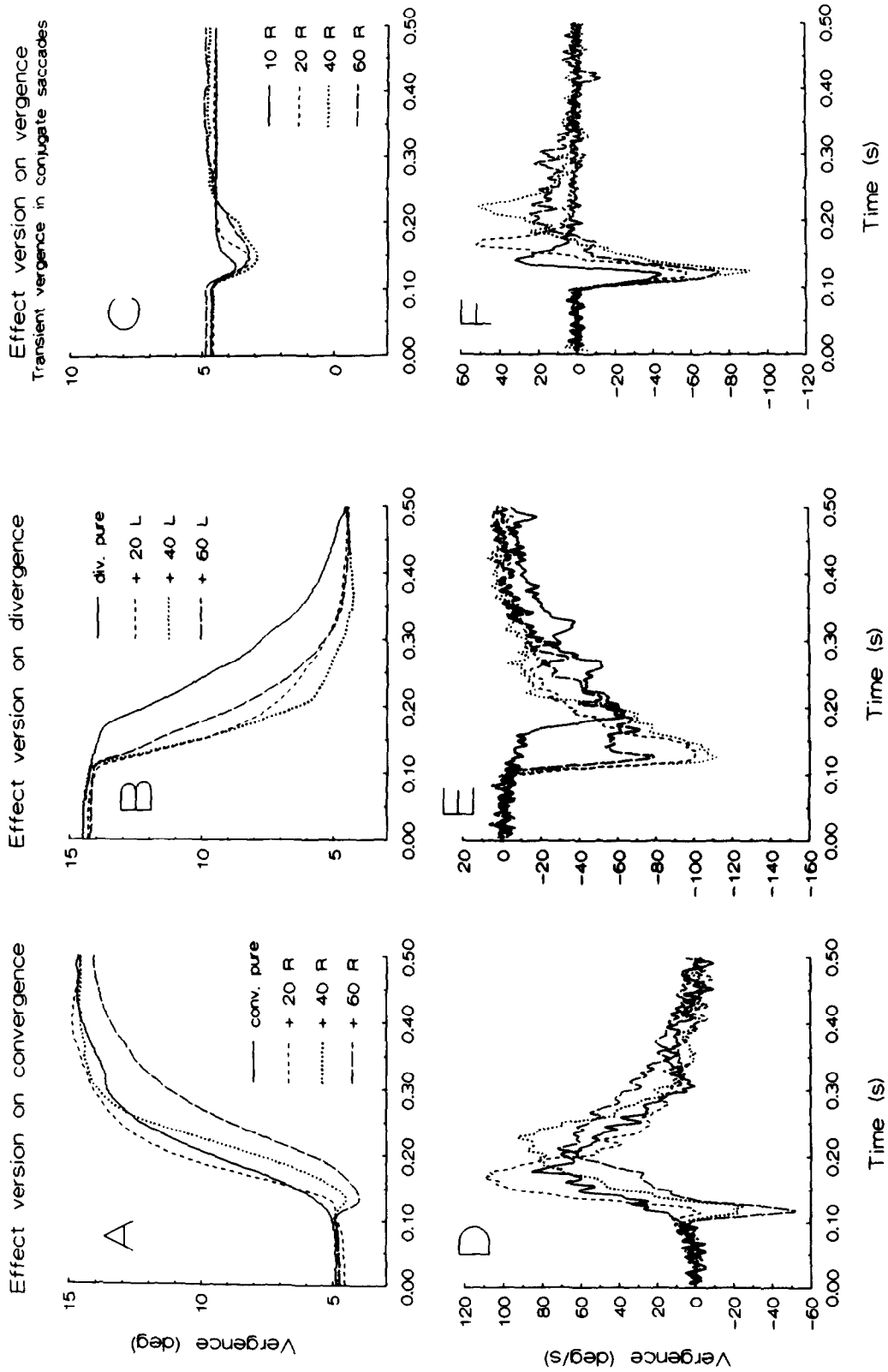
FIGURE 15. Typical plots of vergence position and velocity during convergent (A, D), divergent (B, E) and conjugate (C, F) gaze-shifts. Version is 0 (pure vergence) or 10–60 deg. See text. Subject CE.
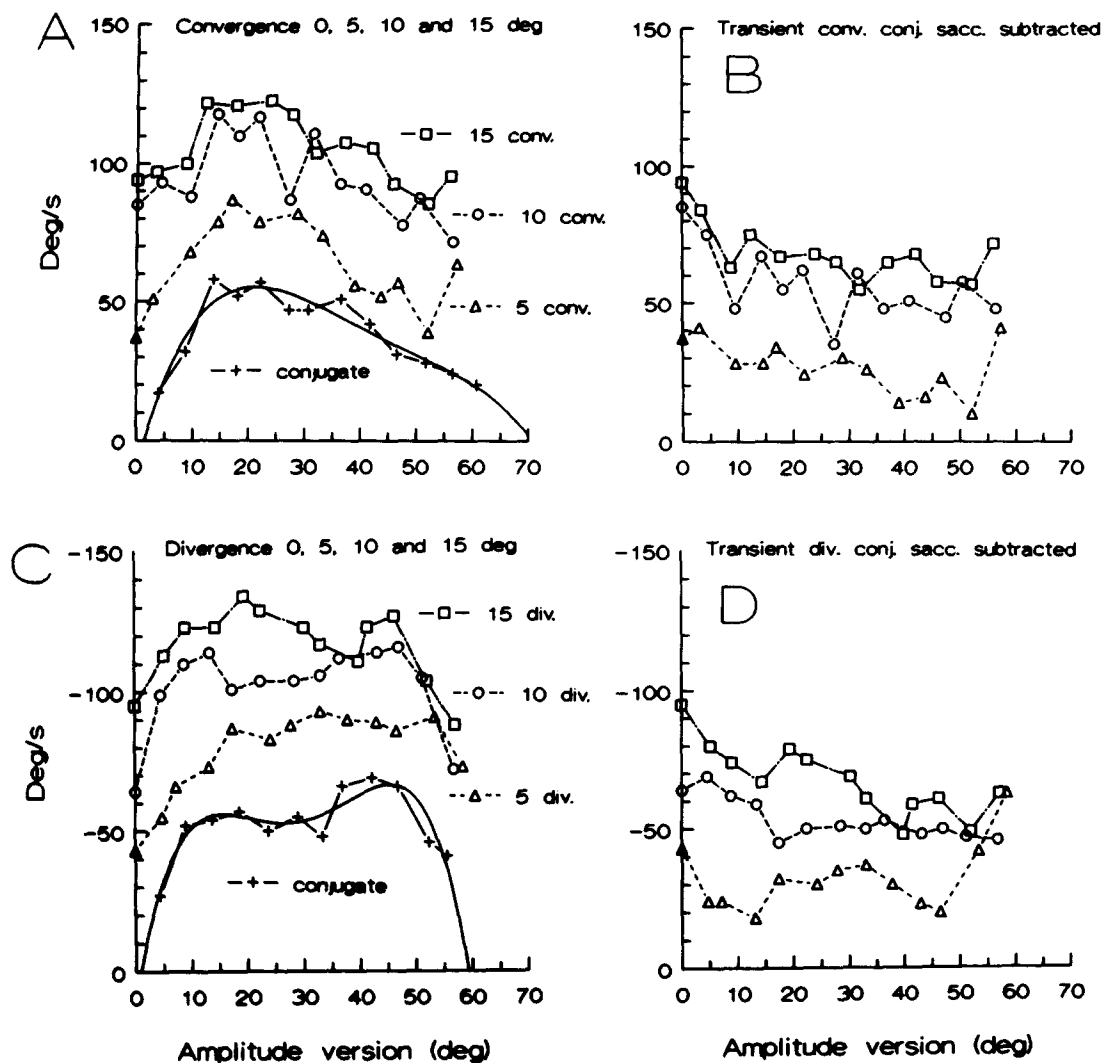
FIGURE 16. Peak velocities of convergence (A) and divergence (C) for disjunctive gaze-shifts with vergence components of 5, 10 or 15 deg, as a function of actual version amplitude. For comparison the peak velocities of transient convergence in conjugate saccades are plotted in (A), and the peak velocities of transient divergence in conjugate saccades in (C). These conjugate graphs have been fitted with fourth-order polynomial to obtain a continuum of values; subtraction of the appropriate transient convergent or divergent velocities of conjugate saccades from the disjunctive graphs leads to diagrams (B) and (D). After this subtraction, increases of vergence velocities above the baseline values for pure vergence (zero version) are abolished.

movement. A comparison respecting time relations could, in principle, be made by simply subtracting conjugate vergence records from disjunctive vergence records with similar version components. We showed such a subtraction (for subject CE) in a preliminary report (Fig. 3 in Collewijn et al., 1994). It is now clear, however, that such a procedure is, in general, problematic because the durations of conjugate and disjunctive version shifts are systematically different, so that the mutual temporal relations become fuzzy. In one of our subjects (ZP) these changes in duration were, as an exception, quite small while the effects of version on vergence were robust and large. For this subject only, we do show the results of a subtraction procedure (disjunctive minus conjugate, transient vergence velocity) in Fig. 4(G, H). Comparison with Fig. 4(A, B) shows that subtraction of the "transient" component does not abolish the advantage of intrasaccadic vs pure vergence.

We have now seen that peak convergence velocities are systematically increased by simultaneous version of intermediate sizes, possibly by incorporating the transient convergence inherent to horizontal saccades. On the other hand, the preceding transient divergence associated with horizontal saccades penetrates only incompletely in disjunctive gaze-shifts. On balance, therefore, the average velocity of convergence should increase when version is added. More direct proof of the accelerating effect of version on convergence, however, should be found in an earlier accomplishment of the required vergence. In this respect, the duration, as defined by the 90% amplitude criterion, is the best evidence. These durations of convergence have been plotted in Fig. 17(C). On the whole, durations (90%) are indeed reduced when version increases from 0 to 20 deg. For 40 deg version further advantage in time is questionable, no doubt due to the delay by the intruding divergence [Fig. 15(A)]. In this

perspective the benefits of version to convergence turn out to be quite modest. Despite the rather impressive increases in peak convergence velocities [Fig. 17(A)], the gain in time at which convergence is accomplished is only on the order of 100 msec at the optimal version amplitude (20 deg). The timing advantage is remarkably similar for the different vergence angles for version up to 20 deg. Obviously, a time advantage of 100 msec is relatively larger for a 5 deg convergence, with a baseline duration of 227 msec, than for a 20 deg convergence, with a baseline duration of 418 msec.

A final way to look at the enhancement of convergence by saccades is to examine the percentage of the *total* achieved vergence that is accomplished within the duration of the version saccade (defined by the 50 deg/sec criterion). These percentages (average values of three subjects) are plotted in Fig. 18(A). They vary from about 40% for 10 deg version to about 60% for 40 deg version. In general, the percentage of intrasaccadic vergence is larger for small vergence demands than for large demands. The upward trend in Fig. 18 is the resultant of two cooperating factors. Firstly, the durations of convergence

are truly reduced by version (Fig. 17). Secondly, the duration of disjunctive version saccades increases linearly with their amplitude (Fig. 14). This latter factor obviously does not represent a true improvement of vergence dynamics. It is clear from Fig. 18 that, in general, only about half of the required convergence is accomplished within the duration of the version saccade.

Effects of version on divergence

The effects of version on divergence largely parallel those discussed above extensively for convergence, but there are a number of differences that make the dynamics faster for divergence. Representative examples are shown in Fig. 15(B, E) (10 deg divergence with 0–60 deg version). Again, gaze responses are aligned to start at $t = 0.1$ by the criteria defined above for convergence. As discussed before, to show "pure" divergence is problematic, because every divergence movement was accompanied by some saccades. [For one of our purest recordings see Fig. 4(B), in which divergence has a very low velocity and very long duration.] Thus, even the pure divergence in Fig. 15 shows some saccadic influence,
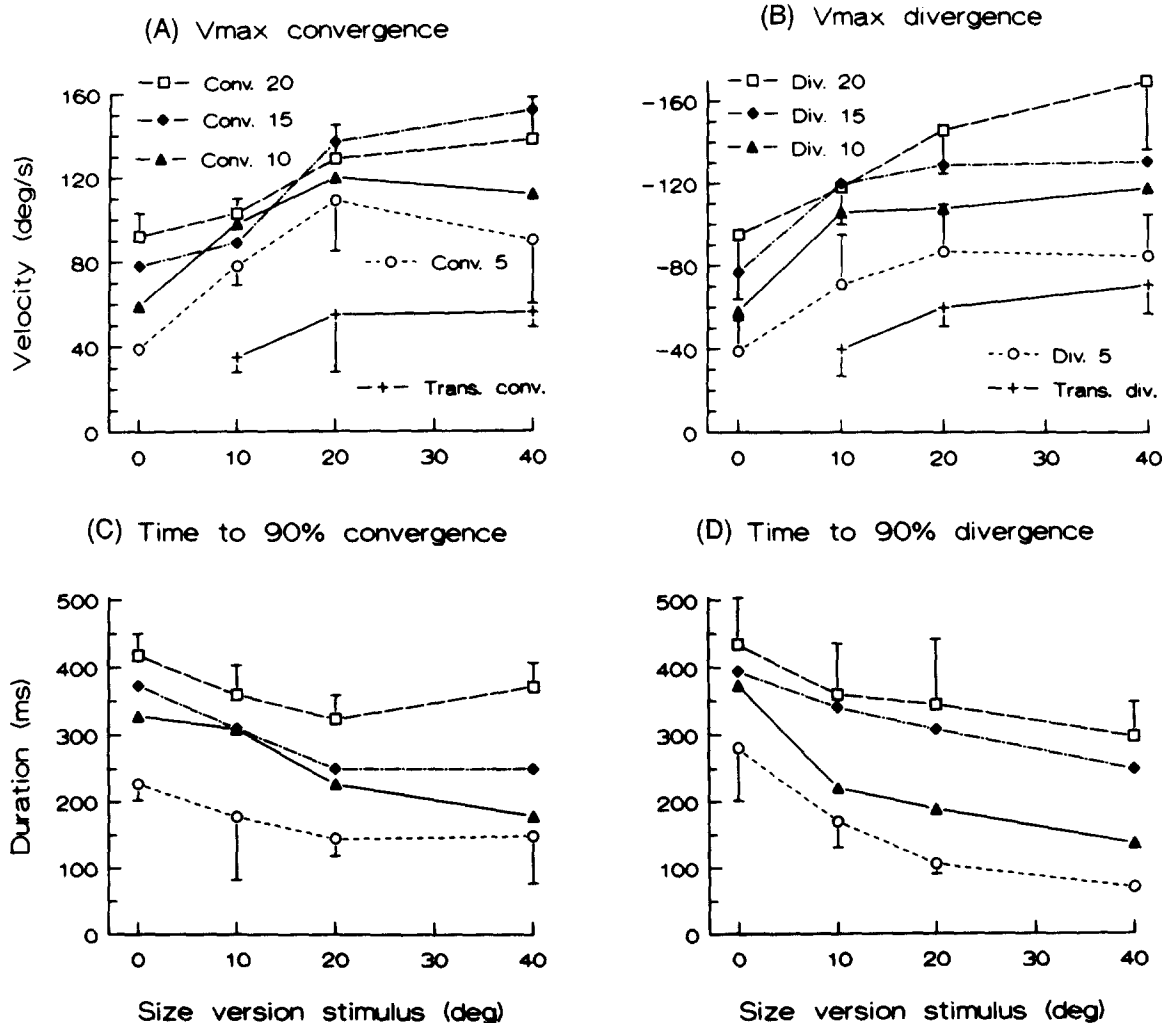

FIGURE 17. Changes in peak velocity and duration (90%) of convergence and divergence when pure vergence (zero version) is combined with 10, 20 or 40 deg of version. The results are shown for vergence demands of 5, 10, 15 and 20 deg. For comparison peak velocities of transient convergence and divergence of conjugate saccades are also shown (+ symbols). Means of three subjects (ZP, CE and AP) for which complete data were available. The vertical bars show typical SDs.

(A) % convergence within version saccade
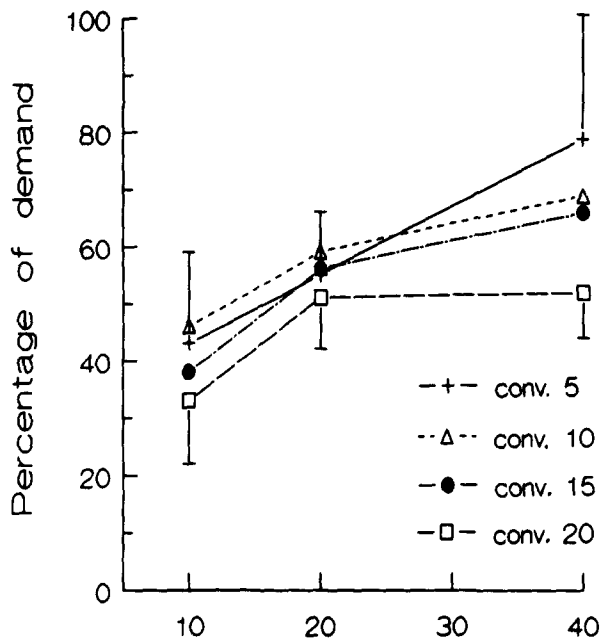
(B) % divergence within version saccade

Amplitude version (deg)

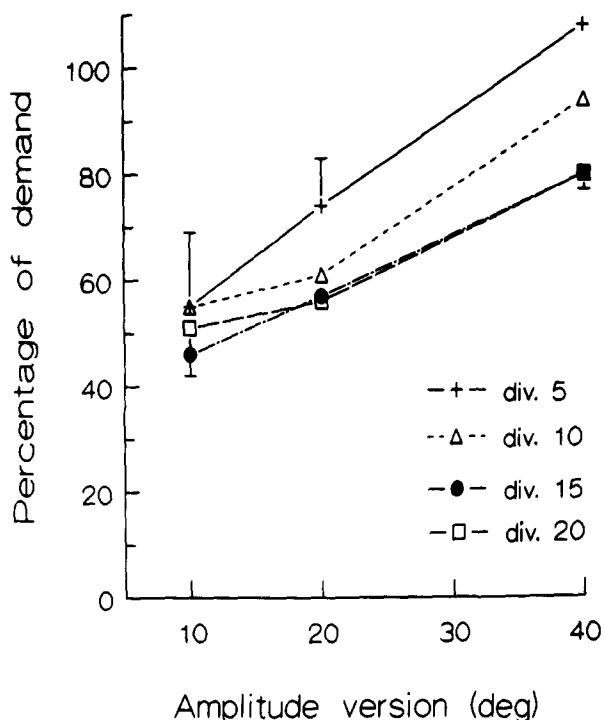FIGURE 18. The percentages of the total vergence, eventually reached after the saccade, that were accomplished within the duration of the version saccade (delimited by the 50 deg/sec criterion). Means and some representative SDs for the same three subjects as shown in Fig. 17.

expressed in the sudden acceleration of divergence after about 60 msec [cf. Fig. 5(B), same subject as Fig. 15; see also Fig. 7(A) for a similar case in a different subject].

The accelerating effect of version on divergence is evident in the examples of combined movements. Comparison between disjunctive and conjugate version [Fig. 15(E, F)] suggests that the early, transient divergence associated with conjugate saccades is fully incorporated in divergent gaze-shifts, while the convergent component that follows the divergence in conjugate saccades is fully abolished in disjunctive gaze-shifts. This makes for faster dynamics than in convergent gaze-shifts, in which the convergent transient component appears to be utilized, but the divergent component is only partially suppressed. Figure 16(C) shows the relation between the peak velocities of transient divergence in conjugate saccades and the peak divergent velocities during disjunctive movements (5, 10 or 15 deg divergence), both as a function of version amplitude. Again, it appears that the increases in peak divergence velocity are on the order of the peak velocities of inherent, transient divergence; subtraction of such peak velocities [Fig. 16(D)] eliminates the gain in velocity. Figure 17(B, D) show the average results for three subjects. The average baseline peak velocities for pure divergence were similar to those for convergence; the durations were slightly longer for divergence. The systematic increase of the peak divergence velocities as a function of increasing version was also not substantially different from the similar increase for convergence, except for details. The effect of version on shortening of the duration of vergence, however, was much larger and more consistent for divergence than for convergence [Fig. 17(D). Shortening continued to progress as version increased to 40 deg; at this version amplitude duration was reduced by about a factor of 3 for 5 deg divergence, and by a factor of 2 for 10 deg divergence. For larger divergence angles, the gains in time were relatively smaller but still substantial. These faster dynamics in comparison to convergence is easily explained by the adverse effects of the intrusion of initial divergence when version is combined with convergence. A further corroboration of this difference is found in the percentage of intrasaccadic divergence [Fig. 18(B)], which is higher than for convergence at all amplitudes of version, and can even exceed 100% (5 deg divergence with 40 deg version; obviously a postsaccadic convergence followed in such cases).

DISCUSSION

In analyzing version–vergence interactions, it is important to consider first the perspective from which we look into the various forms of oculomotor activity. The striking feature of human oculomotor behavior is that the two eyes move as "a single double-eye", such that the two lines of sight intersect with the target (or at least very nearly so) when humans look at an object of interest. This is the essence of Hering's (1868) view of oculomotor behavior. His additional description of binocular eye movements in terms of changes in version and vergence angles was little more than a mathematical abstraction (or even a truism). It certainly was no plea for separate mechanisms controlling version and vergence independently; on the contrary, Hering emphasized the

integrative motion of the eyes. Later on, it has become customary to dissect oculomotor behavior in terms of the activities of "subsystems". As has been argued elsewhere (e.g. Steinman et al., 1990), such subsystems are often primarily defined in an operational way, by the use of limiting configurations or the isolation of sensory channels for the stimuli. Thus, a vergence subsystem is isolated by the use of iso-direction stimuli, and a conjugate, saccadic system is inferred from conditions that do not require vergence. However, such subsystems may reflect limiting modes of operation rather than truly separate functional modules of the oculomotor system. Therefore, it may be erroneous to expect that responses to stimuli requiring both version and vergence will reflect a mere addition of the responses to similar version and vergence stimuli offered separately. On the contrary, limiting conditions, such as isolated vergence, may yield borderline performance by the integrated system that has evolved and been trained to deal with version and vergence in natural combinations.

The difficulty in eliciting gaze-shifts consisting of pure vergence without saccades is illustrative in this respect. Pure vergence, especially pure divergence, proved to be elusive because subjects virtually always made some (small) saccades, even when the stimuli were carefully aligned to exclude any demand for version. This tendency has been reported before (Erkelens et al., 1989b; Zee et al., 1992; Oohira, 1993). The elusiveness of pure vergence responses may be related to the stimulus conditions prevailing in daily behavior. Gaze-shifts requiring pure vergence appear to be exceedingly rare in natural behavior. Pairs of targets requiring pure vergence can be set up in the laboratory only when the subject's head is fixed and targets are meticulously aligned horizontally and vertically. Such perfectly aligned stimuli are most unlikely to occur or be maintained for any length of time for a freely moving subject. In practice, gaze-shifts that require vergence will also require version. Furthermore, the combination of version with vergence turns out to facilitate vergence (divergence even more than convergence). In this light, it is understandable that subjects, confronted with the demand to shift gaze between targets that differ only in vergence angle, are very much inclined to circumvent a pure vergence response by adding some saccades.

In addition, gaze-shifts between similar targets that differ only (by a modest amount) in vergence proved to elicit ambiguous vergence responses. We believe that part of the difficulty in shifting vergence between similar, perfectly aligned targets arises from sensory confusion: the visual system has difficulty in establishing the appropriate correspondence between the (closely adjacent) disparate retinal images and this may result in ambiguous motor responses. Related sensory (Krol & Van de Grind, 1980) and oculomotor (Cogan, 1978) ambiguities, based on mismatching of retinal images, have been described before. In this respect, it is important to emphasize that in our stimulus conditions, both targets of a pair were continuously visible, like in natural surroundings. Conditions were fundamentally different in the experiments of Zee et al. (1992), in which only one

target of a pair was lit at any time, the switch in lighting being the trigger for the eye movement. Obviously, this arrangement eliminates any sensory problems in identifying the target for each eye correctly.

In our experiments the ambiguous responses were eliminated by slight vertical offsets between the near and far targets; this appears to be an aspect of the facilitation of vergence by vertical saccades (Enright, 1984, 1986, 1989; Zee et al., 1992; Oohira, 1993) which has been overlooked before. These previous papers emphasize the more general interaction of vertical saccades with vergence, in a somewhat analogous, although probably less effective way as horizontal saccades. The role of vertical saccades is of theoretical importance in so far as links have been inferred between the saccadic facilitation of vergence and the inhibition of omnidirectional saccadic pause neurons (Zee et al., 1992). We collected some data on the effects of vertical saccades, which suggest that divergence is especially facilitated by upward saccades; all other interactions are much weaker. However, our data on the effects of vertical saccades are not complete enough at present for an adequate analysis of what appear to be rather complex effects.

The fact that gaze-shifts requiring pure vergence are highly unusual does not imply that pure vergence stimuli and responses do not play a role in natural behavior. On the contrary, they occur whenever the two eyes are not aimed at the same target so that disparity results. Such disparity-driven vergence was described in the classical work of Rashbass and Westheimer (1961) and in some more recent work from our group (Erkelens, 1987; Pobuda & Erkelens, 1993). This type of vergence is relatively slow and optimally activated by disparities not larger than a few degrees. It is probably of primary importance in controlling binocular correspondence not during, but in between gaze-shifts, specifically in fine-tuning binocular fixation at the end of gaze-shifts, when imperfections in binocular coordination have to be minimized. A goal-directed vergence component of postsaccadic drift has been described (Collewijn et al., 1988). In this respect, it is of great interest that Busettini, Krauzlis and Miles (1994a) and Busettini, Miles and Krauzlis (1994b) have found a strong facilitation of disparity-driven vergence in the wake of saccades. In conclusion, this classical, slow type of disparity-driven vergence seems to be typically associated with the correction and maintenance of binocular correspondence, not with the shift of gaze to a new target.

The general goal of the present study was a systematic evaluation of the dynamic properties of binocular eye movements during voluntary gaze-shifts in which various demands for vergence (0–20 deg) were combined with various demands for version (0–65 deg). Our present analysis confirms earlier reports that horizontal changes in direction, effected by saccades, increase the velocity and shorten the duration of vergence. These effects are consistently stronger for divergence than for convergence in terms of velocity enhancement, shortening of duration and the percentage of vergence accomplished within the duration of the saccade (Figs 17 and 18). [This larger

acceleration by saccades of divergence than of convergence contrasts with a recent report by Oohira (1993), who found an opposite tendency.] The major new aspects of our analysis are: (i) the systematic description of combinations of a broad range of vergence and version angles, showing the interactions between the transient vergence changes inherent to conjugate version and the demands for a net change in vergence; (ii) the description of systematic changes in velocity–duration–amplitude relations of each of the eyes when version changes from conjugate to disjunctive.

How does version, or more specifically, a saccade, facilitate vergence? On the basis of our present analysis we may speculate on a possible mechanism that has not been considered before. The main elements to be considered are: (i) the transient vergence changes during conjugate saccades; (ii) the differences in vergence velocity between disjunctive saccades and pure vergence; (iii) the differences in the main sequence properties of disjunctive and conjugate saccades.

Transient divergence, followed by convergence during horizontal saccades, found in humans and also in monkeys (Maxwell & King, 1992), is usually considered as an accidental result of slight differences in the mechanical properties of the medial and lateral rectus muscles, and has been modeled by differences in the time constants of abducting and adducting movements (Zee et al., 1992). Bruno, Inchingolo and Van der Steen (1995) discuss central mechanisms of compensation for asymmetries in the peripheral plant, and their possible role in nonconjugate adaptation of saccades. On the other hand, a central generation of these transients has not been excluded; such central generation could imply a purpose in gaze control. It seems possible to consider the hypothesis that the short intrasaccadic episodes of divergence and convergence at rather high velocities are generated as "starters" for an actual, net vergence movement. In this view, during a conjugate saccade, without a stimulus for vergence, the initial divergence is followed by a (more or less) symmetrical convergence. When divergence is needed, the initial divergent peak velocity is maintained and added on top of the divergence velocity that would be generated by the vergence stimulus alone. The secondary convergence is then abolished. On the other hand, when convergence is needed the transient convergent peak velocity associated with the version could be added to the convergent velocity elicited by the convergence stimulus as such, while the initial divergence would be possibly inhibited. The latter process is apparently not completely effective, because divergence penetrates in convergent, disjunctive saccades except for small version amplitudes.

The possibility that peak vergence velocity in disjunctive version movements is generated by a "summation" of the peak velocity generated by a pure vergence stimulus and the peak velocity of the *appropriate* component of "transient" vergence is supported by Figs 16 and 17. On the whole, peak vergence velocities during disjunctive saccades prove to be approximated by adding the transient peak velocity in the appropriate

direction to the peak velocity of pure vergence. Such an addition of peak velocities is very different from a simple moment-to-moment addition of a pure vergence and a pure version movement. It has been shown repeatedly (Ono et al., 1978; Enright, 1984; Zee et al., 1992; Collewijn et al., 1994) that such a straightforward summation does not predict vergence–version interactions, despite Yarbus' (1967) original claims. The mechanism considered here would differ from such a simple addition in that in disjunctive saccades (i) peak velocities are summated, which do not occur at similar times when version and vergence are tested separately; (ii) only (or mainly) the transient vergence component of conjugate saccades in the appropriate direction is utilized in this summation. Obviously, this "peak velocity summation hypothesis" has to remain speculative at this moment. For a better evaluation and understanding of the mechanisms three directions of work are needed: (i) more extensive behavioral testing of the hypothesis; (ii) more neurophysiological investigations on the generation of binocular saccades that are conjugate or disjunctive; (iii) a formal modeling approach based on adequate behavioral and neurophysiological data.

Eventually, version and vergence are the resultants of the movements of the two eyes, and the main sequence diagrams of conjugate vs disjunctive eye movements (Figs 11 and 12) provide some suggestions on the mechanisms involved in the generation of disjunctive saccades. First of all, the velocity–duration–amplitude relations of disjunctive saccades are in general markedly different from those of conjugate saccades. This finding seems to rule out the possibility that disjunctive saccades are the result of the independent generation for each eye of saccades that are different in size, but that otherwise have main sequence characteristics similar to conjugate saccades. Disjunctive saccades are not only unequal in size; their altered shape (lower velocity and longer duration) indicates that they are also generated in a way different from conjugate saccades. Zee et al. (1992) arrived at a similar conclusion, on the basis of simulation studies.

There is, however, a partial exception, which may illuminate the mechanism of disjunctive saccade generation. The abducting eye follows virtually the same main sequence in a divergent, disjunctive saccade as in a conjugate saccade of the same size for that eye. This is evident from Figs 11 and 12, in which actual amplitudes are compared. This suggests that, in disjunctive, divergent saccades, the abducting eye (which has to make the larger movement, the target angle being equal to the version angle + half the vergence angle) follows the parameters of a conjugate saccade of the same size, while all the divergence is achieved at the expense of the adducting eye, which makes a smaller saccade that is both slower and longer lasting than a conjugate, adducting saccade of comparable size for that eye.

Conditions for generating convergent, disjunctive saccades are apparently more complex. Neither of the eyes makes a saccade that fits the main sequence for conjugate saccades; both eyes move considerably slower

than in a conjugate saccade. Especially the abducting eye is slowed down much. The abduction–adduction asymmetry in peak velocity is reversed, compared to conjugate saccades, but this is not done by simply slowing down the abducting eye; both eyes are slowed down, but to an unequal extent.

We conclude that the main sequence velocity–duration–amplitude relations for conjugate saccades represent only one set out of a whole family of such relations that is needed to describe three-dimensional binocular gaze-shifts in general. The relations vary characteristically as a function of vergence amplitude, and as a function of the directions of version (abduction vs adduction) and vergence (convergence vs divergence); the general trend is for vergence to slow down saccades. In addition, many other factors influence main sequence parameters. Preliminary analysis indicated that saccades are faster in free-head conditions than on the biteboard, used in the experiments presented here (Collewijn et al., 1990, 1992; Steinman et al., 1990). Also, considerable asymmetries are found between centripetal and centrifugal saccades, which end or begin in the mid-orbital position, centripetal saccades being the faster ones (Collewijn et al., 1988). Our present analysis was restricted to saccades that were virtually symmetrical about the mid-orbital position.

Our present experiments specifically addressed gaze-shifts between targets located in the manual working space, an area in which most of human visuo-motor activity takes place. In this area, virtually all gaze-shifts require changes in version as well as in vergence. Our present data show that over large parts of manual working space version and vergence are well integrated to accomplish three-dimensional binocular gaze-shifts in a fast and efficient way. This integrated control appears to be of vital importance in the fruitful use of human binocular vision, including stereopsis, in the appreciation of the three-dimensional lay-out of the immediate surroundings and in the guidance of hand movements (see Epelboim et al., 1995). Thus, in near space, binocular gaze-shifts are nearly always disjunctive and saccades are nonconjugate. This contrasts with gaze behavior at distance, where vergence requirements are minor and gaze-shifts are predominantly conjugate, even during monocular viewing, and including variations between the trajectories of successive saccades between identical targets (Collewijn et al., 1988; Lemij & Collewijn, 1992; Bains, Crawford, Cadera & Vilis, 1992; Erkelens & Sloot, 1995). The subtle and tight functional coordination between vergence and version is further corroborated by parallel work by Van der Steen and Bruno (1995), dealing with nonconjugate adaptation of saccades. Briefly, they found that aniseikonic images, viewed at far distance, are not immediately scanned with nonconjugate saccades, but that such nonconjugacy is gradually learned in an adaptive process, which persists for some time in the absence of the driving difference in size, in agreement with previous work (Erkelens et al., 1989a; Lemij & Collewijn, 1991a,b, 1992). However, the same stimuli, viewed at near distance, were immediately scanned with the appropriate nonconjugate saccades, and such nonconjugate scanning did not induce any adaptive changes.

In conclusion, it seems appropriate to conceive of binocular gaze-shifting as the highly integrated operation of conjugate and disjunctive mechanisms. In manual working space, gaze-shift related vergence is largely and preferentially achieved by disjunctive saccades. Pure vergence gaze-shifts without saccades are avoided and, when forced, such isolated vergence is slower than in any combination with saccades. It is hypothesized that the transient vergence components, that are inherent to all conjugate horizontal saccades, may be instrumental components in building up fast and effective vergence in gaze-shifts, rather than being a mere accident of muscular asymmetries.

REFERENCES

Bahill, A. T., Clark, M. R. & Stark, L. (1975). Dynamic overshoot in saccadic eye movements is caused by neurological control signal reversals. Experimental Neurology, 48, 107–122.

Bains, R. A., Crawford, J. D., Cadera, W. & Vilis, T. (1992). The conjugacy of human saccadic eye movements. Vision Research, 32, 1677–1684.

Bruno, P., Inchingolo, P. & Van der Steen, J. (1995). Unequal saccades produced by aniseikonic patterns: A model approach. Vision Research, 35, 3473–3492.

Busettini, C., Krauzlis, R. J. & Miles, F. A. (1994a). Short-latency vergence responses. In Fuchs, A. F., Brandt, T., Büttner, U. & Zee, D. (Eds), Contemporary ocular motor and vestibular research: A tribute to David A. Robinson (pp. 312–319). Stuttgart: Thieme.

Busettini, C., Miles, F. A. & Krauzlis, R. J. (1994b). Short-latency disparity vergence responses in humans. Society for Neuroscience Abstracts, 20, 1403.

Cogan, A. I. (1978). Qualitative observations in visual science: 'The Farnsworth shelf'. Fusion at the site of the "ghosts". Vision Research, 18, 657–664.

Collewijn, H., Erkelens, C. J. & Steinman, R. M. (1988). Binocular co-ordination of human horizontal saccadic eye movements. Journal of Physiology, 404, 157–182.

Collewijn, H., Erkelens, C. J., Pizlo, Z. & Steinman, R. M. (1994). Binocular gaze movements: Coordination of vergence and version. In Ygge, J. & Lennerstrand, G. (Eds), Eye movements in reading (pp. 97–115). Oxford: Pergamon.

Collewijn, H., Steinman, R. M., Erkelens, C. J., Pizlo, Z. & Van der Steen, J. (1990). The effect of freeing the head on eye movement characteristics during 3-D shifts of gaze and tracking. In Berthoz, A., Vidal, P. P. & Graf, W. (Eds), The head–neck sensory motor system (pp. 412–418). New York: Oxford University Press.

Collewijn, H., Steinman, R. M., Erkelens, C. J., Pizlo, Z., Kowler E. & Van der Steen, J. (1992). In Shimazu, H. & Shinoda, Y. (Eds), Vestibular and brain stem control of eye, head and body movements (pp. 203–220). Tokyo: Japan Scientific Societies Press.

Enright, J. T. (1984). Changes in vergence mediated by saccades. Journal of Physiology, 350, 9–31.

Enright, J. T. (1986). Facilitation of vergence changes by saccades: Influences of misfocused images and of disparity stimuli in man. Journal of Physiology, 371, 69–87.

Enright, J. T. (1989). Convergence during human vertical saccades: Probable causes and perceptual consequences. Journal of Physiology, 410, 45–65.

Epelboim, J., Steinman, R. M., Kowler, E., Edwards, M., Pizlo, Z., Erkelens, C. J. & Collewijn, H. (1995). The function of visual search and memory in sequential looking tasks. Vision Research, 35, 3401–3422.

Erkelens, C. J. (1987). Adaptation of ocular vergence to stimulation with large disparities. Experimental Brain Research, 66, 507–516.

Erkelens, C. J. & Sloot, O. B. (1995). Initial directions and landing positions of binocular saccades. *Vision Research, 35*, 3297–3303.

Erkelens, C. J., Collewijn, H. & Steinman, R. M. (1989a). Asymmetrical adaptation of human saccades to anisometropic spectacles. *Investigative Ophthalmology and Visual Science, 30*, 1132–1145.

Erkelens, C. J., Steinman, R. M. & Collewijn, H. (1989b). Ocular vergence under natural conditions. II. Gaze shifts between real targets differing in distance and direction. *Proceedings of the Royal Society of London B, 236*, 441–465.

Hering, E. (1868). *Die Lehre vom binokularen Sehen*. Leipzig: Engelman. [English edition: Bridgeman, B. & Stark, L. (1977). *The theory of binocular vision*. New York: Plenum.]

Judge, S. J. & Cumming, B. G. (1986). Neurons in the monkey midbrain with activity related to vergence eye movement and accommodation. *Journal of Neurophysiology, 55*, 915–930.

Kenyon, R. V., Ciuffreda, K. J. & Stark, L. (1978). Binocular eye movements during accommodative vergence. *Vision Research, 18*, 545–555.

Kenyon, R. V., Ciuffreda, K. J. & Stark, L. (1980a). Dynamic vergence eye movements in strabismus and amblyopia: Symmetric vergence. *Investigative Ophthalmology, 19*, 60–74.

Kenyon, R. V., Ciuffreda, K. J. & Stark, L. (1980b). Unequal saccades during vergence. *American Journal of Optometry and Physiological Optics, 57*, 586–594.

Krol, J. D. & Van de Grind, W. A. (1980). The double-nail illusion: Experiments on binocular vision with nails, needles and pins. *Perception, 9*, 651–669.

Lemij, H. G. & Collewijn, H. (1991a). Long-term nonconjugate adaptation of human saccades to anisometropic spectacles. *Vision Research, 31*, 1939–1953.

Lemij, H. G. & Collewijn, H. (1991b). Short-term nonconjugate adaptation of human saccades to anisometropic spectacles. *Vision Research, 31*, 1955–1966.

Lemij, H. G. & Collewijn, H. (1992). Nonconjugate adaptation of human saccades to anisometropic spectacles: Meridian-specificity. *Vision Research, 32*, 453–464.

Mays, L. E. (1984). Neural control of vergence eye movements: Convergence and divergence neurons in midbrain. *Journal of Neurophysiology, 51*, 1091–1108.

Mays, L. E. & Gamlin, P. D. R. (1992). Role of omnipause neurons in saccade–vergence interactions. *Society for Neuroscience Abstracts, 18*, 27.

Mays, L. E., Porter, J. D., Gamlin, P. D. R. & Tello, C. A. (1986). Neural control of vergence eye movements: Neurons encoding vergence velocity. *Journal of Neurophysiology, 56*, 1007–1021.

Maxwell, J. S. & King, W. M. (1992). Dynamics and efficacy of saccade-facilitated vergence eye movements in monkeys. *Journal of Neurophysiology, 68*, 1248–1260.

Ono, H. & Nakamizo, S. (1978). Changing fixation in the transverse plain at eye level and Hering's law of equal innervation. *Vision Research, 18*, 511–519.

Ono, H., Nakamizo, S. & Steinbach, M. J. (1978). Nonadditivity of vergence and saccadic eye movement. *Vision Research, 18*, 735–739.

Oohira, A. (1993). Vergence eye movements facilitated by saccades. *Japanese Journal of Ophthalmology, 37*, 400–413.

Pobuda, M. & Erkelens, C. J. (1993). The relationship between absolute disparity and ocular vergence. *Biological Cybernetics, 68*, 221–228.

Rashbass, C. & Westheimer, G. (1961). Disjunctive eye movements. *Journal of Physiology, 159*, 339–360.

Steinman, R. M., Kowler, E. & Collewijn, H. (1990). New directions for oculomotor research. *Vision Research, 30*, 1845–1864.

Van der Steen, J. & Bruno, P. (1995). Unequal amplitude saccades produced by aniseikonic patterns: Effects of viewing distance. *Vision Research, 35*, 3459–3471.

Westheimer, G. (1954). Mechanism of saccadic eye movements. *A.M.A. Archives of Ophthalmology, 52*, 710–724.

Yarbus, A. L. (1967). *Eye movements and vision*. New York: Plenum.

Zee, D. S., Fitzgibbon, E. J. & Optican, L. M. (1992). Saccade–vergence interactions in humans. *Journal of Neurophysiology, 68*, 1624–1641.