Pergamon

PII: S0042-6989(96)00245-3

Vision Res., Vol. 37, No. 8, pp. 1049–1069, 1997

Printed in Great Britain
0042-6989/97 $17.00 + 0.00

Trajectories of the Human Binocular Fixation Point during Conjugate and Non-conjugate Gaze-shifts

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

Received 11 January 1996; in revised form 28 May 1996; in final form 9 August 1996

This paper describes the spatial trajectories of the binocular fixation point (the intersection point of the two lines of sight) during gaze-shifts within a horizontal plane of regard. Gaze was voluntarily shifted between pairs of real, continuously visible LED targets that were either iso-vergent at 5–25 deg convergence (conjugate version saccades) or differed in vergence angle (by 5–20 deg) as well as in direction (by 5–60 deg; combined version and vergence). Orientations of both eyes were recorded by phase detection in a homogeneous magnetic field with scleral sensor coils. "Conjugate" saccades showed an outward-looping, curved trajectory as a result of transient divergence, typically associated with horizontal saccades. These outward loops were disproportionately larger for far than for near targets, due to the non-linear relation between vergence and distance. Transient divergence increased moderately in magnitude and duration when basic vergence increased from 5 to 25 deg. As a result, transient saccadic disparities increased in angular magnitude as targets got close. Increasing tonic vergence did not, however, slow down conjugate saccades, in contrast to the previously described dynamic slowing effects of vergence on version during gaze-shifts involving simultaneous vergence and version changes. Convergent and divergent non-conjugate gaze-shifts each had characteristic trajectories; outward loops were much reduced in convergent and virtually absent in divergent movements. The saccadic component of non-conjugate gaze-shifts was preceded by a pre-saccadic vergence component in the direction of the imminent gaze-shift; its magnitude increased systematically with the increase in vergence demand and with the decrease in version demand. For both pre-saccadic convergence and divergence, this pre-saccadic part of the trajectory tended to follow an iso-direction line through the target of origin; directional change did not start until the saccade began. This suggests that for targets that differ in direction as well as distance, control of the vergence and version components of the gaze-shift can be dissociated to some degree. This seems to argue against models of binocular oculomotor control which assume that each eye responds primarily to its own target, and suggests rather that target vergence and target direction may be processed and responded to separately by ocular vergence and version, with a strong interaction between the two oculomotor activities whenever they occur at the same time.

Binocular gaze   Saccades   Vergence   Version   Spatial trajectory   Non-conjugate

INTRODUCTION

In human vision, gaze-direction for each eye is defined by the orientation of the line of sight, i.e., the line extending from the center of the fovea through the nodal points of the eye into visual space. Thus, the locus of monocular foveate vision is essentially a line, and not any single point in space. Shifts in monocular gaze are adequately described by changes in gaze-angles, not by the displacement of a fixation point with a specific spatial location, unless this is defined by the intersection of the line of sight with some surface (e.g. a page of text that is being read). For binocular viewing the situation is fundamentally different. Assuming good alignment, the two eyes, behaving as one single "double eye" (Hering, 1868) or "cyclopean eye", will have their lines of sight oriented towards the same visual target. Thus, the two lines of sight will intersect in a single point in 3-D space, which is the unique, binocular point of fixation. Therefore, it is possible to describe not only the locus of binocular gaze as a unique point in space, but also the trajectory of binocular gaze during shifts of gaze between

*Department of Physiology, Faculty of Medicine, Erasmus University Rotterdam, P.O. Box 1738, 3000 DR Rotterdam, The Netherlands.
†Department of Physics of Man, Utrecht University, Utrecht, The Netherlands.
‡Helmholtz Institute, Utrecht University, Utrecht, The Netherlands.
§Department of Psychology, University of Maryland, College Park, MD 20742-4411, U.S.A.
¶To whom all correspondence should be addressed [*Tel* +31-10-408 7560; *Fax* +31-10-436 7594; *Email* Collewijn@FYS1.fgg.eur.NL].

different objects. Gaze-trajectories in a fronto-parallel plane have been analyzed previously (Viviani *et al.*, 1977; Smit & Van Gisbergen, 1990; Becker & Jürgens, 1990; Erkelens & Sloot, 1995). Such studies revealed systematic curvatures, i.e., deviations from the shortest, straight path between successive fixation points, and addressed the coordination between horizontal and vertical version components.

Adequate descriptions of binocular gaze-trajectories in the plane of regard, which address the coordination between vergence and version, and contain *distance in depth* as a parameter, are not available until now. The only attempts in this direction are the schematic diagrams by Yarbus (1967, Fig. 94) but, despite the frequent reproduction of this figure in the secondary literature, Yarbus' scheme is no longer taken seriously. Note, for example, that Yarbus (1967) insisted on the complete independence and separation in time and space between the conjugate (version) and non-conjugate (vergence) components of the oculomotor pattern, despite the fact that his own published records contradicted this scheme. More recent studies of binocular gaze (e.g. Enright, 1984, 1986; Erkelens *et al.*, 1989b) have amply demonstrated strong interactions between vergence and version. A large component of the vergence required to shift binocular gaze between targets at different distances is accomplished by making the saccadic part of the gaze-shift non-conjugate. Furthermore, "conjugate", horizontal saccades between iso-vergent targets typically contain a major vergence component in the form of an intra-saccadic, transient divergence, amounting to as much as several degrees. This divergence originates from an asymmetry between abducting and adducting saccadic movements that is found in the large majority of subjects with normal binocular functioning. In a typical horizontal saccade, the abducting (i.e., temporalward moving) eye has a higher acceleration, reaches a higher peak velocity, and is on-target somewhat earlier than its fellow, adducting (i.e., nasalward moving) eye (Collewijn *et al.*, 1988a, 1995; Collewijn *et al.*, 1994; for a study in the monkey see Maxwell & King, 1992). The mechanism (central or peripheral) causing this asymmetry has not yet been established. Moreover, transient divergence has been described mainly for saccades between targets subtending relatively small convergence angles (at most about 5 deg). The effect of increased convergence angles (saccades between close targets) on transient divergence has not yet been studied systematically.

Recently, Collewijn *et al.* (1995) published a detailed analysis of the interactions of vergence and version during non-conjugate gaze-shifts. This analysis, based on accurate and precise scleral sensor-coil recordings, was confined to descriptions of gaze-changes as a function of time. The present analysis will address, in particular, the spatial trajectories of the binocular fixation point that are associated with various conjugate and non-conjugate gaze-shifts within a single plane of regard. It will be shown that the trajectories of conjugate and convergent gaze-shifts are highly curved, while rather straight trajectories are followed in divergent gaze-shifts.

METHODS

General considerations

For the practical determination of the binocular fixation point as the intersection of the two lines of sight, we require some simplifying assumptions. Firstly, these "lines" can be only approximately determined and they are also not infinitely thin. During steady, monocular fixation of a point target, under the best laboratory conditions, standard deviations of horizontal and vertical eye position are about 2–5 min arc (Steinman, 1965). We have no way to further narrow down the orientation of the line of sight. Secondly, we do not know whether the two lines of sight generally intersect or merely cross at a short distance. The most critical factor in this respect is the coordination of the vertical positions of each eye: expressed in Helmholtz angles, elevation of both eyes has to be equal (iso-elevation) or else the lines of sight will not be confined to a single plane of regard and there will be no binocular fixation point in any strict sense. Our present investigation was not aimed at resolving the existence of genuine and continuous intersection of the lines of sight at the level of precision of maintained fixation, where precision is within the range of only several minutes of arc. Instead, we shall pragmatically assume in our analysis that both lines of sight were indeed in a single plane of regard, and that, therefore, a unique binocular fixation point was defined within this plane by the azimuth angles of the two eyes. This approach is justified by three arguments: (1) previous work (Collewijn *et al.*, 1988b; Lemij & Collewijn, 1992) has demonstrated very good (though not perfect) vertical conjugacy for vertical saccades; (2) our present recordings of the vertical components of binocular eye movements did not indicate any remarkable violation of iso-elevation; (3) even if the lines of sight did not truly intersect under all conditions, our simplified analysis would still closely approach the trajectories of the *site of shortest distance between the two lines of sight*, which would be a reasonable operational definition for the binocular fixation point in the more general case of near crossing, rather than perfect intersection.

Subjects

Four subjects, one female (AP) and three males (AM, CE and ZP), aged between 29 and 38 years, provided the main body of data. From previous experiments, these subjects were known to perform reliably and accurately in binocular experiments and to tolerate binocular sensor coils well. They had no known visual or oculomotor defects except for mild myopia (CE, AM, ZP) that was corrected by hard contact lenses (CE), required no correction (AM) during the experiments, or was corrected by spectacles (ZP). The latter condition was, in hindsight, not optimal because ZP's negative spectacles shrank the retinal images by refracting the lines of sight at the site of

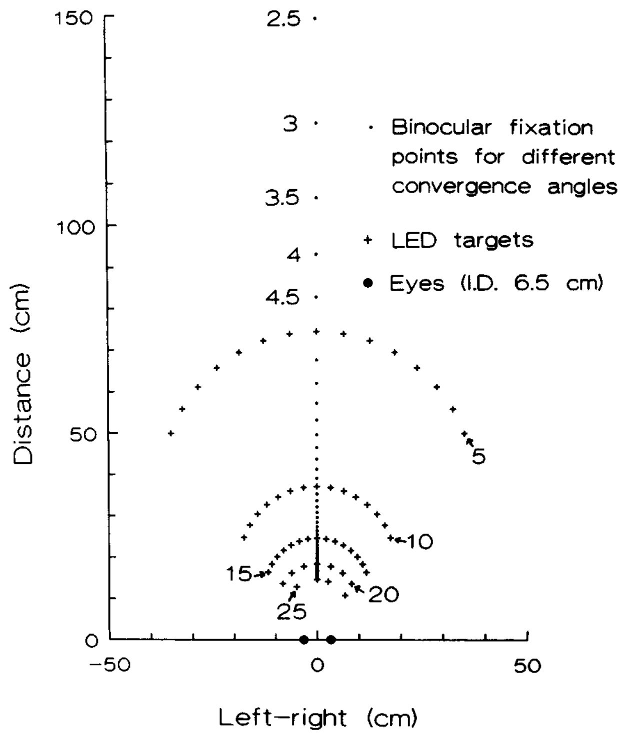

FIGURE 1. Top view of the horizontal plane in which all targets (crosses) and the two eyes (large dots on the abscissa) were located. Targets were positioned on five iso-vergence circles (5–25 deg convergence). Distances are scaled in cm, in Cartesian coordinates with the origin in the midpoint between the centers of the eyes. The small dots represent the binocular fixation points for symmetrical convergence angles ranging from 2.5 to 25 deg, at increments of 0.5 deg. Notice the strongly non-linear relation between fixation distance and convergence angle.

the lenses, so that recorded gaze-directions did not strictly correspond to stimulus directions. For this reason, ZP's reconstructed trajectories showed systematic inaccuracies. The general shape of his trajectories, however, showed the same characteristic as found in the other subjects. Two other subjects provided additional results that supported the main findings but were less suitable for inclusion in the main body of data due to specific anomalies. Only conjugate saccades were recorded in AM, due to limited availability of this subject. RS (61 yr) had a degree of presbyopia that prevented him from seeing any of the closer targets distinctly. Subjectively, he noticed his inability to focus on these targets, and his recordings showed marked imprecision of vergence. Therefore, data collection and analysis was limited in his case. HC (53 yr) habitually wears anisometric spectacles (L −6.5D, R −3.5D), resulting in adaptive non-conjugacy of all eye movements, as described previously (Erkelens *et al.*, 1989a; Lemij & Collewijn, 1991). Such non-conjugacy interferes fundamentally with the purpose of the present analysis. HC's conjugacy was restored to a large degree by taking off his spectacles, but even then his intrasaccadic vergence showed unusual features that we attribute to a complex mixture of adaptations, making his eye movements unrepresentative of normal binocular behavior.

Visual conditions

Arrangements were as described in Collewijn *et al.* (1995). LED targets were positioned on five iso-vergence circles (circles passing through the rotational centers of the two eyes and through the targets; Collewijn *et al.*, 1988a) subtending 5, 10, 15, 20 and 25 deg of convergence for an inter-ocular distance of 65 mm. All targets, as shown in Fig. 1 (crosses), were in a horizontal plane at eye level. Subjects were carefully aligned and maintained with their eyes (Fig. 1, large dots) in the correct position relative to the targets by the use of individually molded dental impression bite boards. Targets ranged in direction from 35 deg left to 35 deg right at 5 or 10 deg intervals.

In any trial, two LEDs (either on a same or on different iso-vergence circles) were constantly lit and subjects were instructed to make voluntary gaze-shifts between those (continuously visible) targets, in alternating directions, at intervals of about 1.5 sec. The surroundings were illuminated to allow the targets to be seen in a relatively natural and rather rich visual context that provided good information about both the directions and distances of the target with respect to the subject, and other objects and frames in the visual array.

Figure 1 also shows the positions of the binocular fixation point for symmetrical convergence ranging between 2.5 and 25 deg, at increments of 0.5 deg. This clearly illustrates the strongly non-linearly increasing effect of decrements in vergence on fixation distance for decreasing angles of convergence. The angles in Fig. 1 are exact for an inter-ocular distance of 65 mm. Actual inter-ocular distances in our subjects differed somewhat from this value; as target positions remained fixed, this resulted in slight deviations from the nominal values of the five iso-vergence angles for each subject. However, variations in interocular distance (range: 58–68 mm) did not appreciably affect the iso-vergent condition as such, nor the directions in which targets were viewed.

Data collection and analysis

Each trial was started by the subject when (s)he felt ready. Trials lasted 10 sec, during which 3 ± 1 saccades were made in each direction between the two targets selected for the particular condition. Sessions contained about 40 trials. Each subject participated in several sessions with different protocols to allow the collection of sufficient data on conjugate and non-conjugate gaze-shifts. Not all protocols were completed for all subjects; the minimum was three subjects for any protocol.

All data were collected with binocularly mounted scleral sensor coils (Skalar, Delft, The Netherlands) in the Maryland Revolving Field Monitor, a phase-detection based electromagnetic eye movement recording system with superior qualities, which has been described in previous publications (e.g. Collewijn *et al.*, 1988a; Epelboim *et al.*, 1995). To summarize very briefly: the system had absolute calibration, linearity better than 0.01% and 1 min arc resolution throughout a range of 360 deg; all data were stored in digital format at 488 samples/sec. Only one type of calibration was needed in

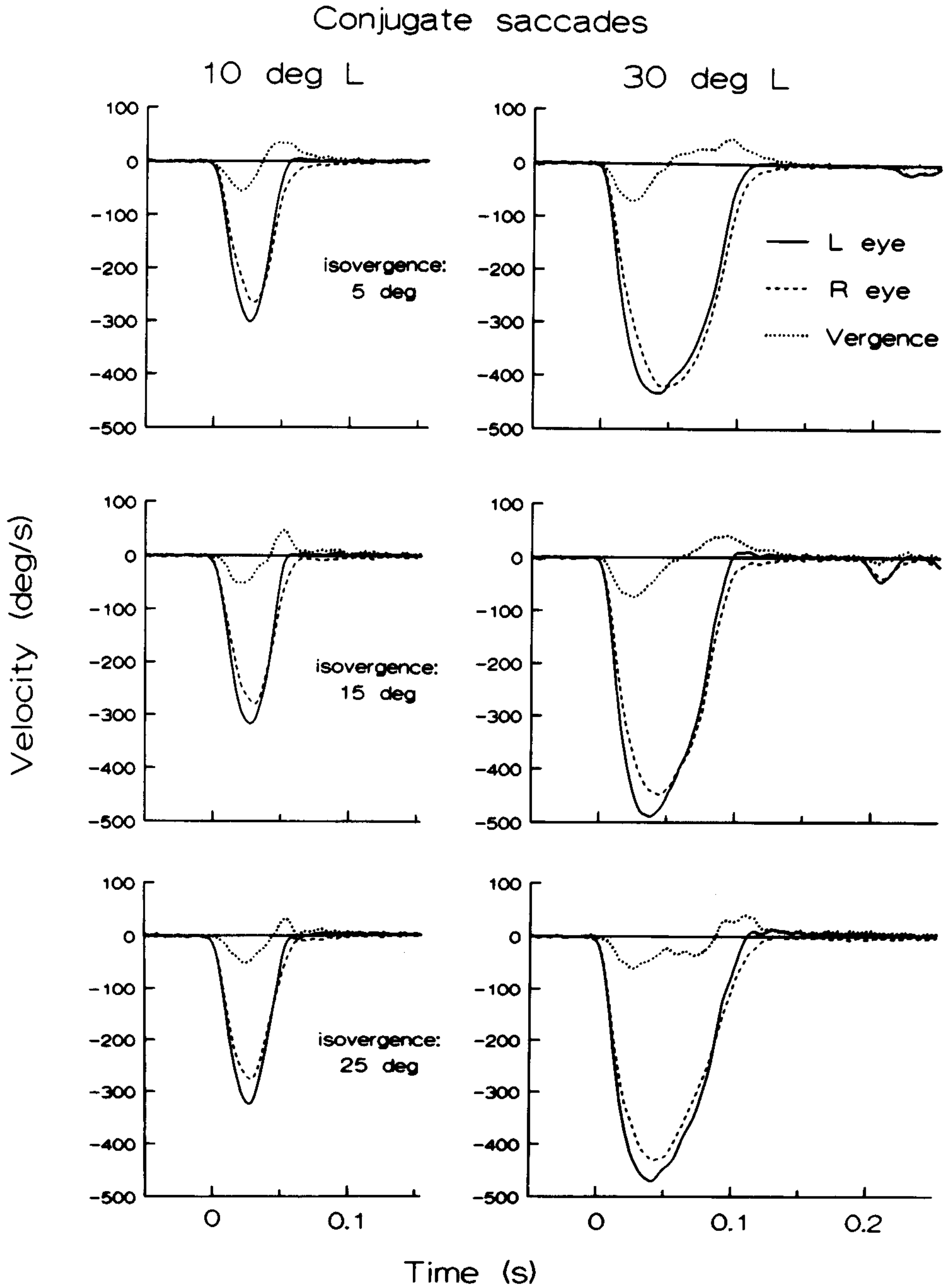

FIGURE 2. Representative examples from one session (subject: CE) of 10 and 30 deg leftward saccades, made between isovergent targets subtending 5, 15 or 25 deg of convergence. Velocity profiles of both eyes and their difference (vergence velocity) are shown.

each session: the offset angles of the coils on the eyes, relative to the line of sight because the head was supported on a dental bite-board. For this measurement, a mirror was placed before the subject, orthogonal to the zero-direction of the stimulus configuration. Each of the eyes was covered in turn, and the subject fixated the center of the pupil of his viewing eye in the mirror for 10 sec. In this way, horizontal and vertical coil-offsets were obtained for straight-ahead fixation (relative to the stimuli) of each eye. After subtraction of the appropriate offsets from all recorded values in a session, the corrected values represented absolute horizontal and vertical gaze-angles, with "zero" representing looking straight ahead for each eye; binocular zero gaze-angles would, thus, correspond to fixation of a very distant target along the zero-direction of the stimuli. Rightward and upward rotations were treated as positive; vergence was calculated as left eye position minus right eye position (convergence thus being positive). Version was defined as the average between left and right eye positions.

For all analysis and illustrations, signals associated with saccades in one direction (and satisfying amplitude criteria) within one trial ($n = 3 \pm 1$) were averaged (trigger signal: version exceeding 15 deg/sec). Variability among these averaged saccades in a trial was small enough to be negligible for our present purposes.

Velocities were derived by differencing without time shift and with a minimum of smoothing (Collewijn *et al.*, 1995).

All stimuli were in the horizontal plane of regard and (as will be shown) all gaze-movements were essentially confined to this plane. Therefore, the reconstruction of binocular gaze-trajectories was simplified to a reconstruction of the position of the top of a triangle in the horizontal plane of regard with the line connecting the ocular rotation centers (length: b) as its base and the horizontal left and right eye angles (azimuths) μR and μL as its base angles. Binocular gaze-position was expressed as Y (distance) and X (lateral position) in a horizontal Cartesian coordinate system, with its origin in the midpoint between the centers of the eyes:

$$Y = b/(\tan\mu L - \tan\mu R)$$

$$X = 0.5Y(\tan\mu L + \tan\mu R).$$

Individual values of b were used in all reconstructions.

RESULTS

Conjugate saccades: effects of iso-vergence magnitude on dynamics

The first aspect that needed to be explored for this study of spatial trajectories of gaze-shift was the effect of varying levels of tonic iso-vergence on the dynamics of saccades. Our previous analysis of conjugate, horizontal saccades was restricted to saccades between targets on a 5 deg iso-vergence circle (Collewijn *et al.*, 1995); increasing levels of tonic convergence might lead to systematic changes in saccadic dynamics. This had to be known before the significance of differences in the spatial trajectories of gaze-shifts could be interpreted. Accordingly, horizontal saccades of 5, 10, 20 and 30 deg amplitude between targets at 5, 10, 15, 20 and 25 deg iso-vergence were analyzed. Recordings from a representative session, illustrating saccadic dynamics, are shown in Fig. 2.

Velocity profiles of left and right eye and their difference (vergence velocity) are shown for 10 and 30 deg, leftward, conjugate saccades at 5, 15 and 25 deg iso-vergence. A few conclusions are immediately suggested by comparing the three rows of panels in Fig. 2. Firstly, the change in basic convergence angle from 5 to 25 deg did not change the well-known abduction–adduction asymmetry in any gross manner. Throughout the convergence range, the abducting eye accelerated faster, reached a higher peak velocity, and ended earlier than the adducting saccade of the fellow eye. Thus, the transient divergence–convergence pattern during horizontal saccades was not basically changed as a function of iso-vergence, although subtle changes appeared in the transient vergence, which will be examined in detail later. Secondly, no systematic changes in the ocular velocity profiles were evident as a function of iso-vergence. Peak velocities, durations and overall shape remained unaffected by the increase of iso-vergence from 5 to 25 deg for both eyes, and thus also for their average, version.

This latter impression was verified by a systematic analysis of "main sequence" parameters (peak velocity and duration) of version for 5–30 deg saccades (leftward and rightward pooled), executed at 5–25 deg iso-vergence, for three subjects (AP, AM and CE), shown in Fig. 3. (Only the primary saccades were considered; secondary, corrective saccades were neglected). There was no systematic effect of the magnitude of iso-vergence on the main sequence parameters of saccadic version, including the actual amplitudes of the primary saccades. This was true for each individual subject as well. We conclude that the dynamics of saccadic version-shifts are not affected by the constant level of convergence, and thus that the *version* component of saccades is effected similarly between pairs of iso-vergent targets that are either near or far.

Some subtle differences were detected, however, in a more detailed analysis of the dynamics of the transient *vergence* component. Series of position and velocity traces of transient vergence, associated with conjugate saccades of 10, 20 and 30 deg at iso-vergences of 5–25 deg are shown in Fig. 4. The trends in this figure are representative, although the magnitude of transient divergence was somewhat above average in these particular recordings.

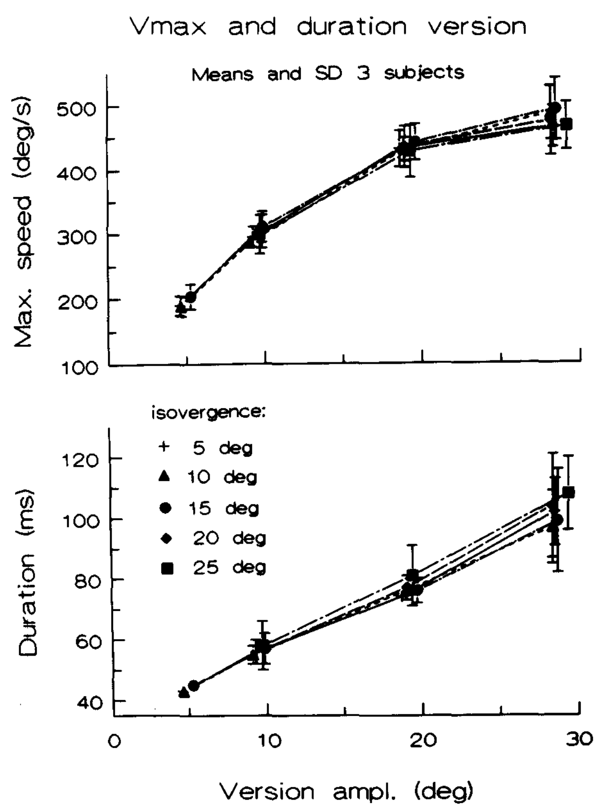

FIGURE 3. Peak velocity and duration of the version component (average of left and right eye movement) of 5–30 deg, horizontal, rightward and leftward saccades, executed at iso-vergence angles of 5–25 deg. Means are shown for three subjects (CE, AM, AP), with the vertical bars representing ± 1 SD of inter-subject variability. Horizontal axes represent the actual mean version amplitudes (which are only slightly smaller than the target amplitudes). Duration (and amplitude) of saccadic version was determined by the criterion of velocity exceeding 15 deg/sec.

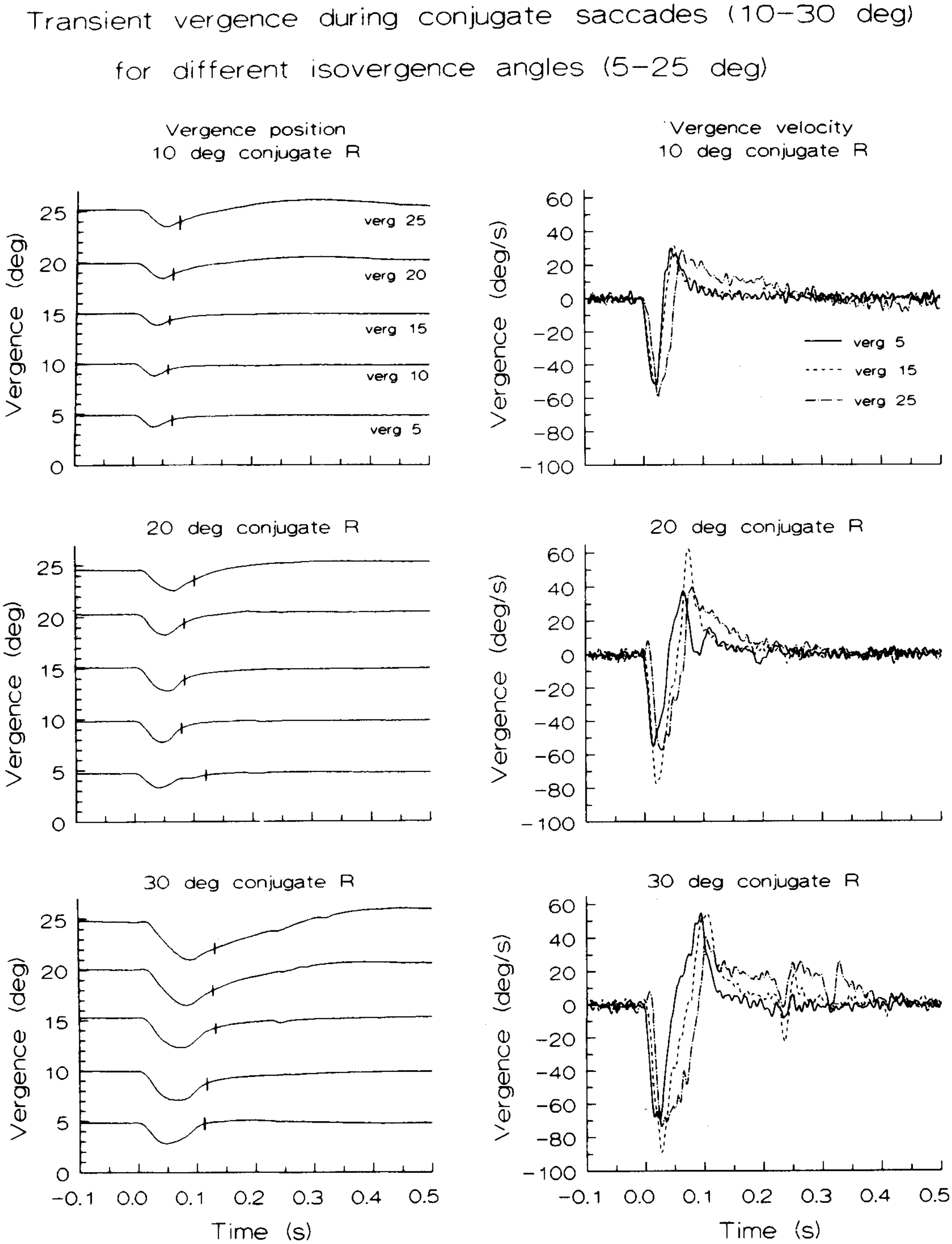

FIGURE 4. Position and velocity traces of transient vergence, associated with rightward, conjugate saccades of 10, 20 and 30 deg at iso-vergences of 5–25 deg, which are reflected in the baseline levels of the various position traces. The rightward saccades of subject CE, shown here, have somewhat larger than average transient divergence, and therefore show the effects of iso-vergence and version magnitude (present in all subjects) particularly clearly. Velocity traces are shown for three values of iso-vergence only, to avoid cluttering. Vertical bars on the position traces mark the end (velocity <15 deg/sec) of the associated version movement.

Several systematic trends can be seen in this figure. As was described before (Collewijn *et al.*, 1995), the magnitude of transient divergence increased with saccadic amplitude in the range 10–30 deg. This effect proved to be robust for all iso-vergence angles. For a constant saccadic amplitude, transient divergence increased as a function of the magnitude of the iso-vergence angle. This is most readily seen for the 30 deg saccades (Fig. 4, lower panels), which show relatively large transient divergence, but the trend is similarly present for the smaller saccades. This increase in magnitude of transient divergence seems to originate mostly from an increased duration of the divergent phase, not from an increase in divergence velocity. The increase in transient divergence as a function of increasing iso-vergence was associated with a marked increase in duration (up to several hundreds of

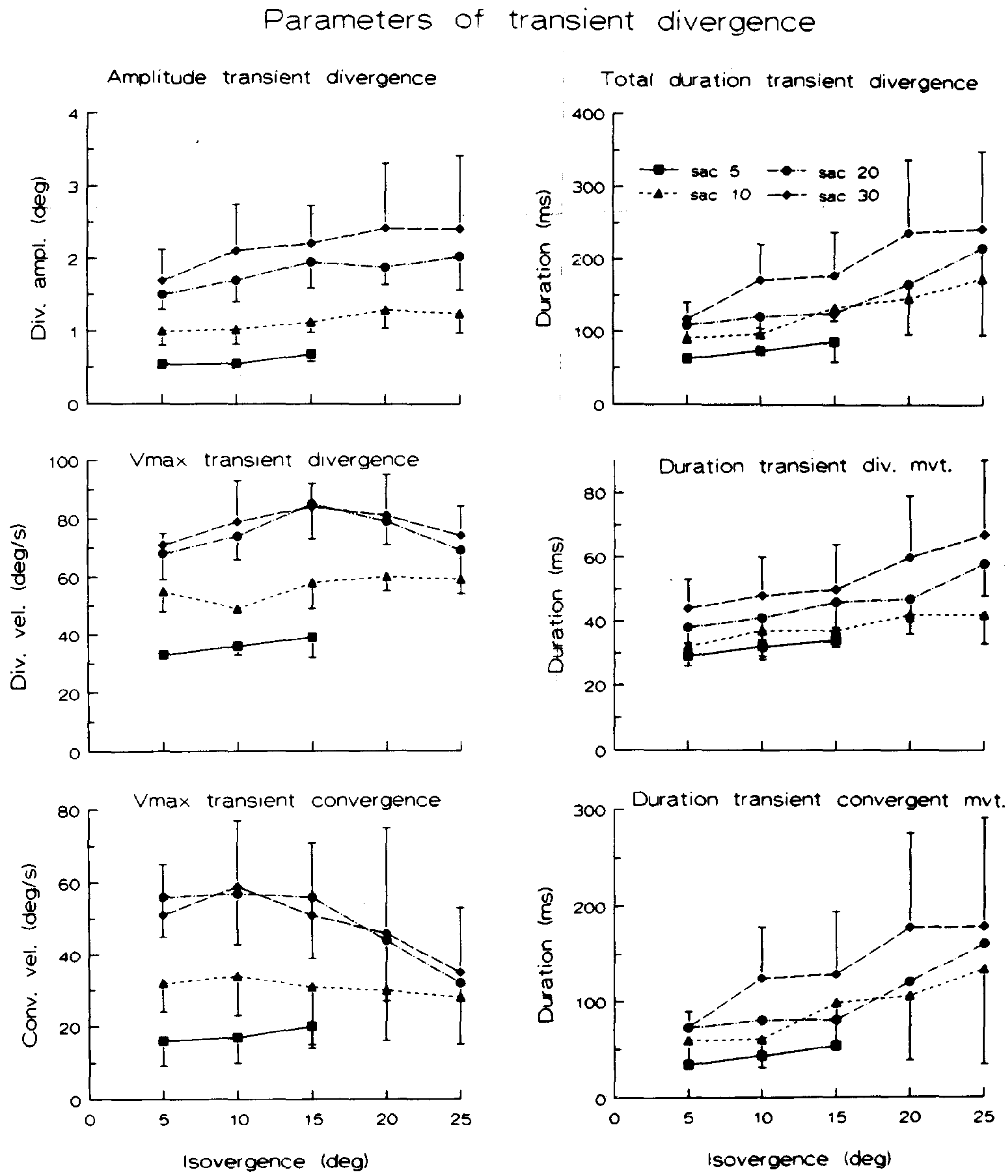

FIGURE 5. Parameters of transient vergence during conjugate saccades of 5–30 deg amplitude, executed at 5–25 deg iso-vergence. Means of three subjects (CE, AP, AM), all of which showed the main trends as described in the text. Vertical bars represent 1 SD (omitted in a few cases to avoid cluttering). Durations were defined as follows: start of divergence was synchronous with start of version (version velocity >15 deg/sec); end of divergence (= beginning of convergence) was the moment at which vergence velocity changed from negative to positive; end of convergence was marked by the consistent (for at least three samples) decrease of vergence velocity to <5 deg/sec.

milliseconds) of the subsequent convergent phase, which restores binocular fixation.

A systematic analysis of the parameters characterizing transient vergence during conjugate saccades of 5–30 deg at iso-vergence angles of 5–25 deg is given in Fig. 5, which shows the mean values (and cross-subject standard deviations) of three subjects (AP, AM and CE). Each of the trends described was present in each of these individual subjects. The upper-left panel shows the systematic increase of the amplitude of transient divergence as a function of saccadic amplitude and as a function of increasing iso-vergence. (The effect of increasing iso-vergence is, in this average plot, smaller than in the examples of Fig. 4). It should be noticed that extrapolation of the graphs to an iso-vergence of 0 deg does not suggest that transient divergence will be absent or even significantly lowered when a subject looks at a target at optical infinity, a condition that we were unable to test in our present experiments. (Experiments by Van der Steen and Bruno in Rotterdam, which are in preparation for publication, have confirmed that transient divergence is indeed maintained under conditions simulating targets at infinite distance.) Changes in peak velocity of transient divergence are shown in the middle-left panel of Fig. 5. These changes were small and unsystematic as a function of iso-vergence, although they were clearly related to saccadic amplitude. Peak velocity of the subsequent transient convergence (Fig. 5, lower-left panel) also increased markedly with saccadic amplitude, but did not increase as a function of iso-vergence. On the contrary, peak velocity of convergence velocities showed a downward trend for 20 and 30 deg saccades at iso-vergence angles >15 deg. Obviously, increasing amplitudes of divergence, followed by convergence at unchanged or even reduced velocities, should result in longer durations. These are indeed shown in the right panels of Fig. 5; durations were defined as the periods during which vergence velocity exceeded 5 deg/sec. The total duration of the transient divergence–convergence increased markedly as a function of increasing iso-vergence (Fig. 5, upper-right panel). Part of this total increase originated from a lengthening of the divergent phase [Fig. 5, middle-right panel; see also Fig. 2(b)] but a larger part derived from a prolongation of the convergent phase (Fig. 5, lower-right panel).

Thus, when the basic convergence angle increased, the convergent phase started later, reached a lower peak velocity which was maintained for a shorter time, and continued for increasingly long times at low velocities (Fig. 2).

The durations of transient vergence (Fig. 5) may be compared to the durations of version for the same saccades (Fig. 3, lower panel). Even when their durations were longest (at 25 deg iso-vergence), the divergent movements (negative vergence velocities) always changed into convergent movements (positive vergence velocities) well before the version saccade ended. This convergent movement, needed to complete binocular fixation of the new target, however, always outlasted the duration of version. The difference was small (a few tens of milliseconds) at 5 deg iso-vergence, but large (as much as 150 msec or more) at 25 deg iso-vergence. This effect is also illustrated in the individual vergence position examples in Fig. 4, in which the vertical bars mark the end of the associated version component (vergence velocity <15 deg/sec).

A general conclusion on the effects of increasing iso-vergence on binocular saccades thus emerges: although the common component of the movement of the two eyes (version) remains virtually unaffected, binocular fixation at the end of the version saccade is progressively

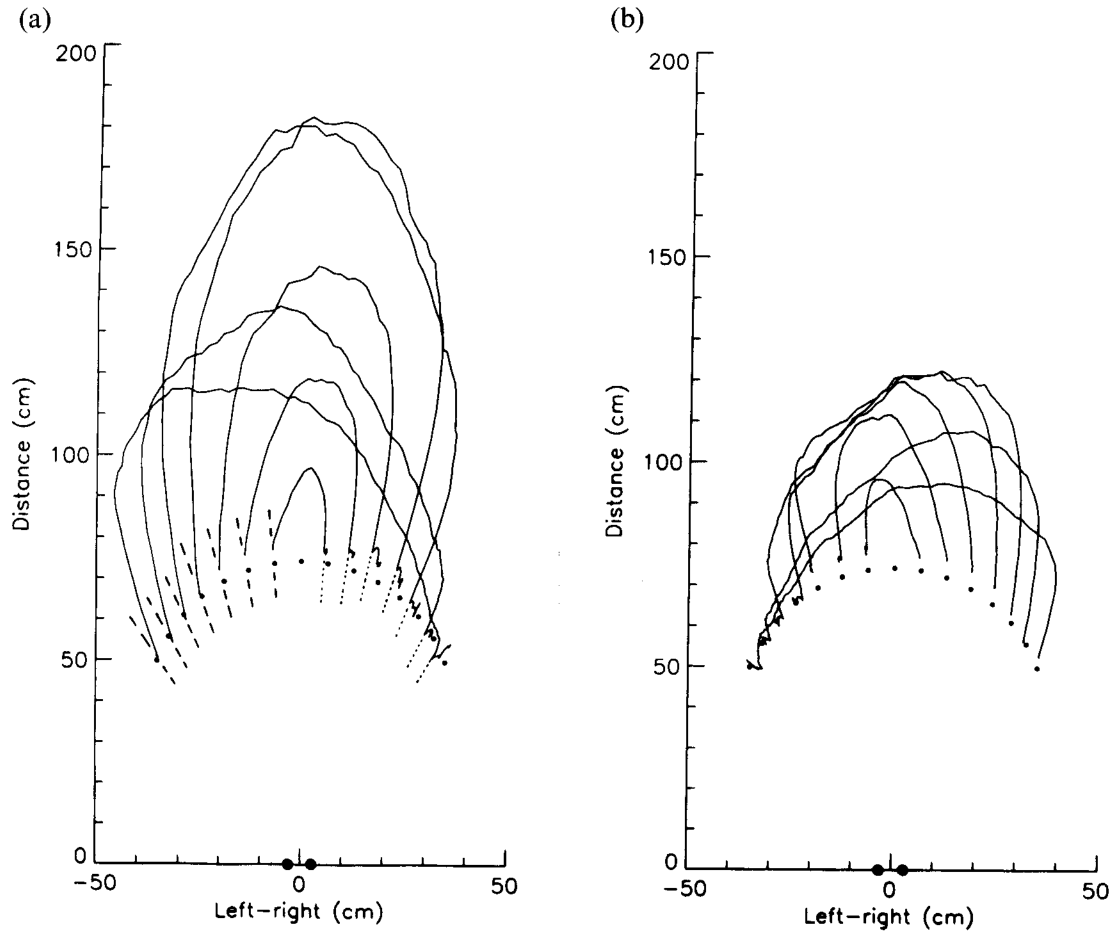

FIGURE 6. Typical trajectories of the binocular fixation point during conjugate saccades (10–70 deg) at 5 deg iso-vergence, projected on the horizontal plane of regard, seen from above. Rightward (a) and leftward (b) saccades of subject CE are shown; the difference in sizes of the loops in the two directions is idiosyncratic, and at the same time marks the overall range that we observed in our subjects. Dots on the X-axis represent positions of the eyes. Iso-direction lines are drawn through the starting (dashed lines) and end positions (dotted lines) of the trajectories.

degraded by transient divergence lingering for a considerable time. This period of continuing convergence may last easily as long as the preceding version saccade at iso-vergence angles of 20–25 deg.

Conjugate saccades: trajectories of binocular fixation point

Typical examples of binocular gaze-trajectories for conjugate saccades are shown in Fig. 6. Figure 6(a) shows rightward saccades of 10–70 deg amplitude at 5 deg iso-vergence; Fig. 6(b) shows similar saccades to the left in the same subject (CE).

The most striking aspect of these trajectories is their strong, outward curvature. Immediately at the start of the saccades, gaze swung away from the iso-vergence circle into the distance. Then, it looped gradually around and swung back towards the new target. The main saccade ended near, but not quite on the new target; this was approached more closely by one or more corrective saccades that show up as small, additional loops appended to the ends of the main trajectories in Fig. 6. The smaller loops for leftward than for rightward saccades in Fig. 6 reflect an idiosyncratic asymmetry of transient divergence in subject CE; the two panels together include the full range that we have encountered in our present sample from three subjects. Figure 7(a) shows examples of trajectories of conjugate (rightward) saccades of 5–30 deg at 5–25 deg iso-vergence in a different subject (AP). For comparison, Fig. 7(b) shows vergence as a function of version *in angular format* for the same set of saccades.

Obviously, the trajectories of conjugate saccades are the result of the combination of version with the effects of transient divergence, superimposed upon the pedestal convergence level. The most distant point of the outward loops is determined by two factors: (1) the absolute magnitude of the transient divergence; (2) its relative magnitude compared to the pedestal iso-vergence. As shown in Fig. 1, a divergence by 2.5 deg from a pedestal convergence of 5 deg will move gaze outward from about 74 cm to about 150 cm, whereas a similar divergence from a pedestal convergence of 10 deg will move gaze outward over only about 12 cm. Thus, the eccentric looping of gaze will increase disproportionally as pedestal convergence decreases.

For a given iso-vergence, the distance of the farthest point of the gaze-trajectory is determined by the amplitude of the transient divergence. This amplitude

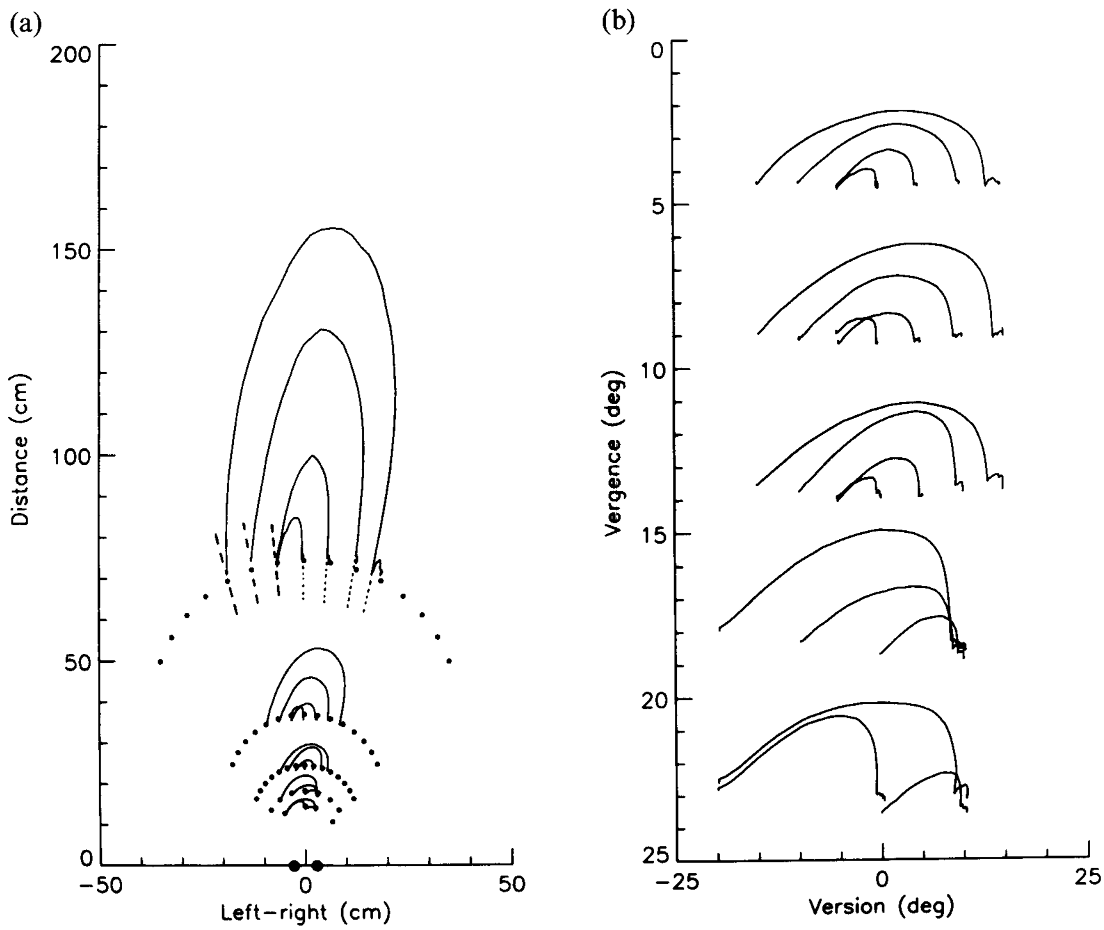

FIGURE 7. Typical trajectories of conjugate saccades (5–30 deg) at different iso-vergence angles (5–25 deg). Rightward saccades of subject AP are shown. (a) Trajectories, plotted in metric coordinates (as in Fig. 6). (b) Same set of saccades, plotted in angular coordinates (vergence vs version angles). Notice that, due to the geometric relations (see Fig. 1) the outward loops of conjugate saccades decrease strongly in amplitude for increasing iso-vergence (a), even though the absolute magnitude of transient divergence increases at the same time (b).

increases with saccadic amplitude (Fig. 5) to a maximum of several degrees, which is often reached for saccades of 40–50 deg. For saccades of still larger size, transient divergence became smaller again in about half of the subject–direction combinations (as in Fig. 8), resulting in flatter loops for the largest saccades (as in Fig. 6). The remaining cases showed transient divergence that was more or less constant, or tended to increase even further for saccades larger than 50 deg.

Especially for the saccades between our farthest targets (5 deg iso-vergence), transient divergence had very large effects on the distance of the binocular gaze-point. In fact, our 5 deg iso-vergence targets are probably about the farthest possible targets for which the trajectories of conjugate, binocular gaze-shifts can be reasonably plotted, or for which a real, continuous trajectory even exists. For more distant targets, the lines of sight will be nearly parallel and further transient divergence during saccades will result in negative vergence angles and the loss of any real binocular gaze-point. On the other hand, for the closer targets, transient vergence, though similar or even larger in absolute size [Fig. 7(b)], remains small compared to the pedestal vergence level. Accordingly, the outward loops shrink dramatically as pedestal convergence increases [Fig. 7(a)].

Other than the most distant point, the main characteristics of trajectory are the orientations of the initial and final segments of the loop. These are determined, in turn, by the evolution of vergence and version as a function of time. The interplay of version and vergence is somewhat difficult to perceive from the trajectories in Fig. 6; the saccadic loops sometimes seem to suggest that divergence precedes version, because gaze seems initially to recede much more than to move toward the new

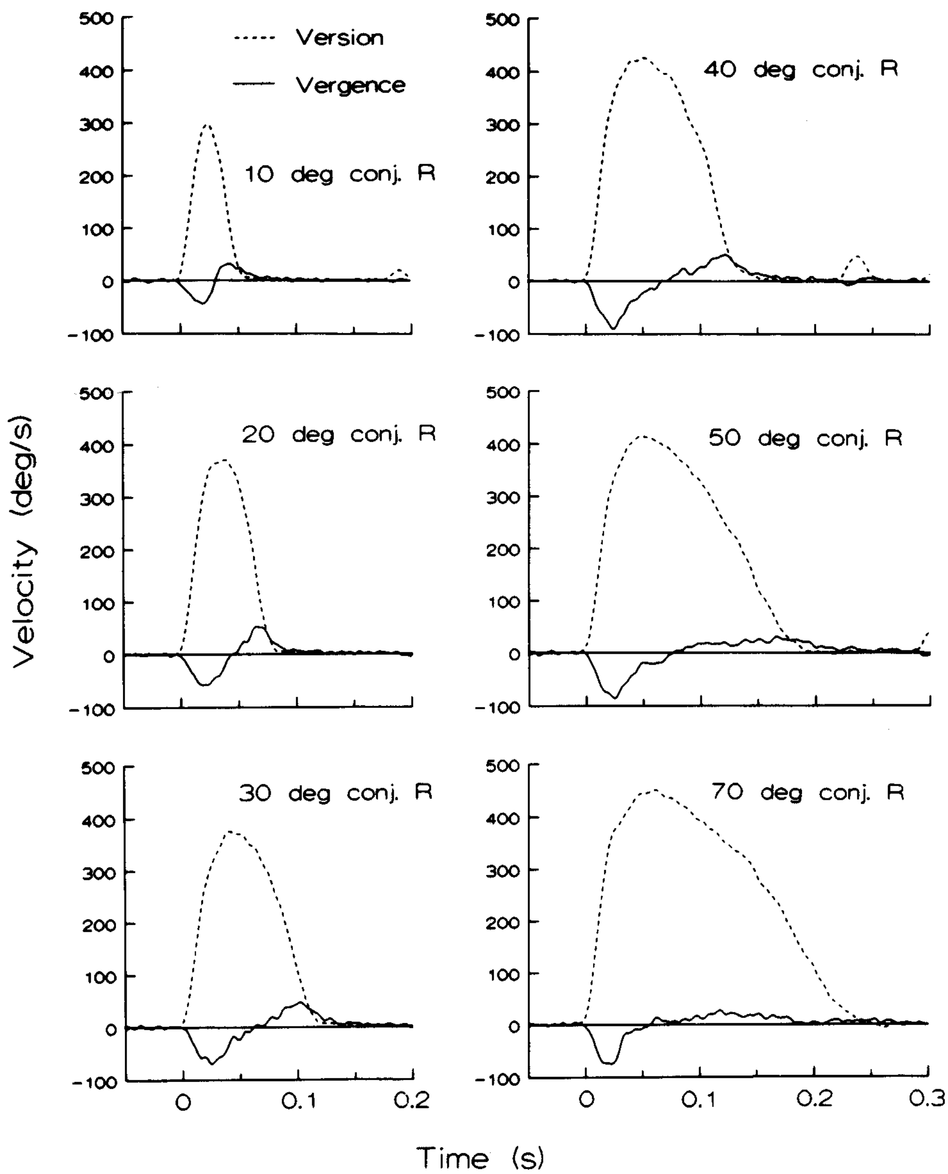

FIGURE 8. Version and vergence velocities as a function of time for rightward saccades of 10–70 deg. The same saccades are plotted as trajectories in Fig. 6(a). The amplitudes of transient divergence are represented by the integral (i.e., the area) of the vergence velocity graphs below the zero lines.

direction. For the largest saccades [Fig. 6(a)], superficial inspection seems even to suggest that the initial trajectory is in the wrong direction, e.g. the 70 deg rightward saccade trajectory swings left before curving to the right. This impression is, however, wrong, and also not supported by angular plots such as in Fig. 7(b).

To illustrate this aspect further, Fig. 8 shows version and vergence velocities as a function of time for most of the saccades plotted also in Fig. 6(a). These time plots document that, invariably, version and vergence movements start simultaneously, and that version always starts in the correct direction. Peak velocity and duration of divergence increased, in this case, as a function of saccadic amplitude for amplitudes up to 40–50 deg; this trend was reversed for larger saccades. The amplitude of divergence is equal to the integral (i.e., the area) of the vergence velocity below the zero line; maximum divergence is reached when vergence velocity crosses from negative to positive values. This point in Fig. 8 corresponds to the attainment of the most distant point in the trajectories in Fig. 6. The relations between version and vergence are further clarified in Fig. 6(a) by the iso-direction lines, drawn from the midpoint between the eyes through the start and end points of the trajectories (dashed and dotted lines, respectively). The initial segments of all trajectories make a positive (rightward) angle with the iso-direction line through the starting point, which means that in all cases gaze-direction (version) started to move immediately in the direction of the new target. On the other hand, the final segments of the trajectories make a much smaller angle, and are often almost aligned, with the iso-direction lines through the endpoint of the trajectories. This means that the last part of the trajectories consists almost totally of a convergent movement; this is also evident in the time graphs of Fig. 8.

Vertical components of horizontal gaze-shifts

The trajectories in Figs 6 and 7 have been drawn as if both lines of sight moved within the horizontal plane of regard containing the targets and the centers of the eyes. Two assumptions were implicitly made here: (1) absence of vertical vergence; (2) absence of vertical version. As we have pointed out in the Methods section, absence of vertical *vergence* is a condition for the existence of a real binocular gaze-point. In practice, this condition is probably not satisfied perfectly. Our recordings of vertical eye movements showed erratic vertical vergence movements during the gaze-shifts; these were of the order of 1 deg at most. We have no firm basis for attributing these minor deviations to either real oculomotor errors or errors of measurement, but consider them small enough to be neglected for our present purpose.

Absence of vertical *version* is not a condition for the

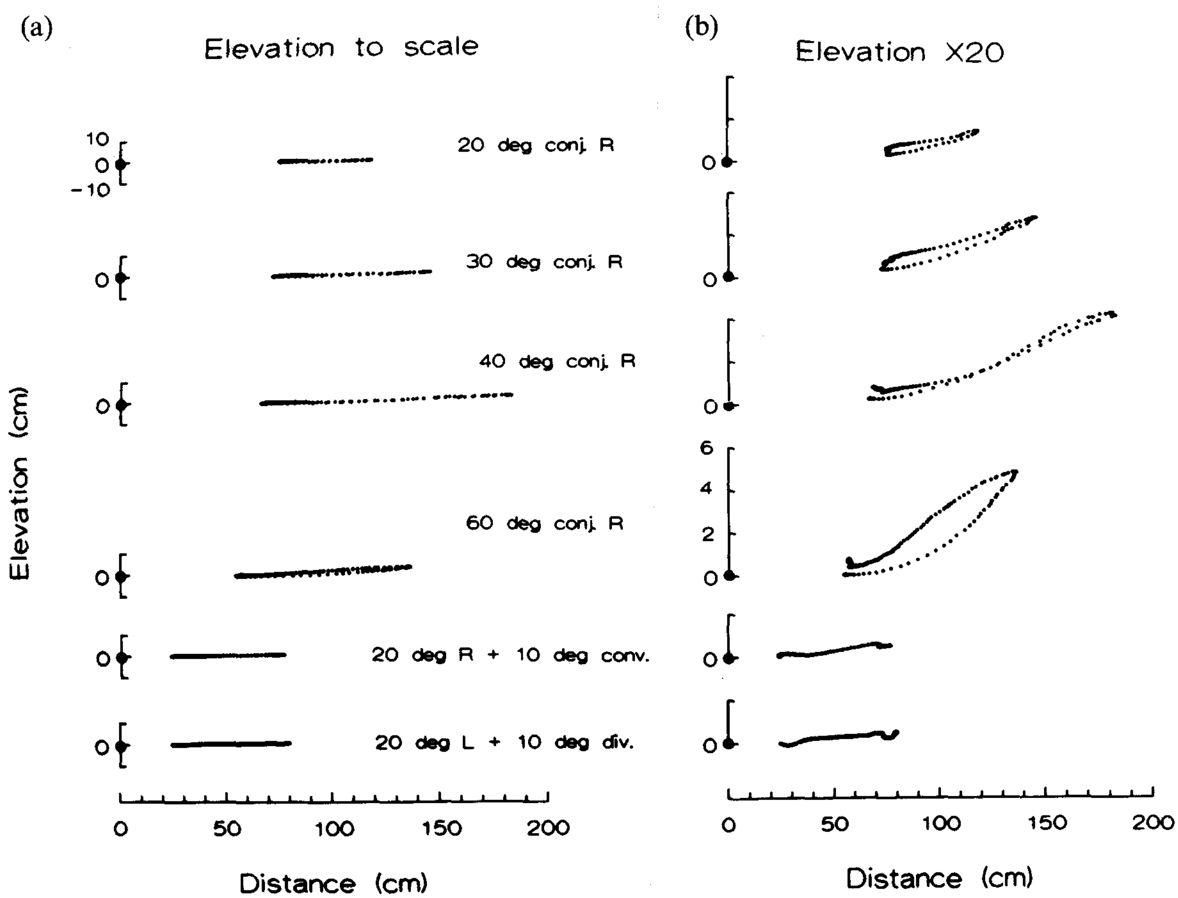

FIGURE 9. Projections of gaze-trajectories (subject: CE) on the sagittal plane, viewed from the right side, to illustrate that vertical components of horizontal gaze-shifts were very small. (a) Vertical and horizontal movements plotted on equal scales. (b) Vertical scale magnified ×20. The conjugate saccades (four upper traces) are also plotted in Fig. 6(a).

calculation of the binocular gaze-point, but any substantial vertical version would have to be taken into account in the calculation of gaze-trajectories, as projected on the horizontal plane of regard. To explore this point, the vertical position of the binocular gaze-point as a function of distance was plotted for a number of representative gaze-shifts in Fig. 9. Elevation in cm (Z) was calculated from distance (Y) and the vertical version angle λ:

$$Z = Y * \tan\lambda.$$

Vertical version was calculated as the average of the vertical positions of the two eyes:

$$\lambda = (\lambda L + \lambda R)/2.$$

Figure 9 represents the trajectories of horizontal gaze-shifts projected on a sagittal plane, seen from the right. The dots on the Y-axes represent the position of the eye. The important aspect of Fig. 9 is that the vertical component in the gaze-movements is very small. In Fig. 9(a), vertical and in-depth movements are plotted at equal scales. The upper four graphs represent conjugate saccades to the right at 5 deg iso-vergence for which the horizontal trajectories were also shown in Fig. 6(a). The deviations from a purely horizontal movement are so small, that for all practical purposes the simplified calculation of the gaze-trajectories, such as that shown in Fig. 6 is equivalent to a complete 3-D calculation of the gaze-trajectory with correct projection on the horizontal plane. Figure 9(b) shows the same trajectories as Fig. 9(a) with the vertical scale magnified by a factor of 20. These plots emphasize the small upward swing of the gaze-trajectory that appears to be characteristic of this subject (CE) and was shown in a different form previously (Fig. 11 in Collewijn *et al.*, 1988a). Somewhat similar vertical components, with idiosyncratic differences of detail, were also seen in the other subjects. In all cases, these vertical components were very small compared to the horizontal component. Therefore, the neglect of vertical components in plotting horizontal gaze-trajectories is justified for our present purposes.

Trajectories of non-conjugate gaze-shifts: a typical case

Trajectories of non-conjugate gaze-shifts were very different from those of conjugate gaze-shifts. Typical examples of trajectories (subject: AP) are shown in Fig. 10, which compares 20 deg version shifts with and without 10 deg simultaneous vergence. To give an impression of the time relations, separate data points were plotted after reduction by a factor of 2 to improve resolution (interval between successive plotted points: 4.1 msec). The conjugate trajectories were as described above [Fig. 7(a)]. The trajectory of a 20 deg rightward and 10 deg convergent movement [Fig. 10(a)] was very different from the conjugate 20 deg rightward movements, and showed characteristic successive phases: (1) the movement started with a convergent movement, which preceded the version component and followed an iso-direction line through the first (not the second) target; (2) when version started, the trajectory bent sharply towards the new direction, while convergence was halted or slowed down; (3) the new target was approached with a curved trajectory, resembling the middle and later segments of a conjugate trajectory; (4) the last part of the

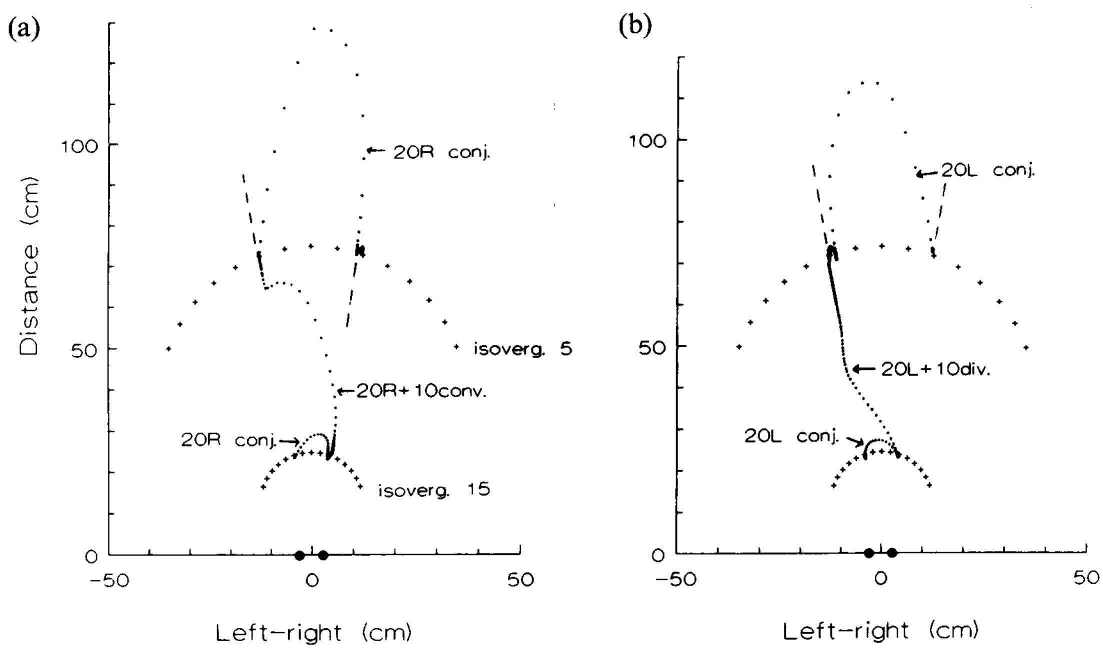

FIGURE 10. Representative examples of trajectories of non-conjugate gaze-shifts, in comparison to conjugate gaze-shifts. Subject: AP. To give an impression of time, data points are not connected by a continuous line. For optimal resolution, the number of data points has been reduced by a factor of 2; the interval between two successive data points is thus 4.1 msec. (a) Shows three separate movements: two conjugate, 20 deg rightward saccades at 5 and at 15 deg iso-vergence, and the non-conjugate combination of 20 deg rightward and 10 deg convergence. (b) Shows the same gaze-shifts in opposite directions (i.e., with divergence). The small loops that terminate the conjugate saccades at 5 deg iso-vergence are corrective saccades.

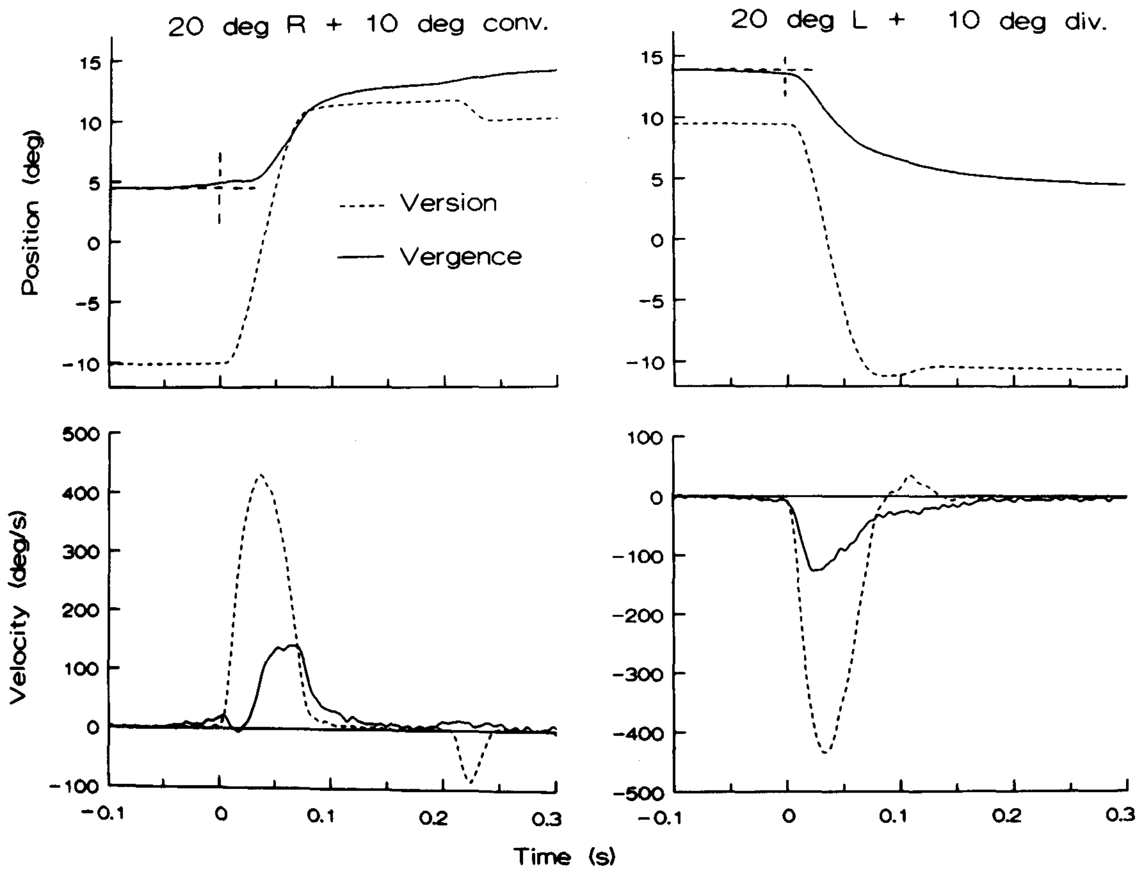

FIGURE 11. Vergence and version, plotted as a function of time, for the same non-conjugate gaze-shifts shown as trajectories in Fig. 10.

trajectory was slow again and consisted mainly of convergence along the iso-direction line through the new target.

The temporal relations between vergence and version are illustrated more directly in Fig. 11, which shows examples of version and vergence velocities plotted as a function of time. As will be elaborated in the next section, the precedence of version by convergence was consistently found among stimulus configurations and subjects, in agreement with earlier descriptions by Yarbus (1967). Although this first convergence component was small, it had a significant effect on the first part of the non-conjugate trajectory, because even small changes in vergence have a relatively large effect on gaze-position at low convergence angles. When version started, the trajectory showed a very much smaller tendency to swing outward than it showed during a conjugate saccade. Much of the transient divergence occurring during a conjugate saccade was suppressed during the convergent, non-conjugate gaze-shift, as can be seen also in Fig. 10. This interaction, which was systematically described in Collewijn *et al.* (1995), clearly had a large effect on the shape and range of the gaze-trajectory.

For the opposite non-conjugate movement, 20 deg left and 10 deg divergence [Figs 10 and 11(b)], the trajectory was very different. Although also in this case divergence started prior to version (Fig. 11), this change in vergence was not obvious in the initial phase of the trajectory, because this change started at a larger pedestal convergence (15 deg), where gaze-position is much less sensitive to small changes in vergence. The divergent trajectory could be roughly divided into two segments. In the first segment, there was a rapid displacement of gaze with divergence and version towards the new direction occurring together. In the second segment, gaze-movement was mostly confined to divergence, along the iso-direction line through the new target. As shown by the density of the data points in this later segment [Fig. 10(b)] and by the time-plot [Fig. 11(b)], this final divergence movement was relatively slow. Both segments were fairly straight.

Reconstruction of the trajectories in the other subjects corroborated the general validity of the description as given for Fig. 10 (subject AP). The trajectories of CE were virtually identical. ZP showed generally similar forms, except for the systematic distortions due to his spectacles; pre-saccadic divergence was expressed more clearly in his trajectories than in Fig. 10. HC showed atypical loops during conjugate saccades, which we relate to his habitual adaptation to non-isometric spectacles. These caused HC to make habitually smaller saccades with the left than with the right eye, a condition that would favor convergence during leftward version and vice versa. Our stimulus configuration happened to demand exactly the opposite combinations; this could be the reason that HC had to accomplish most of his

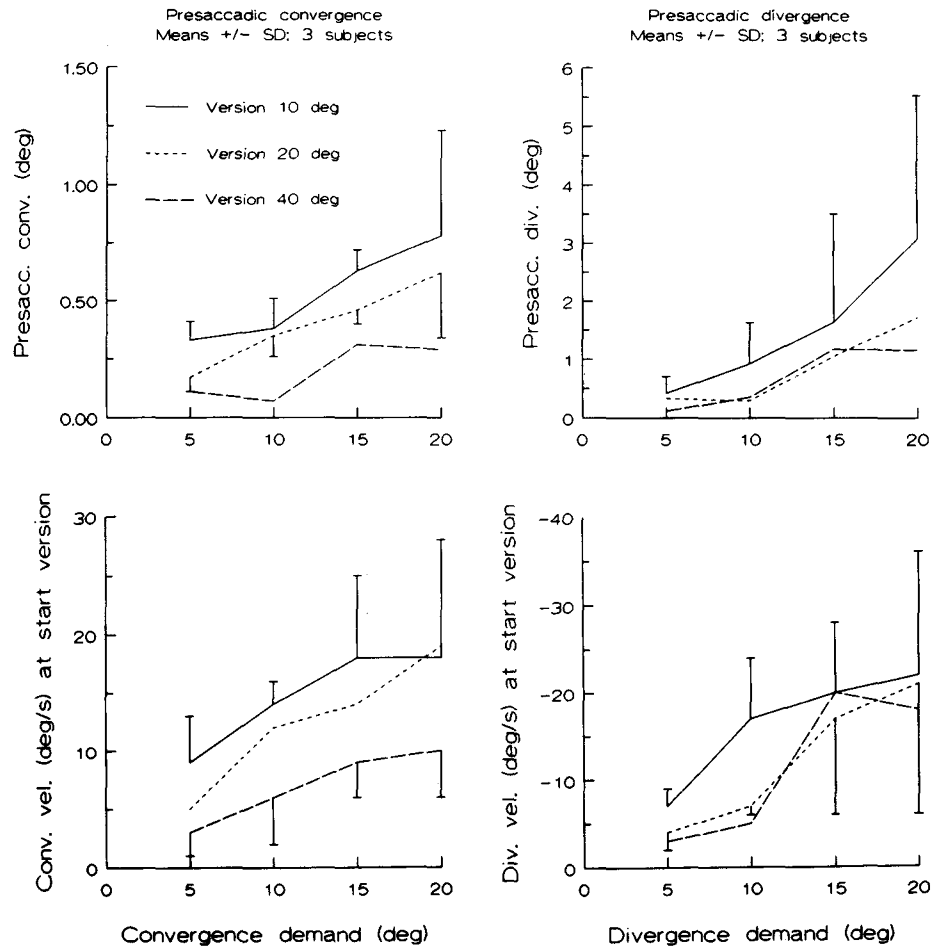

FIGURE 12. Summary of pre-saccadic convergence and divergence as a function of vergence and version demands. Means and some representative SD values for three subjects (AP, ZP, CE). Upper panels: amplitude of vergence preceding the version saccade; lower panels: vergence velocity at time of onset of version saccade. The main trends were present in each of the three subjects.

divergence after the saccade. The limited material for RS also showed basically similar forms, except for his inaccuracy in fixation, which may be related to his advanced presbyopia. Although HC was also fairly presbyopic, he had much less of a problem in viewing the present stimuli than RS, because HC is myopic while RS is emmetropic. For AM, only conjugate protocols were recorded.

Pre-saccadic vergence movements

The present way of plotting non-conjugate gaze-movements as trajectories made it very obvious that pre-saccadic vergence contributed significantly to the gaze-path, most obviously to the initial part of convergent non-conjugate gaze-shifts. Therefore, quantitative treatment of this aspect, which was not covered in our recent analysis of vergence–version relations (Collewijn *et al.*, 1995), became necessary at this point. As can be seen in Fig. 11, pre-saccadic vergence movements occurred largely in the period of about 100 msec prior to the beginning of the version saccade. Therefore, measurements were made of the vergence change between −200 and 0 msec. The velocity of vergence at 0 msec (the time of saccadic onset) was also measured. Means and SDs for three subjects (AP, ZP, CE) are shown in Fig. 12, for vergence demands of 5–20 deg and version demands of 10–40 deg.

Given the small number of data points, the large SDs are not reliable statistical estimates but they do illustrate the presence of a large range of magnitudes of pre-saccadic vergence across subjects. However, each of the systematic trends was present in each of these three subjects. Specifically, pre-saccadic convergence was in the appropriate direction in 35 out of 36 combinations, and pre-saccadic divergence was present in all of 36 cases. A less complete sample from HCs data showed the same. As an exception, RS showed no pre-saccadic vergence; given the limitations of his data we do not know whether he is truly different from the other subjects or only different while poorly refracted, as was the case here.

The general trends were as follows. Firstly, pre-saccadic vergence (amplitude and end-velocity) increased when the vergence demand increased, and pre-saccadic vergence was in the direction of the required vergence. Secondly, pre-saccadic vergence was large for small version demands, and much smaller for large version demands. Thirdly, pre-saccadic divergence tended to be larger in amplitude than pre-saccadic convergence (notice the scale differences between the upper panels in Fig. 12). The convergent and divergent vergence speeds at saccadic onset were, however, comparable. We did not analyze the duration of pre-saccadic vergence movements because their beginning was gradual and could not be located unambiguously.

The systematic pre-saccadic start of vergence, as shown in Fig. 12, deserves some further scrutiny because it raises two questions. The first question is: Is what we observe here true, symmetric pre-saccadic vergence movement, or is this vergence the expression of a very early asymmetry in the saccades, already apparent at the moment that we defined as saccadic onset (i.e., version velocity exceeding 15 deg/sec)? The second, related question is: Why is the substantial pre-saccadic divergence (Fig. 12) not at all obvious in the trajectory plots of Fig. 10 (and also Figs 15 and 16)?

To answer the first question, we measured the magnitude of pre-saccadic version associated with pre-saccadic vergence. In the case of symmetric vergence, version should be zero; in the case of a mere asymmetry of the early parts of the non-conjugate saccade, pre-saccadic version should be about half of pre-saccadic vergence.

We determined the pre-saccadic version/vergence ratio for the same body of data used for Fig. 12, with proper signing of the data (convergence and rightward version taken positive, and vice versa). For convergent gaze-shifts, the mean pre-saccadic version/vergence ratio was 0.10 ± 0.31 (SD; $n = 36$); for divergent gaze-shifts the mean ratio was 0.03 ± 0.18 (SD; $n = 36$). This result shows unequivocally that pre-saccadic vergence was, on average, very nearly symmetrical, and not caused by unequal but similarly directed movements of the two eyes. Furthermore, although pre-saccadic vergence was virtually always in the appropriate direction, this was not true for pre-saccadic version.

To illustrate this, Fig. 13 shows representative changes of vergence and version, as a function of time, around saccadic onset, for a convergent [Fig. 13(a)] and divergent [Fig. 13(b)] gaze shift (subject AP). A combination of 20 deg version and 20 deg vergence was chosen to show substantial (but not extreme) pre-saccadic movement (see Fig. 12). (The position signals have been arbitrarily shifted to accommodate the graphs to a scale with high resolution.) Figure 13 shows very clear pre-saccadic convergence and divergence in the directions appropriate for the imminent gaze-shift, whereas pre-saccadic version is much smaller. It also

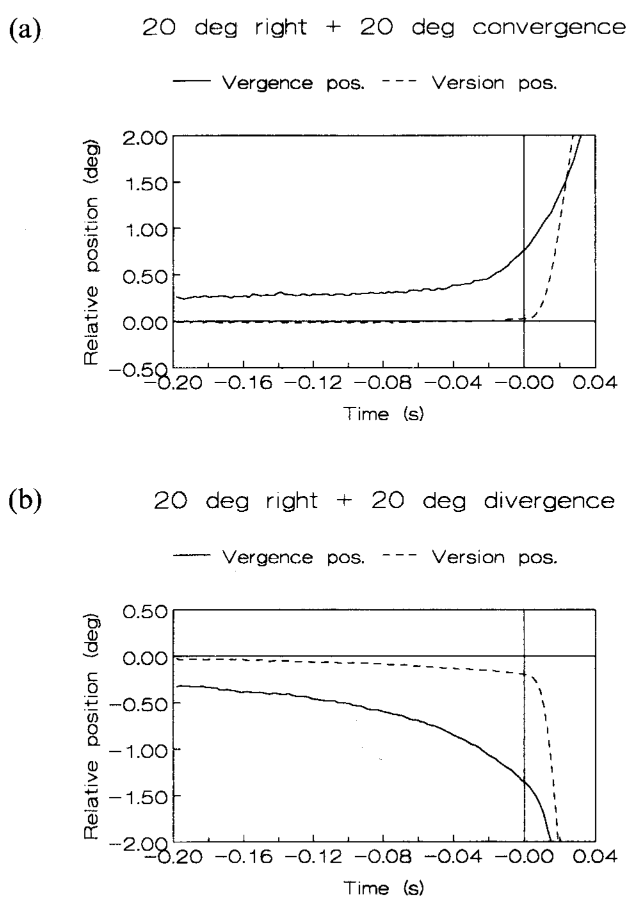

FIGURE 13. Details of pre-saccadic vergence and version angles for convergent (a) and divergent (b) gaze-shifts involving shifts of 20 deg in both vergence and version (subject: AP). This stimulus configuration was chosen for illustration because it elicits, on average (see Fig. 12), substantial (though not extreme) pre-saccadic vergence movements in the direction appropriate for the imminent gaze-shift. Saccadic onset (version velocity >15 deg/sec) is at $t = 0$. Positions have been shifted to fit the high-resolution scale; thus, the numbers on the ordinate do not represent absolute angles.

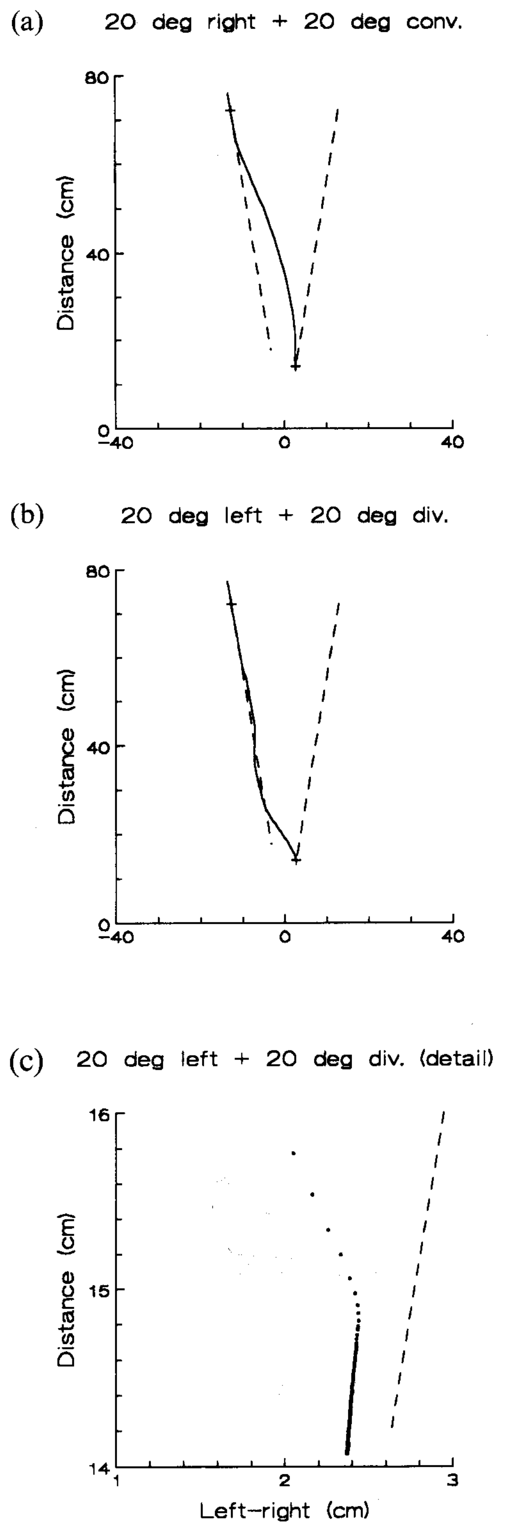

FIGURE 14. Pre-saccadic vergence (same cases as presented in Fig. 13) expressed in trajectories. (a) Convergent, non-conjugate gaze-shift (downward in figure). Targets are represented by crosses, iso-direction lines by dashed lines. Pre-saccadic convergence is visible as an initial segment of the trajectory (continuous line) following the iso-direction line through the first target. (b) Divergent non-conjugate gaze-shift (upward in figure). The final segment of the trajectory consists of pure divergence. The initial part of the trajectory is magnified (×40) in (c), which shows the iso-direction line through the near target (dashed line) and the trajectory as discrete samples (interval: 2.05 msec). The first segment, representing about 1 deg of pre-saccadic, symmetric divergence (corresponding to a change in distance of approx. 6 mm at the pedestal convergence angle of about 25 deg) runs parallel to the iso-direction line.

shows the very abrupt onset of saccadic version at $t = 0$, whereas the acceleration of vergence appears to be more gradual.

The second question, concerning the visibility of pre-saccadic divergence in the trajectory plots, turns out to be a matter of scaling. This is illustrated in Fig. 14, which shows in the upper and middle panels the trajectories of the same convergent and divergent gaze-shifts (subject AP) of which the initial parts are shown in Fig. 13, using similar scales as in Fig. 10. Whereas the initial phase of pure convergence over a distance of about 10 cm is apparent in Fig. 14(a), no initial segment of pure divergence can be distinguished in Fig. 14(b). When, however, the initial part of the divergent trajectory is magnified by a factor 40 [Fig. 14(c)], the initial pure divergence (covering a distance of less than 1 cm) becomes very obvious. Notice that this first segment runs almost parallel to the iso-direction line through the first target. (The offset of about 2 mm between the initial gaze trajectory and this iso-direction line results from accumulated experimental errors of measurement of target and eye positions, as well as the fact that the LED-targets had a width of several millimeters.) A simple calculation shows that is precisely the kind of result that should be expected for a similar change in vergence (about 1 deg) at near and far distances. For an interocular distance of 64 mm, vergence angles of 5 and 6 deg correspond (for midline targets) to distances of 73.3 and 61.1 cm, a difference of 12.2 cm. Vergence angles of 25 and 24 deg, however, correspond to distances of 14.43 and 15.06 cm, a difference of only 0.63 cm. (Compare also Fig. 1.) Thus, the inconspicuousness of initial pure divergence in most of the trajectory plots shown here is purely a matter of geometry and scaling.

Trajectories of non-conjugate gaze-shifts: the general case

The main properties described above for the combination 20 deg version and 10 deg vergence proved to be general for most combinations of vergence and version. This will now be shown in two cross-sections through the data; one with constant vergence (Fig. 15) and one with constant version (Fig. 16). Once again, the examples in Figs 15 and 16 are representative of the subjects in general. In Fig. 15, typical trajectories are shown for 10 deg vergence in combination with 0–60 deg version. Figure 15(a) shows the trajectories for convergent movements (change from 5 to 15 deg convergence). In the absence of a direction change (zero version), gaze moved from the far to the near target in a straight line in the mid-sagittal plane. With the addition of increasing angles of version (10–60 deg) the shape of the trajectory showed some gradual changes. The first part of the trajectory, however, remained straight. Interestingly, these initial gaze-changes followed, to a good approximation, iso-direction lines through the *first* target. Thus, this first part typically consisted of a nearly pure convergence towards the vergence angle of the new target, without expression of the change in direction

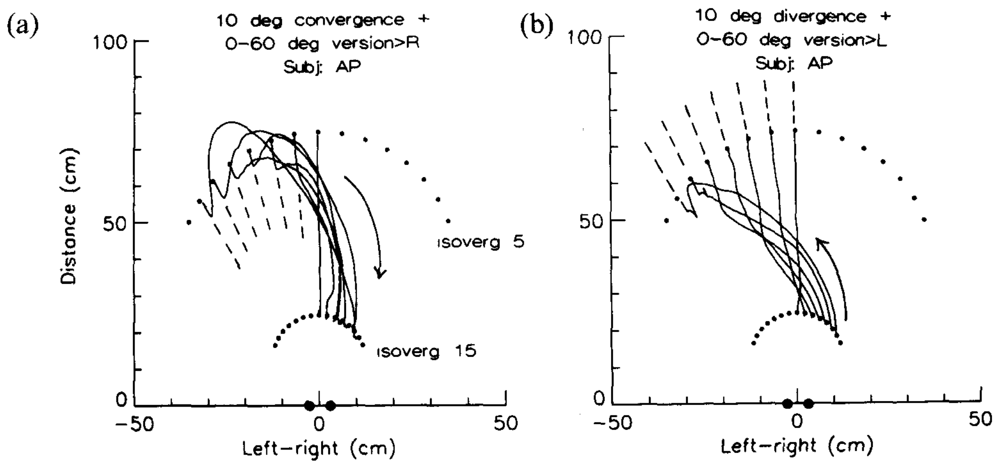

FIGURE 15. Typical families of trajectories for combined vergence and version gaze-shifts. Vergence fixed at 10 deg (changes between 5 and 15 deg convergence); version varying between 0 and 60 deg (in steps of 10 deg). (a) Convergence and rightward version. (b) Divergence and leftward version. Dashed lines are iso-direction lines. Subject: AP.

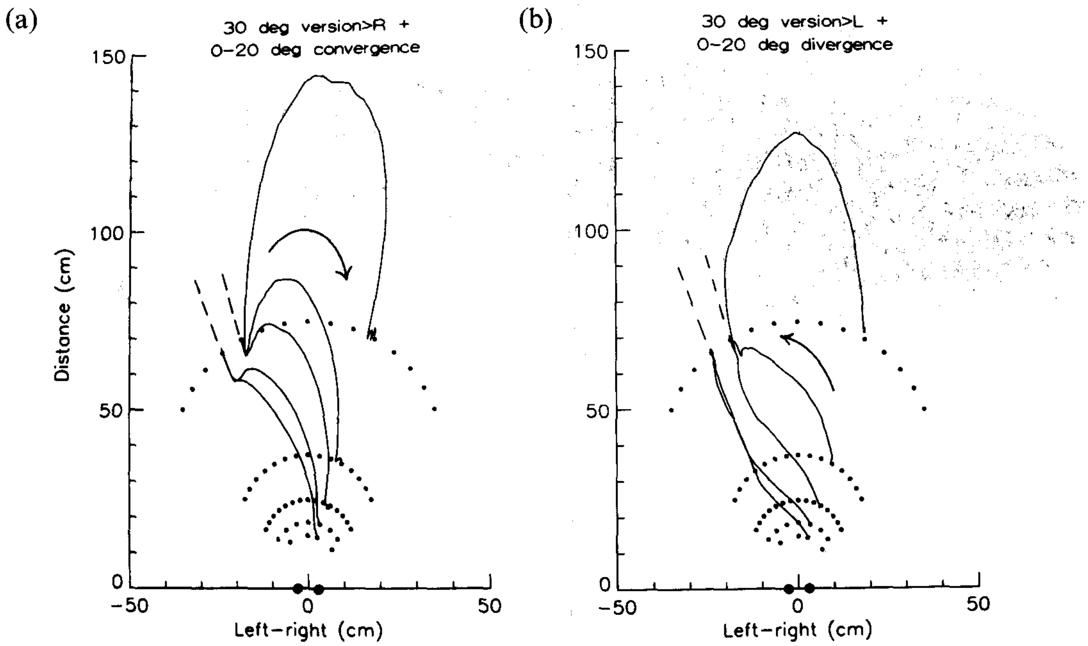

FIGURE 16. Typical families of trajectories for combined vergence and version gaze-shifts. Version fixed at 30 deg; vergence varying between 0 and 20 deg (in steps of 5 deg). (a) Convergence and rightward version. (b) Divergence and leftward version. Dashed lines are iso-direction lines. Subject: AP.

needed to acquire the new target. The second part of the trajectory started with a sharp bend, reflecting the start of the version movement. When the version angle between the targets increased in magnitude, the direction of this second part of the trajectory rotated gradually in a divergent direction, reflecting the tendency for initial divergence during horizontal gaze-shifts. Although this led to the emergence of an outward loop as described for the conjugate saccades, this outward loop remained very modest in size. Even for the largest changes in version (60 deg), the outward loops in the presence of a concomitant convergence stimulus [Fig. 15(a)] remained tiny, compared to the loops that were characteristically observed with conjugate gaze-shifts (Figs 6 and 7). Thus, the stimulus for convergence was apparently sufficiently strong to overcome most of the inherent tendency towards divergence. The further course of the trajectories was as already described, i.e., a gradual combined version and convergence movement towards the new target.

The trajectories of the opposite, divergent gaze-movements are shown in Fig. 15(b). In the absence of a version stimulus, divergence again followed a trajectory close to the mid-sagittal plane. The somewhat less straight course, compared to pure convergence, reflects the strong tendency for making some small saccades during divergence, even in the absence of any stimulus for version (Erkelens *et al.*, 1989b; Collewijn *et al.*, 1995).

The trajectories of combinations of divergence with version started with a nearly pure divergence [small and invisible at the scale of Fig. 15(b)], followed by combined divergence and version, *until* the trajectory reached the iso-direction line through the *new* target. From that point onward, the trajectory followed the appropriate iso-direction line in a nearly pure divergent movement, as was described before and illustrated in Fig. 10. This second segment was relatively long for small version angles, but became shorter as version requirements were increased. This is a consequence of the increasing percentage of divergence that is accomplished within the version saccade when the size of the version angle increases (Collewijn *et al.*, 1995). A divergent–convergent loop, as was typically seen in all conjugate and most convergent gaze-shifts, emerged only sporadically and inconsistently in the divergent gaze-shift trajectories with the largest version components. An example of this is shown in Fig. 15(b), for the largest version amplitude (60 deg). Also in this case, the trajectory terminated with a nearly pure radial movement that started as soon as the iso-direction line of the second target was reached.

Figure 16 shows a complementary cross-section through the data; here the shift in version was constant at 30 deg, while vergence was varied between 0 and 20 deg. The general trends described above are confirmed in this figure. For the convergent gaze-movements [Fig. 16(a)] the outward loop, which is large for the conjugate saccade, shrunk systematically as the additional convergent component was increased (in steps of 5 deg) to 20 deg. Thus, the trajectory became straighter as the convergence demand increased. The very first part of the trajectory consistently kept following a nearly pure convergence course, along the iso-direction line through the first target. The trajectories for divergence [Fig. 16(b)] appeared to start with a combined version and divergent movement; compare, however, Fig. 14(c), which clarifies that the very first, pre-saccadic phase of pure divergence does not show up at the scale of Fig. 16. The only exception is perhaps the trajectory for 5 deg divergence, with a change in vergence angle from 10 to 5 deg, in which a small initial segment of pure divergence is just visible, probably due to the increase in effect of changes in vergence on binocular gaze distance with the decrease in pedestal vergence (see Fig. 1). Also as an exception, this trajectory with the smallest divergence component (5 deg) still showed a vestigial outward loop. The other trajectories appeared to consist, at the scale of Fig. 16, essentially of two approximately straight segments, as described above for divergence. The first visible segment consisted of divergence and version; the second visible segment consisted largely of divergence alone, along iso-direction lines through the new target. The second segment increased in length as the vergence demand increased. This is in agreement with our previous finding that the percentage of divergence accomplished within the version saccades decreases as the vergence demand rises (Collewijn *et al.*, 1995).

DISCUSSION

Gaze-shifts between iso-vergent targets

Due to transient divergence, horizontal, conjugate gaze-trajectories typically follow an outward loop. The first segment of the loop consists of divergence and version, while the last segment consists mainly of convergence. The depth of the loop increases with version amplitude to a maximum for saccades of about 50 deg; some reversal of this trend appears for still larger saccades. The depth of the loop also increases, in an accelerating manner, as pedestal convergence values decrease. This trend implies that during gaze-shifts between targets at a distance, where pedestal convergence becomes smaller than the magnitude of transient divergence, the lines of sight will diverge beyond a parallel position and a real binocular fixation point will cease to exist during horizontal saccades. Independent experiments in Collewijn's laboratory (Van der Steen and Bruno, in preparation) have recently confirmed this trend for targets at simulated infinite distance.

Obviously, the binocular gaze-trajectories during horizontal saccades between iso-vergent targets are very different from the schema proposed by Yarbus (1967), in which he conjectured that trajectories follow a locus of iso-vergence. Strictly speaking, we have documented curved trajectories only for horizontal saccades, but it seems safe to generalize these observations to other planes of movement because almost all natural saccades will contain horizontal components, and even natural vertical saccades contain systematic, transient, horizontal vergence components (Collewijn *et al.*, 1988b; Enright, 1989).

The binocular gaze-trajectory is so curved that retinal projections of the binocular gaze point are unlikely to correspond to any feature of a real object in the surroundings. In particular, during horizontal saccades the binocular gaze trajectory will not follow anything like an iso-vergence, let alone an iso-distance surface. This implies that for approximately flat stimulus arrays, such as monitors, projection screens and printed text, gaze-shifts will be associated with substantial, transient, absolute disparities. As shown in Fig. 5, such disparities will vary, on average, between about 0.5 deg for small saccades to about 2 deg and more for larger saccades. Furthermore, their magnitude as well as their duration increase when the pedestal convergence angle increases (Figs. 4 and 5). Conditions for binocular correspondence will be worst in a task where large horizontal saccades have to be made at a short working distance; as shown in Fig. 5, disparities may then exceed 2 deg and last for more than 200 msec.

Why don't we, then, experience diplopia during and after horizontal saccades? A number of factors may mitigate this problem. First of all, we usually avoid such rather extreme demands as sketched above, and prefer to work under conditions that are appreciably more favorable. For instance, a typical reading task (see e.g. Kowler *et al.*, 1992) will involve a viewing distance of about 30 cm (vergence about 12 deg), and horizontal saccades of about 3 deg. Figure 5 shows that such working conditions may be associated with saccade-related transient disparities of about 0.5 deg amplitude and about 80 msec total duration. As the duration of the main part of 3 deg saccades is about 40 msec (e.g. Collewijn *et al.*, 1988a), substantial disparity would exist only during approx. the first 40 msec of the subsequent inter-saccadic interval, which lasts typically about 150 msec (Kowler *et al.*, 1992). This suggests that inter-saccadic fixations during reading will be binocularly correspondent for periods of about 100 msec, i.e., about two-thirds of the inter-saccadic interval. Admittedly, this is only a rough estimate, which takes into account only stability of vergence and neglects absolute errors of binocular fixation, as well as any effects of the width of the fusional area (Panum's area). This fusional zone may extend to as much as 1–2 deg. This extension was first documented as a special case when stabilized images were slowly diverged (Fender & Julesz, 1967). Later, dynamic disparities of similar size were shown to occur routinely, without interruption of fusion, during voluntary head movements (Steinman & Collewijn, 1980; Steinman *et al.*, 1982). Subsequent analytical experiments have further corroborated this phenomenon (Erkelens & Collewijn, 1985; Steinman *et al.*, 1985; Erkelens, 1988; see also Collewijn *et al.*, 1991). Robustness of fusion for transient disparities as large as 1–2 deg would easily accommodate the effects of saccadic transient divergence. In addition, transient increases in visual thresholds associated with saccades (usually known as "saccadic suppression", see Sperling, 1990) will contribute to the absence of clear perceptual correlates of the transient non-conjugacies.

Despite the rather marked effects of increasing tonic vergence on the dynamic yoking of the eyes, the peak velocity and duration of version saccades (i.e., the average movements of the two eyes) remained unaffected (Fig. 3). Version saccades between nearby targets were as fast as saccades between distant targets. Thus, the tonic vergence level influenced the (relatively small) *differences* between the saccades of the two eyes, but not the average saccadic movement as such. The possibility may be considered that these effects are not simply due to tonic vergence as such but also, or even wholly, to the different range in which the saccades are effected. Whereas at 5 deg convergence the saccades of both eyes are made nearly symmetrically about the mid-position, at 25 deg convergence the saccades of the two eyes are eccentric in opposite directions. For example, during a 30 deg leftward saccade, the left eye will make a centripetal saccade from 27.5 deg right to 2.5 deg left of its mid-position, while the right eye will move centrifugally from 2.5 deg right to 27.5 deg left. It has been shown that centrifugal saccades are slower, last longer and are more skewed than equally large centripetal saccades of the same eye (Collewijn *et al.*, 1988a). Such differences would work in the proper direction to account, at least qualitatively, for (part of) the effects of increased convergence on transient divergence; on the other hand, they would tend to average out for version. As all of these effects are fairly subtle, however, a quantitative evaluation of the effects of tonic vergence *vs* eccentricity would require a set of recordings dedicated specifically to this issue.

The lack of an effect of tonic vergence on the dynamics of version contrasts with the effects of dynamic changes of vergence. We showed before (Collewijn *et al.*, 1995) that saccadic version is slowed down during combined vergence and version gaze-shifts, compared to shifts of version alone. During such combined version–vergence gaze-shifts the saccades become strongly non-conjugate, especially when convergence is involved. As this non-conjugacy is associated with the slowing down (in comparison to conjugate saccades) of at least one and often both of the eyes, slowing down of version is the inevitable correlate (Collewijn *et al.*, 1995). Our present results show that this effect is related strictly to the change in vergence, not to its absolute level.

Gaze-shifts between non-isovergent targets

For four of the five subjects, the trajectories of convergent gaze-shifts in combination with version nearly always started with a pure convergence segment along the iso-direction line through the first target. This was followed by a sharp inflection marking the onset of version. The ensuing version–convergence trajectory showed an outward loop, but this was much smaller than in conjugate gaze-shifts with a similar version. The size of this loop increased when the version demand increased and decreased when the convergence demand increased. The trajectories of divergent gaze-shifts in combination with version generally consisted of three segments. The first segment consisted of pure divergence; due to the geometric relations (Fig. 1) this segment was too small to be visible in most of the trajectory plots presented here, although proper scaling [Fig. 14(c)] reveals it unambiguously. The second, much larger segment carried gaze in a combined divergence–version movement toward the iso-direction line of the new target. The final, third segment ran close to this line, and thus, consisted once more mainly of divergence. (Even if final divergence was not strictly symmetrical between the eyes, the trajectory would still be largely iso-directional in this phase because, at moderate convergence angles, the effect of changes in vergence on the distance of the binocular gaze point is much larger than the effect of a similar change in version on the lateral position of the gaze point; cf. Fig. 1). The length of this final segment increased when the divergence demand increased, and decreased when the version demand increased. An outward loop was usually absent in divergent gaze-shifts, but did appear in vestigial form when version was large or when vergence was small.

The trajectories of non-conjugate gaze-shifts differed substantially from those of conjugate gaze-shifts with a similar version component. The outward loop was absent or very much reduced in size. The vergence demand strongly affected the transient vergence so that the initial divergence was largely suppressed in convergent gaze-movements, while the convergence phase was suppressed in divergent gaze-movements. These basic effects have been noticed previously in our analysis of non-conjugate eye movements as a function of time (Collewijn *et al.*, 1995), but the present reconstructions, which are not easily visualized intuitively from time plots, make it particularly clear how strongly the vergence activity influenced the trajectory of the ongoing version.

The non-conjugate trajectories also revealed very clearly that the saccadic part of non-conjugate gaze-shifts is very commonly preceded by a beginning of vergence in the appropriate direction, whereas the transient divergence during conjugate saccades never had a pre-saccadic component and always started strictly synchronously with version (Fig. 8). This finding vindicates, at least qualitatively, Yarbus' (1967) observation of the initiation of non-conjugate gaze-shifts by vergence. The magnitude of the pre-saccadic vergence is related to the ratio *vergence demand/version demand*; it is larger for divergence than for convergence (Fig. 12). It is most clearly expressed in the trajectories of convergent gaze-shifts (Figs. 10, 15, 16). This is due to the stronger effect of small changes in vergence when pedestal vergence is low; the convergence movements started from about 5 deg convergence. As we established by measuring the concomitant version, pre-saccadic convergence is a relatively pure, symmetrical vergence movement, that follows the vergence demand of the new target, without being affected by its direction. Therefore, the initial, pre-saccadic convergence tends to follow an iso-direction line through the initial target. Pre-saccadic divergence was less distinct in most of the trajectory plots presented here, but this is essentially accounted for by the relatively smaller effect of small vergence changes at closer ranges. Plotting at a suitable scale (Fig. 14) clearly reveals a pre-saccadic divergence segment in the trajectory, and analysis of concomitant version suggested that pre-saccadic vergence in divergent gaze-shifts is even more symmetrical than pre-saccadic convergence in convergent gaze-shifts.

The finding of a segmentation of non-conjugate trajectories into pure vergence and mixed vergence–version parts seems to argue rather strongly for separate mechanisms controlling vergence and version. It appears as if the response to the "closeness" of a new stimulus can be dissociated, at least for a certain period, from the response to its direction. This seems to argue against a control system in which each eye more or less responds to its own stimulus, a possibility once raised by Ditchburn (1973) and recently advocated by Enright (1984, 1992). Rather in contrast, our findings suggest that target vergence and target direction may be processed and responded to separately, by ocular vergence and version oculomotor behaviors that do not necessarily completely overlap in time. In the very rare circumstances when only one system, vergence or version, is active, it shows its own characteristics. During the rest of the time in which both are operating, as they do whenever the head is free and the targets are within the range in which demands on vergence changes are large, the systems interact strongly: vergence is accelerated and version is modified to become non-conjugate.

REFERENCES

Becker, W. & Jürgens, R. (1990). Human oblique saccades: quantitative analysis of the relation between horizontal and vertical components. *Vision Research, 30*, 893–920.

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 Press.

Collewijn, H., Erkelens, C. J. & Steinman, R. M. (1995). Voluntary binocular gaze-shifts in the plane of regard: dynamics of version and vergence. *Vision Research, 35*, 3335–3358.

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

Collewijn, H., Erkelens, C. J. & Steinman, R. M. (1988b) Binocular coordination of human vertical saccadic eye movements. *Journal of Physiology, 404*, 183–197.

Collewijn, H., Steinman, R. M., Erkelens, C. J. & Regan, D. (1991). Binocular fusion, stereopsis and stereoacuity with a moving head. In Regan, D. (Ed.), *Binocular vision* Vol. 9 of Cronly-Dillon, J. (Ed.), *Vision and visual dysfunction* (pp. 121–136). Macmillan: London.

Ditchburn, R. W. (1973). Eye-movements and visual perception. (p. 353). Oxford: Clarendon 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 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.

Enright, J. T. (1992). The remarkable saccades of asymmetrical vergence. *Vision Research, 32*, 2261–2276.

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. (1988). Fusional limits for a large random-dot stereogram. *Vision Research, 28*, 345–355.

Erkelens, C. J. & Collewijn, H. (1985). Eye movements and stereopsis during dichoptic viewing of moving random-dot stereograms. *Vision Research, 25*, 1689–1700.

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

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.

Fender, D. & Julesz, B. (1967). Extension of Panum's fusional area in binocularly stabilized vision. *Journal of the Optical Society of America, 57*, 819–830.

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.)

Kowler, E., Pizlo, Z., Zhu, G., Erkelens, C. J., Steinman, R.M. & Collewijn, H. (1992). Coordination of head and eyes during the performance of natural (and unnatural) visual tasks. In Berthoz, A., Vidal, P. P. & Graf, W. (Eds), *The head–neck sensory motor system* (pp. 419–426). New York: Oxford University Press.

Lemij, H. G. & Collewijn, H. (1991). Long-term nonconjugate adaptation of human saccades to anisometropic spectacles. *Vision Research, 31*, 1939–1954.

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

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

Smit, A. C. & Van Gisbergen, J. A. M. (1990). An analysis of curvature in fast and slow human saccades. *Experimental Brain Research, 81*, 335–345.

Sperling, G. (1990). Comparison of perception in the moving and stationary eye. In Kowler, E. (Ed.), *Eye movements and their role in visual and cognitive processes* (pp. 307–351). Amsterdam: Elsevier.

Steinman, R. M. (1965). Effect of target size, luminance, and color on monocular fixation. *Journal of the Optical Society of America, 55*, 1158–1165.

Steinman, R. M. & Collewijn, H. (1980). Binocular retinal image motion during active head rotation. *Vision Research, 20*, 415–429.

Steinman, R. M., Cushman, W. B. & Martins, A. J. (1982) The precision of gaze. *Human Neurobiology, 1*, 97–109.

Steinman, R. M., Levinson, J. Z., Collewijn, H. & Van der Steen, J. (1985). Vision in the presence of known natural retinal image motion. *Journal of the Optical Society of America A, 2*, 226–233.

Viviani, P., Berthoz, A. & Tracey, D. (1977). The curvature of oblique saccades. *Vision Research, 17*, 661–664.

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

Acknowledgements—We gratefully acknowledge the assistance provided by Dr J. van der Steen in the development of part of the analysis software and thank Al Martins and Agnieszka Pizlo for serving as subjects. We also thank an anonymous reviewer, whose "skeptical" attitude helped us to strengthen this paper. This research was supported in part by AFOSR Grants 91-0124 and F49620-94-1-0333 and EEC Contract Nr. SC1*-CT91-0747 (TSTS).