

Binocular Gaze Movements: Coordination of Vergence and Version

HAN COLLEWIJN^{1*}, CASPER J. ERKELENS², ZYGMUNT PIZLO³
AND ROBERT M. STEINMAN⁴

¹*Department of Physiology, Erasmus University Rotterdam, The Netherlands,*

²*Utrecht Biophysics Institute, University of Utrecht, The Netherlands,*

³*Department of Psychological Sciences, Purdue University, West Lafayette, IN, USA*

⁴*Department of Psychology, University of Maryland, College Park, MD, USA*

Introduction

In traditional concepts of the oculomotor system, control of direction and distance of the binocular fixation point is attributed to two essentially independent subsystems. 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 by Hering (1868), has been supported by the finding of characteristic differences in the dynamic properties of saccadic and vergence movements, when investigated separately.

*Corresponding author

Classical investigations (Westheimer, 1954; Rashbass and 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/s, vergence velocities appeared to reach only tens of deg/s. This difference strongly argued for separate neurophysiological mechanisms controlling binocular direction and distance, a view which was 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.

From a functional perspective this straightforward dichotomy is puzzling because it would imply that the overall dynamics of natural binocular gaze shifts, which usually involve changes in distance as well as direction, are limited by the slow vergence component, so that targets distributed in 3-D space would typically not be foveated with saccadic velocities. Several more recent observations have, however, suggested a revised view of version and vergence control, with a less absolute separation between these subsystems.

Firstly, the very low vergence velocities elicited under laboratory conditions by changes in disparity as the only input (Rashbass and Westheimer, 1961; confirmed recently by Erkelens, 1987) are untypical for normal behavior. Natural gaze shifts between real targets that differ in distance but not in direction typically reach much higher vergence velocities. Erkelens *et al.* (1989a) measured an approximately linear relation between vergence velocity and vergence amplitude, with a slope on the order of 5 deg/s per deg of vergence, in agreement with earlier but incompletely documented data reported by Bahill *et al.* (1975). Thus, vergence shifts of 20 deg between real targets typically have peak velocities on the order of 100 deg/s.

Secondly, nonconjugate saccades that can not be accounted for by a linear summation of conjugate saccades with ongoing, smooth vergence have been documented first as curious exceptions (Ono and Nakamizo, 1978; Ono *et al.*, 1978; Kenyon *et al.*, 1980a,b) and later as the regular mode of operation in combined version-vergence shifts (Enright, 1984, 1986; Erkelens *et al.*, 1989a; Zee *et al.*, 1992). Similar version-vergence interactions have been reported for monkeys (Maxwell and King, 1992). The mechanism underlying these fast, nonconjugate gaze shifts is still unclear, although various possibilities have been proposed. Erkelens *et al.* (1989a) advocated that the saccadic system has an inherent ability to generate nonconjugate saccades, which is used in natural 3-D gaze shifts. The ability to generate nonconjugate saccades was further supported by experiments on adaptation to anisometric spectacles,

which clearly demonstrated plasticity in the size ratio between the saccades executed by the two eyes (Erkelens *et al.*, 1989b; Lemij and 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 and King, 1992). Zee *et al.* (1992) have proposed a mechanism for such facilitation in which 'vergence burst neurons' are disinhibited during saccades by the inactivity of pause cells.

Previous investigations of version-vergence interactions have been limited to a small range of combinations of changes in gaze angles. In more recent experiments, we have collected data covering a large range of combinations of changes in vergence (0–20 deg) and version (0–70 deg). The present report supplies a partial analysis of these data which suggests that the acceleration of vergence is not uniform throughout the range of version, that the interaction between version and vergence shows several systematic asymmetries, and that version is generally slowed down by the simultaneous occurrence of vergence.

Methods

Real targets (LEDs) were positioned on isovergence circles, subtending vergence angles of 5–25 deg with intervals of 5 deg. Directions ranged between 35 deg left and 35 deg right, likewise with intervals of 5 deg. In most conditions, all targets were in a horizontal plane at eye level. Differences in vertical direction were sometimes introduced: (1) targets on 5 deg isovergence circles were available at 4 elevation levels: (+10, 0, -10 and -20 deg); (2) the elevation of the closer targets could be continuously adjusted to arbitrary levels. 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 (usually about once per s). Nine subjects (two women, seven men; ages between 25 and 60 years) participated in some or all of the experiments. They were recruited from the authors and their colleagues and had no known deficiencies of binocular vision or oculomotor control. The results described in this report were obtained with the subject's head stabilized on a dental impression board, so that target viewing angles could be fully controlled.

Horizontal and vertical motions of both eyes were measured with the scleral coil technique and sampled at a rate of 488/s with a resolution of 1 min arc or better during trials lasting 10–16 s (for details of recording technique, see e.g. Collewijn *et al.*, 1988). Analysis of the digitized signals

involved detection of saccades fulfilling velocity and size criteria, in most cases averaging of a number (3–16) of successive saccades in a same direction between the same targets, and differentiation with a minimum of smoothing and no time shift. Version was calculated as the average of, and vergence as the difference between the positions of the two eyes. In all cases, time relations between the two eyes were conserved.

Results

Introductory remarks

Idiosyncracies

A first round of analysis of the extensive data sets of our nine 'normal' subjects showed that (a) performance was very reproducible throughout and between sessions within each subject; (b) very considerable and consistent differences existed between subjects. In fact, almost every subject had his or her own, unmistakable idiosyncracies lending a unique signature to eye movements. Individual variability included the level of saturated peak velocity during large saccades (between 400 and 600 deg/s) and the degree of facilitation of vergence by version (from slight to strong). This kind of variability is within the scope of the investigation and is part of the result. Other idiosyncracies were actually (borderline) deficiencies of binocular oculomotor control, making binocular eye movements less than perfect in five out of the nine subjects. Two subjects showed incomplete vergence at larger version angles; a third subject had nonconjugate saccades as a baseline condition due to the wearing of anisometric spectacles; a fourth subject showed a latent phoria that worsened during a session; a fifth subject was unable to make single, approximately accurate saccades and habitually made multiple, large secondary saccades to reach a target. The large inter-individual variability and the high frequency of manifest functional imperfections in a 'normal' population calls for caution in the interpretation of the findings; we have verified that the main trends described below do indeed occur to a considerable degree in all subjects.

The difficulty of executing 'pure' vergence

Execution of vergence was least efficient, and experienced as most difficult, when the vergence system was totally isolated, i.e. when two targets were aligned exactly in the same horizontal and vertical directions. Especially when target vergence differences were relatively small (5 deg), ocular vergence was often slow and even ambiguous. In many cases, vergence shifts were only half of the required size: one eye

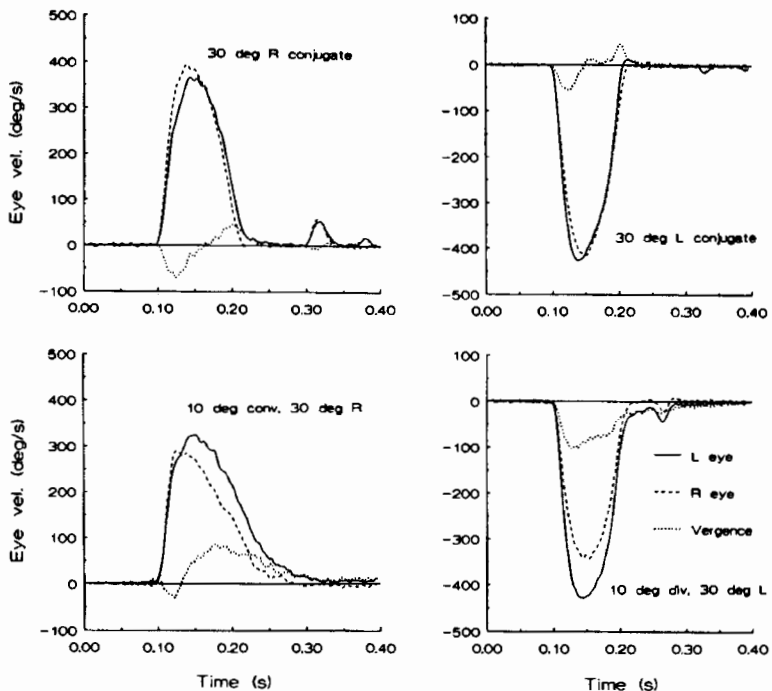


Fig. 1. Velocity profiles of the right and left eye and their difference (vergence) for conjugate saccades of 30 deg to the right and left (upper panels) and for combined version (30 deg) and vergence (10 deg) shifts (lower panels). In Figs 1 through 5, rightward and convergent movements are plotted as positive values. Each profile is the average of 3–4 successive saccades, variability among these saccades being negligible compared to any effect described. For consistency, all figures in this paper relate to the same subject (author CJE), who was one of the subjects showing fully adequate binocular oculomotor control.

continued to fixate the same target, while the other shifted to the nearer or farther target. Saccades often intruded, and indeed it was very hard to find records where vergence was both pure and effective. However, effective and unambiguous vergence was easily obtained by the introduction of a vertical offset (as small as 1 deg) between the near and far targets. We believe that the difficulty in shifting vergence between perfectly aligned, identical targets originates mainly from sensory confusion: the visual system has difficulty in establishing the appropriate correspondence between the (closely adjacent) disparate images in the two eyes and this may result in ambiguous motor control. A similar kind of ambiguity has been described previously both at the sensory (Krol and Van de Grind, 1980) and motor (Cogan, 1978) level. The 'pure vergence' case is obviously rather academic, because it is a limiting case that will be exceedingly rare under natural conditions with a freely

moving head. Actually, it could be very misleading to characterize vergence behavior on the basis of the responses to such unusual stimuli.

Version-vergence interaction: the basic picture

While it was argued above that pure vergence hardly occurs, because virtually every natural change in distance will involve some change in direction, it is also the case that pure version, in which both eyes would make exactly identical angular movements, does not occur. All horizontal saccades are accompanied by a transient divergence in humans (Collewijn *et al.*, 1988; Zee *et al.*, 1992) and monkeys (Maxwell and King, 1992). The phenomenon is illustrated in Fig. 1 (upper panels) for "conjugate" saccades of 30 deg. The velocity profiles of the binocular saccades to the right and to the left show that the abducting eye consistently accelerates faster and reaches a higher peak velocity than the adducting eye. As a result, the eyes diverge in the early (accelerating) phase of each horizontal saccade. This is followed by convergence in the decelerating phase of the saccade, when the adducting eye generally maintains a higher velocity than the abducting eye.

Thus, in horizontal saccades, the abducting eye shows a higher acceleration, a higher peak velocity, a slightly shorter duration and a slightly larger amplitude than the adducting eye (Collewijn *et al.*, 1988). By the end of the saccade, most of the initial divergence has been compensated by the later convergence; any remaining misalignment is usually corrected by postsaccadic drift. The transient divergence associated with all horizontal saccades is a very robust phenomenon that will affect any further interaction between version and vergence: it would be logical to predict an asymmetry in its effects on additional convergence and divergence.

The lower panels of Fig. 1 show that this is indeed the case. The left lower panel shows the typical relations found for a combined version (30 deg rightward) and convergence (10 deg). In the initial phase of the eye movement, the abducting (right) eye still accelerates slightly faster than the adducting (left) eye, but the remaining divergence is much smaller than in the corresponding conjugate saccade (left upper panel) and soon superseded by a strongly enhanced convergent movement, in which the adducting eye actually reaches a higher intrasaccadic peak velocity than the abducting eye. The adducting eye continues to move faster than the abducting eye during the decelerating phase of the saccade. As a result, a major fraction of the required convergence is accomplished within the duration of the saccade, although it is clear that significant postsaccadic vergence and version drifts contribute to the completion of binocular foveation. One could conclude that, due to the demand for convergence along with version, the adducting eye has now made

a larger saccade than the abducting eye: the saccadic velocity profile of the adducting eye shows a higher peak velocity, a longer duration and thus a larger amplitude. Actually, the adducting eye has to move 35 deg, while the abducting eye has to move 25 deg to reach the target. Independent programming of the saccades of both eyes could accomplish this by generating a 35 deg saccade for the left eye and a 25 deg saccade for the right eye. Closer inspection of the velocity profiles (Fig. 1, left panels) suggests, however, that this is not the actual mechanism in operation. In comparison to the conjugate saccade, the saccade incorporating convergence shows a markedly lower peak velocity and longer duration for *both* eyes, which suggests that neither of the eyes makes a typical 'main sequence' saccade. A special difficulty in comparing the conjugate and convergent saccades is the very gradual deceleration of the latter, which makes the determination of the *duration* of these disjunctive saccades rather arbitrary and very dependent on the choice of a criterion for the end of the saccade. Therefore, we shall concentrate here on peak velocities, which can always be determined unambiguously.

The lower right panel of Fig. 1 shows a combined 30 deg version and 10 deg divergence. This case is clearly different from the convergent case: the abduction-adduction asymmetry of conjugate saccades is enhanced rather than reduced, and as a result the required divergence is built up right from the beginning of the saccade. The early divergence becomes permanent instead of transient, and is not followed by convergence during the decelerating phase of the saccade. It is apparent that the inherent abduction-adduction asymmetry of horizontal eye movements antagonizes convergence, but is synergic with divergence. The better compatibility of divergence than convergence with horizontal saccades is also evident from the overall velocity profiles (Fig. 1, right panels). The abducting saccade (left eye) in the divergent case is about as fast as in the conjugate case, while the adducting saccade (right eye) is markedly slowed down in the divergent case. Also saccadic duration seems much less affected than in the convergent case, although there is still a significant 'tail' of postsaccadic divergence.

These basic observations illustrate some of the complexities in version-vergence interaction. Next, we shall examine the effect of variation of the amplitude of version, with a similar vergence amplitude.

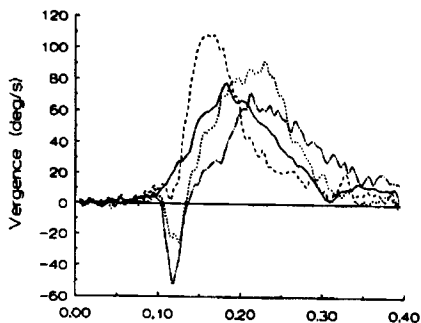
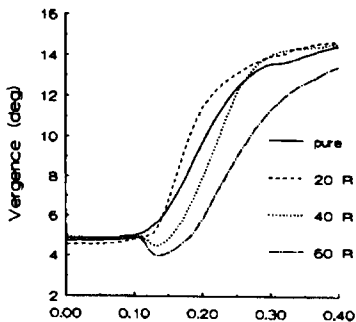
Vergence dynamics as a function of version magnitude

Figure 2 illustrates the basic effects of increasing shifts in direction (0, 20, 40 and 60 deg) on the course of convergence or divergence with a constant size of 10 deg. (Actually, the vergence shifts occurred between 5 and 15 deg convergence.) The "zero version" cases represent "pure" vergence cases, in which the stimulus contained no demand for horizontal

version. This case, however, presented special difficulties, because "ideal" examples of pure vergence, without any saccadic shifts in version, could practically not be found in any of our subjects. In virtually every record, some saccadic component was evident in the traces of the individual eyes. Especially cases of saccade-free divergence were virtually non-existent, whereas saccade-free convergence was found to occur occasionally, and more often with large (20 deg) than small (5 deg) vergence movements. To present the best approximation of pure vergence, we selected records with the least and smallest saccades, to minimize the saccadic contribution to vergence, and we show only the vergence traces.

The left upper panel of Fig. 2 shows the position traces of 10 deg convergent movements as a function of time, for different sizes of version. The right upper panel shows the corresponding vergence velocities.

Effect of version on convergence (10 deg)
Version 0, 20, 40 and 60 deg



Effect of version on divergence (10 deg)
Version 0, 20, 40 and 60 deg

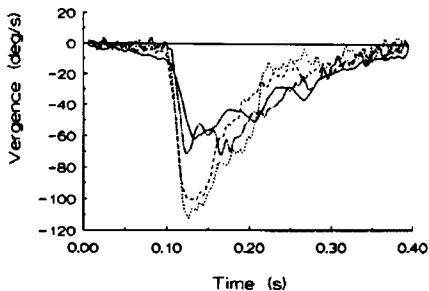
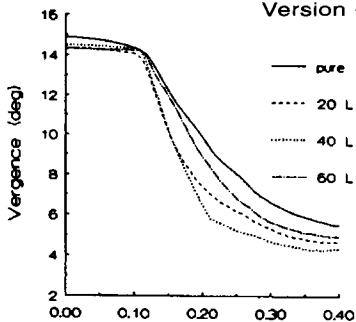


Fig. 2. Position and velocity profiles of vergence during convergence (top) and divergence (bottom) of 10 deg, in combination with 0, 20, 40 or 60 deg of version. All vergence traces are synchronized on the beginning of vergence (for pure vergence) or the beginning of version (when present).

The trends illustrated in these figures were essentially found in all subjects. Essentially, convergence was enhanced by version movements of intermediate sizes, but hampered by large version movements. The position plots show that convergence associated with 20 deg version was faster, and reached the required convergence angle sooner than pure convergence. The velocity profile shows a higher and earlier occurring peak velocity and a shorter duration compared to pure convergence, while the transient divergence is virtually abolished. There is, however, no progressive enhancement of convergence with further increases in the version amplitude. With 40 deg version, initial divergence is manifest again, and causes a marked delay of the convergence movement. Although the latter still shows a higher peak velocity than pure convergence, the overall completion of convergence is only marginally faster than pure convergence. For 60 deg version, the effects on convergence are only detrimental. The large initial divergence movement delays the convergence movement by about 50 ms, without any gain in peak velocity.

For divergence (Fig. 2, lower panels) the results are quite different. Pure divergence (i.e. divergence with a minimum of saccadic contribution) was nearly always slower than pure convergence. On the other hand, additional version always enhanced divergence, although also in this case very large saccades were relatively less beneficial than those of intermediate size. The position profiles (Fig. 2, left lower panel) show a considerable acceleration of divergence by a 20 deg version movement, and an even stronger one by 40 deg version. The effect of 60 deg version shows a diminishing, but still clearly present, enhancement. The velocity profiles also show that version strongly accelerates the initial divergence, with a shortening of duration.

Separating transient vergence from true vergence

The essential effects of version on vergence are somewhat difficult to evaluate from plots such as shown in Fig. 2, because part of the changes in velocity profiles may just reflect the transient vergence associated with any horizontal saccade. As these transients increase progressively with the size of the saccades, at least part of the increase in velocity peaks visible in Fig. 2 might be interpreted as a fairly trivial contamination which does not effectively contribute to vergence. To unravel true enhancement from spurious effects, we attempted to eliminate the transient vergence component by *subtracting* the vergence component of conjugate saccades from the vergence during disjunctive saccades. Obviously, each subtraction involved versions of commensurate amplitude. Despite this precaution, the results are only approximately valid for reasons that will become clear later on.

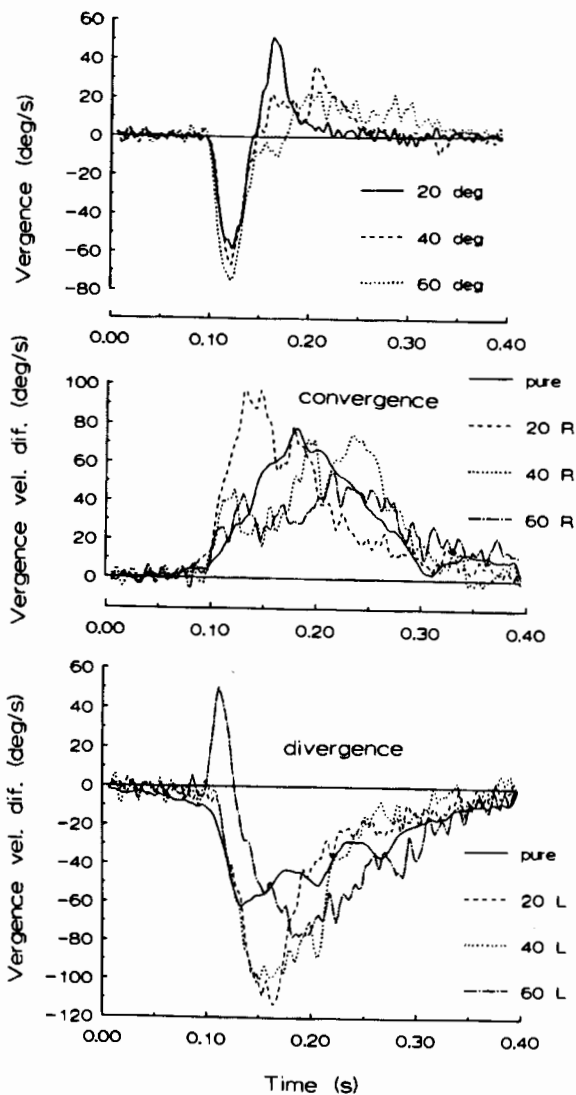


Fig. 3. Removal (by subtraction) of the transient vergence components, associated with conjugate horizontal saccades, from vergence during combined version-vergence movements, in order to show the genuine effects of version on vergence. Upper panel: velocities of transient vergence during conjugate saccades of 20, 40 and 60°. Middle panel: convergence (10°) combined with 0, 20, 40 or 60° version, as in Fig. 2, right upper panel, after subtraction of the transient vergence, shown in the upper panel (except for pure vergence).

Lower panel: analogous to middle panel, for 10° divergence. This panel is equivalent to the right lower panel of Fig. 2, with the upper panel of Fig. 3 subtracted. See text for further explanation.

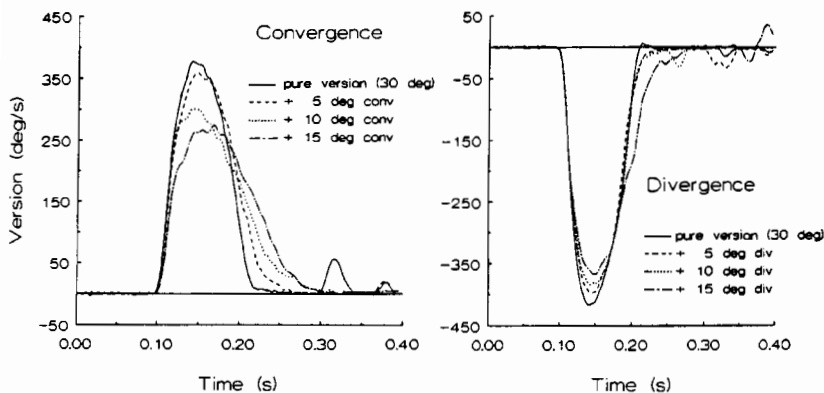


Fig. 4. Velocity profiles of 30 deg version, which was conjugate or combined with 5, 10 and 15 deg vergence. Notice the slowing and lengthening of version with increasing vergence, especially convergence.

The upper panel in Fig. 3 shows the vergence velocities associated with conjugate shifts in version (20, 40 and 60 deg) along the most distant isovergence circle, subtending 5 deg of convergence. Transient vergence clearly depends on version amplitude: the initial divergence peak velocity grows with the saccadic amplitude but remains fixed in time, whereas the subsequent convergence peak velocity is high and comes early for saccades of intermediate size but is progressively lower and arrives progressively later for increasingly large saccades. This general pattern, which was evident in all subjects despite some idiosyncratic variations, shows several features of the velocity diagrams shown in Fig. 2.

The middle panel of Fig. 3, representing convergence, is equal to the right upper panel of Fig. 2 after subtraction of the upper panel of Fig. 3 (except for the pure vergence case, which is unchanged). The result is illuminating. The divergence velocity peaks are neatly eliminated, and the convergence velocity peaks are lowered. The true contribution of version is now clarified: compared to pure convergence, convergence in combination with 20 deg version is markedly faster and shorter. The overall effect of larger versions (40 and 60 deg) on convergence is, however, largely detrimental. The lower panel of Fig. 3, representing divergence, shows the difference between Fig. 2, right lower panel, and Fig. 3, upper panel. Clearly, shifts in vergence of 20 and 40 deg strongly accelerate divergence, while the effects of a 60 deg version are somewhat mixed, though positive on balance.

Essentially similar results as for 10 deg vergence movements were seen for 5, 15 and 20 deg vergence shifts. The general conclusion is that vergence is indeed accelerated by saccadic version, but within certain limits. For convergence, only saccades with angular amplitudes up to

about twice the vergence amplitude are helpful; larger saccades have a negative effect. For divergence, the effect of saccades is positive throughout the range of version, although the best effect is seen with saccades of intermediate size.

The effects of vergence on version

Until now, the discussion of the interaction between version and vergence has focused on the enhancement of vergence, while any reciprocal effects have received little attention. It was mentioned, however, in connection to Fig. 1, that vergence also appears to affect the overall properties of saccades. To examine any such effects more in general we have plotted in Fig. 4 the velocity profiles of version (the average of right and left eye) with a constant amplitude of 30 deg for conjugate saccades and combinations with 5, 10 and 15 deg vergence.

Very clear effects are indeed demonstrated. For convergence, there is a strong and systematic decrease in peak velocity and a commensurate increase in duration as a function of the increase in convergence. For divergence, the effect is similar, though clearly smaller. These effects diminish the validity of the subtraction operation, practised in Fig. 3, somewhat because the actual time course of the vergence components in conjugate and disjunctive version can no longer be assumed to be synchronous.

We have to conclude that version-vergence interaction works in two directions: version accelerates vergence, but vergence decelerates version.

The effects of vergence on the saccades of individual eyes

In view of the significant asymmetries between abduction and adduction on the one hand, and convergence and divergence on the other hand, it is necessary to investigate the general effects of vergence on version, indicated above, in more detail for each eye apart. As a starting hypothesis, one might suppose that the asymmetries might make some combinations more easy to execute than others. For instance, abduction and divergence would seem to work in similar directions; thus, one might expect that an eye that abducts during a divergence might move as fast, or even faster than during a conjugate saccade of comparable size. A similar effect might apply for the combination of convergence and adduction. In contrast, the combinations convergence with abduction or divergence with adduction would seem to be antagonistic and more likely to slow the eye movements down. The actual effects are shown in Fig. 5.

The left upper panel shows the combination adduction and

Convergence

Divergence

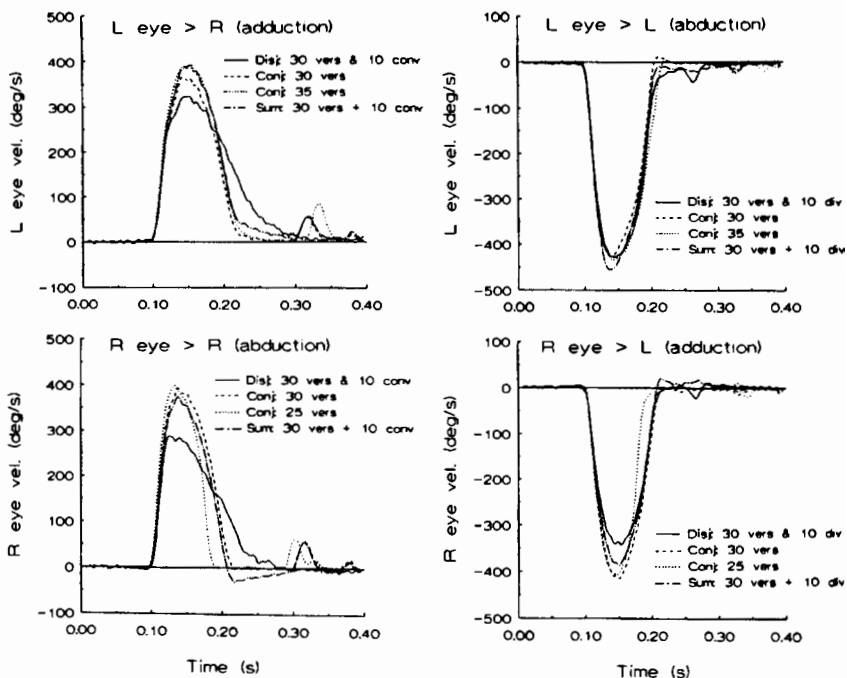


Fig. 5. Comparisons of velocity profiles of different types (convergent, divergent and conjugate) and directions (abduction or adduction) of eye movements. All records from same subject, same session. See main text for further explanation.

convergence (left eye moving rightward). The actual disjunctive movement (30 deg version and 10 deg convergence) is represented by the solid line. For comparison, two version movements (same eye, same subject, same session) which were part of conjugate saccades are shown, with amplitudes of 30 deg (dashed) and 35 deg (dotted). The 30 deg conjugate saccade corresponds in size to the 30 deg overall version, while the 35 deg saccade corresponds in size to the actual motion of the eye. The plot shows that the actual disjunctive eye movement resembled neither of these conjugate saccades: it was substantially slower and lasted longer. A further comparison was made by generating a synthesized, theoretical eye movement ('sum'; dash-dot line), consisting of the summation of the 30 deg conjugate motion and the appropriate half of a pure convergence movement of 10 deg. (Half the vergence was used instead of the real recorded motion of the particular eye, to minimize contamination by saccades.) Again, this theoretical curve did not match at all with the real disjunctive movement. Thus, our expectation that

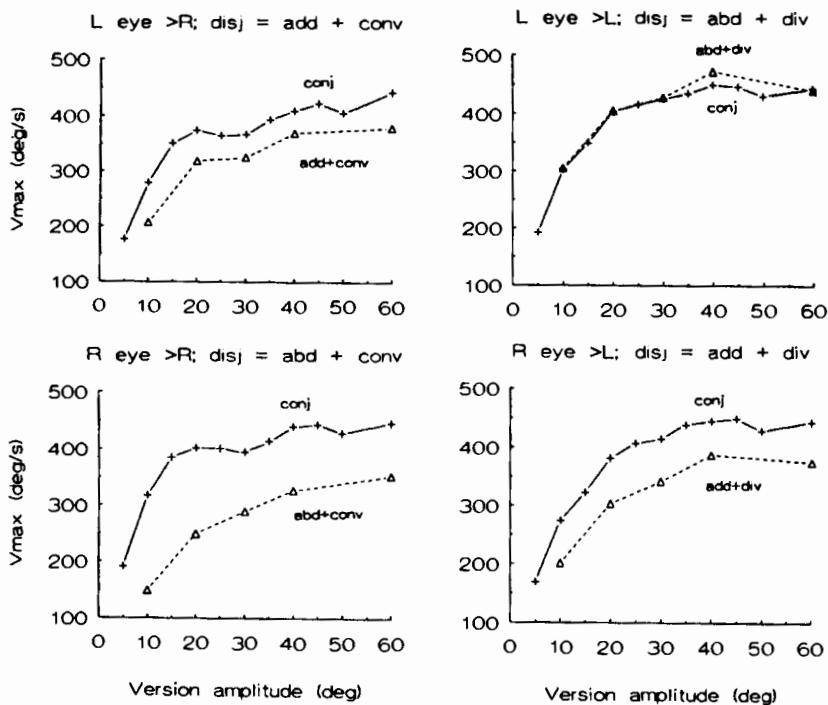


Fig. 6. Peak velocity-amplitude diagrams for various conjugate and disjunctive gaze shifts. The four possible combinations of abduction, adduction, convergence and divergence are shown in conjunction with conjugate saccades. The lay-out of the four panels corresponds to the combinations shown in Fig. 5, except that all velocities have been plotted as absolute values.

the combination of adduction and convergence might result in relatively fast eye movements was disproved: the actual eye movements were slow.

The other theoretically favorable combination, abduction with divergence, is illustrated in the right upper panel of Fig. 5. Different types of movement, including the theoretical sum of pure version and pure divergence, are plotted in an analogous way as for the case discussed above. This time, the discrepancy between the real disjunctive movement and the corresponding conjugate components is very minor, and it appears that the diverging and abducting eye executes a saccade which is almost identical to a conjugate, main-sequence saccade of similar size. This is the only combination for which this seems to be true.

The left lower panel of Fig. 5 gives the results for the combination abduction and convergence for the right eye. The correct conjugate movements to compare are in this case 30 deg (the version component)

and 25 deg (the actual amplitude of the disjunctive eye movement). Once more, the real disjunctive movement deviates strongly from both of these conjugate saccades and from the sum of pure version and pure convergence: peak velocity is much lower and duration much longer. For the combination adduction and divergence (Fig. 5, right lower panel) the discrepancies are smaller: the real disjunctive eye movement has a peak velocity lower than that of a 25 or 30 deg saccade but has the same duration as a 30 deg saccade (the actual amplitude of the disjunctive movement being 25 deg).

A more systematic analysis, for the same subject shown in Fig. 5, is given in the peak velocity–amplitude relations of Fig. 6. Peak velocities of conjugate movements are plotted in conjunction with peak velocities of disjunctive eye movements with corresponding version components and 10 deg vergence components. The lay-out of the diagrams corresponds to that of the combinations in Fig. 5, except that all velocities have been plotted as absolute values, as customary for 'main sequence' diagrams. These data show that the trends described above can be generalized across the whole oculomotor range of amplitudes. The exceptional combination (right upper panel) is abduction with divergence, which occasionally even shows hints of peak velocities exceeding conjugate saccadic peak velocities; a trend which was noticed in several other subjects for whom a similar analysis was completed. All other combinations consistently generated peak velocities lower than conjugate peak velocities, the worst combination being abduction with convergence.

The effect of vertical saccades on horizontal vergence

Finally, we studied the systematic effects of vertical shifts in version on horizontal vergence. This aspect is important in the light of suggestions for a model in which the acceleration of vergence by saccades is related to the saccadic inhibition of (omnidirectional) pause-cells (Zee *et al.*, 1992). The systematic effects of vertical gaze shifts are anisotropic. Upward saccades strongly accelerate divergence. Downward saccades accelerate convergence mildly. The maximum convergence and divergence speeds reached in these conditions (for vertical saccades of 30 deg) were about equal; however, convergence was already much faster than divergence in the condition without a vertical saccade. This difference in baseline speed for convergence and divergence may underlie the asymmetry. The other combinations, i.e., downward saccades with divergence or upward saccades with convergence, have only very modest enhancing effects on vergence for small (10 deg) vertical saccades, while the effect of larger saccades (20 and 30 deg) is mostly unfavorable (vergence being slowed down and delayed). This anisotropy was consistently present

in the 4 subjects tested for effects of vertical saccades.

Discussion

Analysis of version-vergence interactions over a larger range of amplitudes than was explored in previous studies (Erkelens *et al.*, 1989; Zee *et al.*, 1992; Maxwell and King, 1992) reveals that facilitation of vergence by directional gaze shifts (saccades) is not uniform across the range of version amplitudes. Convergence is facilitated during saccades that are not larger than about twice the vergence amplitude; larger saccades cause a progressive delay of convergence, combined with progressively lower peak convergence velocities. On the other hand, divergence is facilitated by saccades throughout the range of version, although in this case too the effect is most pronounced for saccades of intermediate size. The effects of vertical saccades also show a marked anisotropy, the combination upward saccade with divergence being far more effective in accelerating vergence than any of the other possible combinations.

This great variability in facilitation of vergence by version, with strong dependence on direction and size, seems to argue against models in which the saccadic interruption of activity of omnidirectional pause cells releases the activity of saccade-related vergence burst neurons (Zee *et al.*, 1992). In such a model one would expect a progressive enhancement of vergence with increasing size of saccades, because inactivity of pause neurons will be longer for larger saccades; moreover, the effects of vertical saccades would be as large as of horizontal saccades, and independent of direction. The actual results do not follow this straightforward pattern, and suggest a more diversified type of interaction.

A second important finding is the large effect of vergence on version: while version facilitates vergence, vergence clearly slows down version. These effects show a marked, specific differentiation for combinations of convergence or divergence with abduction or adduction of each individual eye. Only the combination abduction with divergence yields eye movements that are very similar to conjugate saccades; all other combined movement types are considerably slower than conjugate saccades of comparable sizes, particularly the combination abduction with convergence. These findings suggest that version and vergence are tightly interconnected and that each of these subsystems influences the other profoundly. Neither version nor vergence are likely to be seen in a 'pure form'. Pure vergence is very hard to obtain; particularly divergence without some small saccades is most exceptional. This may be a consequence of the divergence associated with each horizontal saccade; it is so much easier to diverge with the assistance of this transient divergence that asking for 'pure' divergence amounts to requesting very

unnatural behavior.

It seems not feasible at this moment to incorporate all the particulars of version-vergence interaction in a functional model, without making abundant ad-hoc assumptions. More neurophysiological facts will be needed about the control of conjugate and disjunctive binocular eye movements; behavioral evidence (Maxwell and King, 1992) suggests that the monkey may be a reasonable model for human behavior in some respects. Nevertheless, the present findings seem to make certain classes of models less plausible. The strong deviations of disjunctive eye movements from regular saccades argue against models in which disjunctive eye movements are simply generated by independently controlled, separate saccade generators for the left and right eye. Neither is it generally the case that the eye making the larger movement makes a saccade obeying the main sequence for conjugate saccades, while the fellow eye is just slowed down, retaining a similar duration: this situation may be approximated in divergent movements, but certainly not in convergent movements, during which both eyes are always very much slowed down compared to conjugate movements.

Our findings seem to also exclude models which assume a one-way action of version on vergence. The substantial changes in version during vergence argue for a mutual interaction, in which both subsystems strongly affect each other. We conclude that version and vergence operate in a strongly integrated way; this integration seems in the interest of 3-D binocular gaze control avoiding dissociations between fast version and slow vergence movements, that would be disruptive to binocular vision.

Acknowledgements

This research was supported, in part, by AFOSR Grant 91-0124.

References

- Bahill, A. T., Clark, M. R. and Stark, L. (1975). Dynamic overshoot in saccadic eye movements is caused by neurological control signal reversals. *Expl. Neurol.* **48**: 107-122.
- Cogan, A. I. (1978). Qualitative observations in visual science: 'the Farnsworth shelf'. Fusion at the site of the "ghosts". *Vision Res.* **18**: 657-664.
- Collewijn, H., Erkelens, C. J. and Steinman, R. M. (1988). Binocular co-ordination of human horizontal saccadic eye movements. *J. Physiol.*

Lond. **404**: 157–182.

Enright, J. T. (1984). Changes in vergence mediated by saccades. *J. Physiol. Lond.* **350**: 9–31.

Enright, J. T. (1986). Facilitation of vergence changes by saccades: influences of misfocused images and of disparity stimuli in man. *J. Physiol. Lond.* **371**: 69–87.

Erkelens, C. J. (1987). Adaptation of ocular vergence to stimulation with large disparities. *Expl Brain Res.* **66**: 507–516.

Erkelens, C. J., Steinman, R. M. and Collewijn, H. (1989a). Ocular vergence under natural conditions. II. Gaze shifts between real targets differing in distance and direction. *Proc. R. Soc. Lond. B* **236**: 441–465.

Erkelens C. J., Collewijn H. and Steinman, R. M. (1989b). Asymmetrical adaptation of human saccades to anisometropic spectacles. *Invest. Ophthalmol. Vis. Sci.* **30**: 1132–1145.

Hering, E. (1868). *Die Lehre vom binokularen Sehen*. Engelmann, Leipzig. (English edition: Bridgeman, B. and Stark, L. (1977). *The Theory of Binocular Vision*. Plenum, New York.)

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

Kenyon, R. V., Ciuffreda, K. J. and Stark, L. (1980b). Unequal saccades during vergence. *Am. J. Optom. Physiol. Opt.* **57**: 586–594.

Krol, J. D., and 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. and Collewijn, H. (1991a). Long-term nonconjugate adaptation of human saccades to anisometropic spectacles. *Vision Res.* **31**: 1939–1954.

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

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

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

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

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

Rashbass, C. and Westheimer, G. (1961). Disjunctive eye movements. *J. Physiol. Lond.* **159**: 339–360.

Westheimer, G. (1954). Mechanism of saccadic eye movements. *Arch. Ophthalmol.* **52**: 710–724.

Yarbus, A. L. (1967). *Eye Movements and Vision*. Plenum, New York.

Zee, D. S., Fitzgibbon, E. J. and Optican, L. M. (1992). Saccade–vergence interactions in humans. *J. Neurophysiol.* **68**: 1624–1641.