Proc. R. Soc. Lond. B **236**, 441–465 (1989)
Printed in Great Britain

Ocular vergence under natural conditions. II. Gaze shifts between real targets differing in distance and direction

By C. J. Erkelens[1], R. M. Steinman[2] and H. Collewijn[1]

[1] *Department of Physiology I, Faculty of Medicine, Erasmus University Rotterdam P.O. Box* 1738, *NL* 3000 *DR Rotterdam, The Netherlands*
[2] *Department of Psychology, University of Maryland, College Park, Maryland* 20742, *U.S.A.*

(*Communicated by G. Westheimer, F.R.S. – Received* 21 *November* 1988)

Horizontal binocular eye movements of three subjects were recorded with the scleral sensor coil – revolving magnetic field technique during voluntary shifts of gaze between pairs of stationary, real, continuously visible targets. The target pairs were located either along the median plane (requiring symmetrical vergence), or on either side of the median plane (requiring asymmetrical vergence).

Symmetrical vergence was primarily smooth, but it was often assisted by small, disjunctive saccades. Peak vergence speeds were very high; they increased from about 50° s^{-1} for vergence changes of 5° to between 150 and 200° s^{-1} for vergence changes of 34°. Differences between convergence and divergence were idiosyncratic.

Asymmetrical vergence, requiring a vergence of 11° combined with a version of 45°, was largely saccadic. Unequal saccades mediated virtually all (95%) of the vergence required in the divergent direction, whereas 75% of the vergence required in the convergent direction was mediated by unequal saccades, with the remaining convergence mediated by smooth vergence, following completion of the saccades. Peak divergence speeds during these saccades were very high (180° s^{-1} for a change of vergence of 11°); much faster than the smooth, symmetrical vergence change of comparable size (14°). Peak convergent saccadic speeds were about 20% lower. This difference in peak speed was caused by an initial, transient divergence, observed at the beginning of all horizontal saccades.

The waveform of disjunctive saccades did not have the same shape as the waveform of conjugate saccades of similar size. The smaller saccade of the disjunctive pair was stretched out in time so as to have the same duration as its larger, companion saccade. These results permitted the conclusion that the subsystems controlling saccades and vergence are not independent.

Vergence responses were relatively slow and incomplete with monocular viewing, which excluded disparity as a cue. Monocularly stimulated vergence decreased as a function of the increasing presbyopia of our three subjects.

Subjects were able to generate some vergence in darkness towards previously seen and remembered targets. Such responses, however, were slow, irregular and evanescent.

In conclusion, vergence shifts between targets, which provided all natural cues to distance, were fast and accurate; they appeared adequate to provide effective binocular vision under natural conditions. This result could not have been expected on the basis of previous observations, all of which had been made with severely reduced cues to depth. We also found that asymmetric vergence was largely saccadic and conclude that the generation of saccades of unequal sizes in each of the eyes is a normal feature of oculomotor performance whenever gaze is shifted between targets that differ in distance as well as direction.

INTRODUCTION

In the preceding paper (Erkelens *et al.* 1989), we reported that the vergence subsystem makes timely and fast responses over a large dynamic range when it is provided with its 'natural input'. By 'natural input', we mean a visually rich environment that contains objects and visual frames which provide effective cues to their depth relative to the observer. We also showed that the vergence subsystem, like other oculomotor subsystems, is largely under voluntary control once it is provided with natural input. Under these conditions, we found that when the subject attended selectively to a continuously moving target object, cues to its motion in depth initiated vergence subsystem reflexes that produced accurate, as well as very fast, smooth convergent and divergent eye movements: movements capable of preventing appreciable vergence tracking errors even when target velocities were relatively high. We demonstrated these properties of the vergence subsystem by asking the subject to maintain fixation on a target object binocularly, while its position in depth was varied by moving the target continuously back and forth or by keeping the target stationary and having the subject move his upper torso in the same way. Changes of depth in these experiments were always produced by continuous movements of the target or by continuous movements of the subject's upper torso. Motions in depth were not only always continuous, they were also always confined to the median plane.

The present experiments extend this line of research in two ways. We examined (1) shifts of gaze between stationary target objects located at different distances from the subject along the median plane: these shifts of gaze could be made exclusively by means of 'symmetrical' vergence responses; and (2) shifts of gaze between objects that lay off to the side of the median plane as well as at different distances from the subject. The second condition required version (conjugate), as well as vergence (disjunctive), eye movements, which we will lump together and call 'asymmetrical' vergence responses.

We examined these conditions because both are required for effective visual functioning in natural situations. We had no basis for predicting the quality of oculomotor performance when symmetrical and asymmetrical vergence responses are made between stationary target objects seen in a relatively natural environment. Our accompanying study of symmetrical vergence responses to continuous motions in depth led us to suspect that the vergence subsystem might prove to be more competent than might be expected on the basis of earlier experiments, in which cues to depth had been severely restricted. This suspicion was borne out.

We found that symmetrical vergence responses, as large as 30°, were largely smooth and attained maximum speeds as high as 200° s^{-1}. When the placement of the targets required asymmetrical vergence responses (a disjunctive response of 11° coupled with a conjugate response of 45°), vergence responses were effective but they were mediated almost exclusively by unequal saccades in each of the eyes; smooth vergence eye movements contributed relatively little to the final orientation of the paired lines of sight. Such a dominant role for saccades in producing large vergence responses consistently has been rarely suspected, although earlier work by Enright (1984, 1986) pointed in a similar direction. An analysis of the velocity profiles of these disjunctive saccades showed that they cannot be accounted for by an addition of conjugate saccades and ongoing smooth vergence. We conclude that unequal saccades are generated normally in asymmetric vergence, and that traditional schemas such as Yarbus's (1967), as well as the current interpretations of Hering's law, are incorrect.

METHODS

Subjects

Three subjects (the authors) participated in the experiments. All had visual acuities of 20/20 or better, without (R.S.) or after correction of refractive errors (C.E. and H.C.). All were very experienced eye movement subjects and none showed any ocular or oculomotor pathologies. R.S. was a 60-year-old emmetropic presbyope. H.C. was a 51-year-old myopic presbyope, and C.E. was a 36-year-old myope. H.C., who normally wears spectacles to correct his myopia, did not wear his spectacles for at least 3 h before each experimental session or during the experiments because he could see all of the targets clearly; the farthest was less than a metre away. H.C. did not wear his spectacles because spectacles introduce the need to correct eye-movement data for the magnification factor introduced by the spectacle lenses. By avoiding spectacles the geometrical–optical–oculomotor relations were simplified, which made it easier to study H.C.'s oculomotor performance. C.E., the other myopic subject, wore his corneal contact lenses during the experiments because they neither introduced a magnification factor nor interfered with the placement or wearing of the silicone annulus sensor coil used to record his eye movements.

Eye-movement recording technique

The revolving magnetic field – sensor coil technique was used to record absolute eye positions of both eyes in space. The principle of the technique and its realization in our specific instrument are described in the preceding paper (Erkelens *et al.* 1989).

Stimuli

The experiments were done in a dimly lighted room that contained a great deal of structure capable of providing good monocular and binocular cues to depth. The visual targets consisted of nine light-emitting diodes (LEDS) arranged in the configuration illustrated in figure 1. Five LEDS, A through E, were located at different distances along the median plane of the subject. Target distances, from A to E, were 91.4, 43, 21, 14, and 10 cm, respectively. The subject's heads were stabilized by bite-boards with individually fitted dental impressions. Target

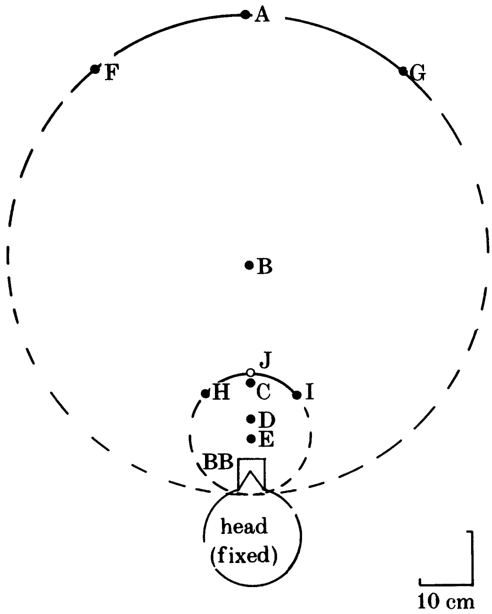

FIGURE 1. Top view of the subject and the arrangement of the LED targets, drawn to scale. The subject's head was supported by a bite-board (BB). The LEDs are shown by solid dots. The significance of their placement and the particular pairs lighted in each experiment are described in the text.

distance was defined as the distance between the target and the midpoint of the line connecting the centres of rotation of the two eyes, which were assumed to lie 13.5 mm posterior to the cornea. By using this definition of target distance, the angle of target vergence follows directly from the target distance and the interocular distance because target vergence is defined as the angle subtended by the centres of rotation of the two eyes at the target (Rashbass 1981). With this definition, target vergence varied from about 4° at A to 36–38° at E. The exact angles were slightly different for each subject, depending on his interocular distance. LEDs F and G were placed on the same isovergence circle (Collewijn *et al.* 1988) as LED A. F was 20° to the left of A, the farthest target (91.4 cm) along the subject's median plane, and G was 20° to the right of A. Their distance to the subject was 86.6 cm. LEDs H and I were much closer, and had a distance of 20.9 cm. They lay on the isovergence circle that passed through J, only 24 cm from the subject along his median plane. H and I were 25° to the left and to the right of J, respectively.

Experimental procedure

Sessions began with two 10 s calibration trials during which horizontal and vertical positions of each eye were recorded while the subject maintained monocular fixation on LED A with the right and left eye. Following these calibration trials, 23 experimental trials were recorded during which the subject shifted gaze (changed fixation) between a pair of LEDs at a comfortable, self-paced rhythm of about one gaze shift per 1.5 s. The subject started each trial whenever he felt prepared after he had been told that the next stimulus pair had been made ready. During each trial, horizontal and vertical eye positions were sampled at 488 Hz. This was four times the sampling rate used in the preceding paper because the asymmetrical vergence condition led us to expect large saccadic eye movements in the research to be described. Large saccades introduce the requirement of relatively high bandwidth for describing saccadic waveforms with reasonable fidelity. Only the two LEDs that served as targets were lighted on any given trial, but the other targets, their mountings, and the frames supporting the magnetic field coils could also be seen clearly. As a result, the location of the LEDs with respect to each other and with respect to many other objects in the visual scene was unambiguous. Different pairs of LEDs were used to study symmetrical and asymmetrical vergence: LED A, paired with one of the other LEDs located long the median plane (LEDs B through E), was used to study symmetrical vergence, and LED F was paired with LED I or LED G was paired with LED H for the study of asymmetrical vergence. Trials during which the LEDs were viewed binocularly were interleaved with trials during which viewing was monocular. The entire experiment was replicated on different days for all subjects.

Data analysis

The storage and analyses of data were similar to the procedures described in the preceding paper. Briefly, ocular vergence was calculated by subtracting the horizontal position of the right eye from the horizontal position of the left eye. Offsets, caused by misalignments of the sensor coils relative to the visual axis of each eye, were obtained from the calibration trials and subtracted from the estimates of ocular vergence. In these calculations, it was assumed that the subjects correctly fixated the target at 91.4 cm (LED A) in the calibration trials with monocular viewing. Zero values of ocular vergence, after these corrections, corresponded to fixation of a target at optical infinity. The measurements included monocular fixations (with either eye) of all targets; the difference between these monocular fixations and binocular fixation was used to calculate fixation disparity for the different targets. Velocities were calculated simply as the difference between adjacent samples, divided by the sampling interval. No filtering or windowing techniques were used. The sampling rate of 488 Hz made the effective bandwidth 244 Hz. The noise associated with estimates of velocity was about 5.4° s^{-1} with the 488 Hz sampling rate, noise arising in the eye movement monitor of about 40″, and the 16-bit data-storage constraint employed (see Erkelens *et al.* (1989) for additional details).

RESULTS

Symmetrical vergence responses during binocular viewing

In the initial experiment subjects alternatively converged and diverged as they shifted gaze between LED A (the farthest target) and one of the other four LEDs located in the median plane. Binocular eye movement recordings of a portion of a representative 20 s trial of each subject are reproduced in figure 2. During these trials, the subject shifted gaze, about once each 1.5 s, between LED A and LED E, a gaze shift requiring a change of vergence between 4° and about 38° of

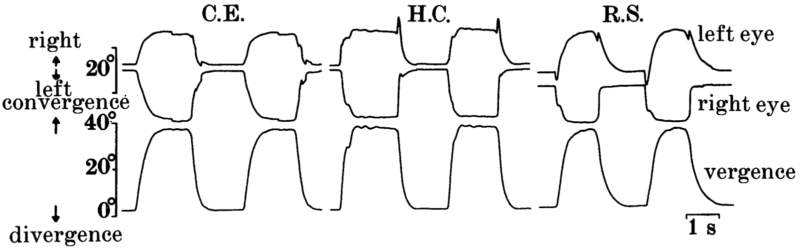

FIGURE 2. Representative eye movements of the three subjects (C.E., H.C. and R.S.) when they shifted gaze between LEDS A and E, both of which were located along each subject's median plane (see figure 1 for their relative distances from the subject). Viewing, as well as eye-movement recording, was binocular.

convergence. Vergence responses were largely smooth and fast. The subjects showed small, idiosyncratic differences in the details of their eye movements (such as the occurrence of concomitant saccades or the stability of convergence); each individual's behaviour was quite characteristic of him. It replicated in each successive cycle to such an extent that it could be described as his binocular oculomotor signature.

Vergence, in all subjects, was 'steady-state' within a second, well within the self-paced interval of each voluntary gaze shift. We compared steady-state ocular vergence with target vergence following each gaze shift and found that, on average, ocular vergence during binocular viewing was invariably too small; it left a residual fixation disparity. These residual fixation disparities, which increased in absolute size as a function of target vergence, are shown in figure 3. Residual fixation disparity was always present, but it amounted to only a small fraction of the vergence required. Even for the nearest target, located at 10 cm where target vergence was about 38°, fixation disparity was not larger than 2% for C.E., 3% for H.C. and 6% for R.S. of target vergence. Its magnitude for all three subjects was under 0.5° for target vergences up to 20° when targets were as close as 20 cm. Table 1 summarizes the percentage of change of target vergence that was corrected by ocular vergence when gaze shifted between targets located along the median plane. It is difficult to imagine any biological motor system performing more competently.

The characteristic dynamics of these symmetrical vergence movements can be seen in more detail in figure 4, which shows typical position and velocity profiles of subject C.E. plotted on an expanded timescale. Both convergent and divergent responses are illustrated. This figure shows that most of the symmetrical vergence was accomplished by smooth eye movements. Small, unequal saccades could also make a relatively minor contribution. C.E. tended to avoid making saccades while converging (figure 4, left side; cf. figure 2), but always made a few while diverging. H.C. showed a similar tendency, whereas R.S. made some saccades both during convergence and divergence. The overall vergence change between targets along the median plane was, however, primarily accomplished by smooth eye movements.

As shown in the typical records in figure 4, C.E. reached a smooth convergence

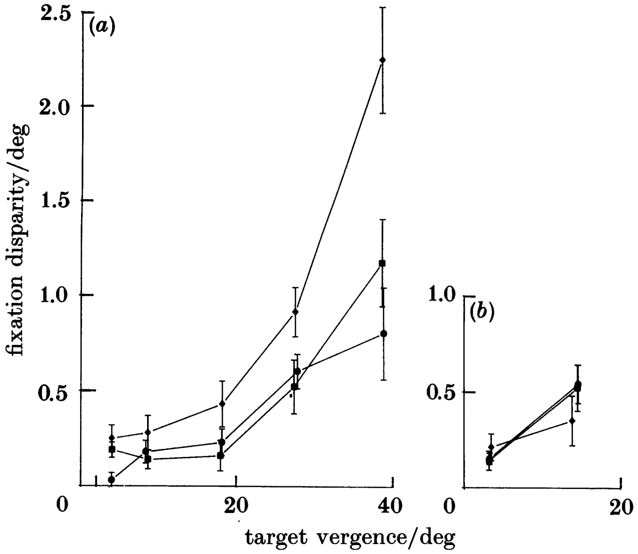

FIGURE 3. Residual fixation disparities (target vergence minus ocular vergence) at the completion of gaze shifts. (*a*) Results for the five targets (A–E) in the median plane (symmetrical condition). (*b*) Results for the asymmetrical targets (F or G opposed to I or H). Viewing was binocular. Subjects: R.S. (diamond), H.C. (square) and C.E. (circle). Bars represent the variability (1 s.d.) between successive fixations.

TABLE 1. PERCENTAGE OF DIFFERENCES IN TARGET VERGENCE, CORRECTED BY CHANGE IN OCULAR VERGENCE, DURING GAZE SHIFTS BETWEEN DIFFERENT PAIRS OF LEDS IN THE MIDLINE

		subject		
targets	difference in target vergence	C.E.	H.C.	R.S.
A–B	4.4°	98%	98%	97%
A–C	14.1°	99%	98%	98%
A–D	23.8°	98%	97%	97%
A–E	34.8°	98%	96%	93%

velocity of more than 100° s^{-1} within about 100 ms; this velocity declined gradually to zero as convergence was completed. Completion took about 1 s. The four saccades that C.E. made when he diverged (figure 4) show that these saccades were clearly distinguishable from the ongoing smooth divergent eye movement. We are confident that our recording and analysis techniques permitted us to be sure that the unexpectedly high smooth-vergence velocity we observed did not originate from hidden saccades. We are also sure that our technique allows us to say that the small saccades that did occur contributed to the effectiveness of vergence. These saccades were not perfectly yoked, and their disjunctive component was always in the correct direction to enhance the effectiveness of the ongoing smooth-vergence eye movement. This can be seen most clearly in the divergence velocity trace of figure 4 (right upper panel), which shows that the brief velocity peaks produced by the saccades always went in the direction that would

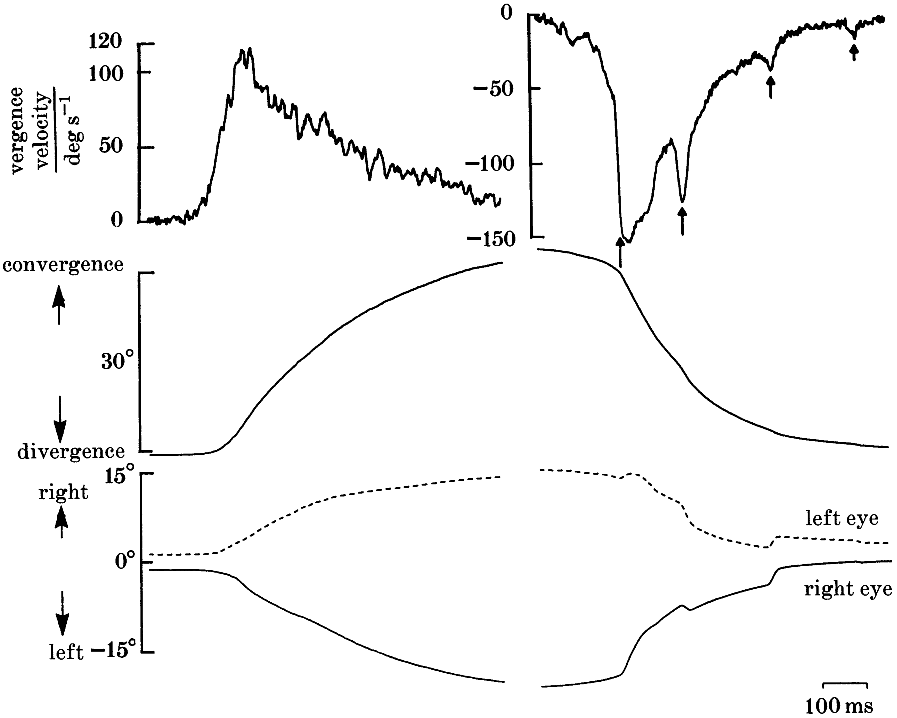

FIGURE 4. The dynamics of gaze shifts along the median plane in the convergent direction (from LED A to LED E; left panels) and in the divergent direction (from E to A; right panels). The representative recordings are from subject C.E. The traces show, from top to bottom: vergence velocity, vergence position, left and right eye position. The arrows in the divergent velocity trace (top right panel) mark the occurrence of a saccade.

facilitate the ongoing smooth divergent movement. The occurrence of these velocity peaks, superimposed on the smooth vergence, also proves that the disjunctive component of the saccades provided an *extra* contribution to vergence. The imperfect yoking of the saccades did not result from the ongoing smooth vergence movement. If this had been the case, the vergence-velocity trace would have remained smooth. The occurrence of these small, unequal saccades in the symmetrical target situation was idiosyncratic with respect to their prevalence during convergence and/or divergence, but in all cases these saccades, when they did occur, contained a disjunctive component that contributed to the effectiveness of the vergence movement. Thus the small, unequal saccades made by all three subjects during smooth vergence eye movements were not a mere contamination of the smooth response or an adventitious effect produced by minute stimulus misalignment, which took the target slightly off the median plane. Rather, these small unequal saccades represented a useful oculomotor strategy that was used idiosyncratically by each of the subjects.

The implication of this finding, which will be further supported in the section on asymmetrical vergence, is that binocular eye movements cannot be described as the linear sum of conjugate, equal saccades and disjunctive, slow vergence.

Now that we have shown that vergence was largely smooth, we can go on to describe the velocity/amplitude relations of this vergence response in a systematic manner. Figure 5 shows mean *maximum* vergence velocities reached during convergent and divergent gaze changes. Figure 6 shows mean *average* velocities during the entire convergent or divergent gaze shift.

Maximum vergence speeds were very high (figure 5); they increased from about

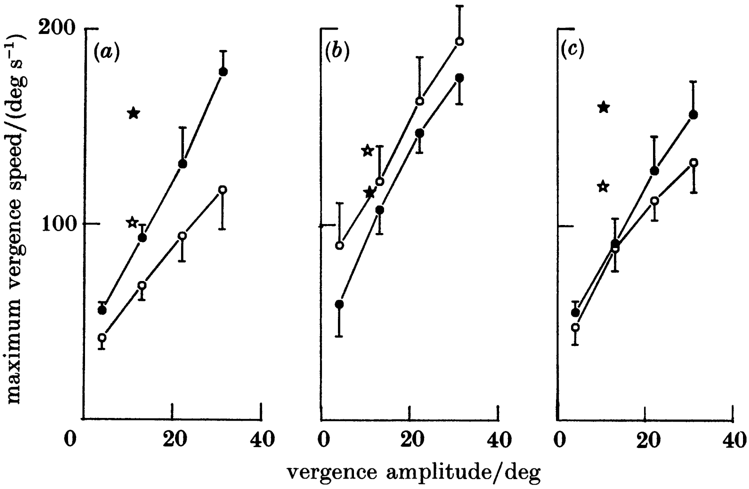

FIGURE. 5. Mean maximum smooth vergence speed of each of the three subjects plotted as a function of the amplitude of the vergence change required. (*a*) R.S.; (*b*) H.C.; (*c*) C.E. The target pairs were located along the subject's median plane (connected symbols) or asymmetrically (asterisks). Means are based on six trials, each containing 4–5 convergent responses and an equal number of divergent responses. Error bars indicate 1 s.d. Open symbols, convergence; closed symbols, divergence.

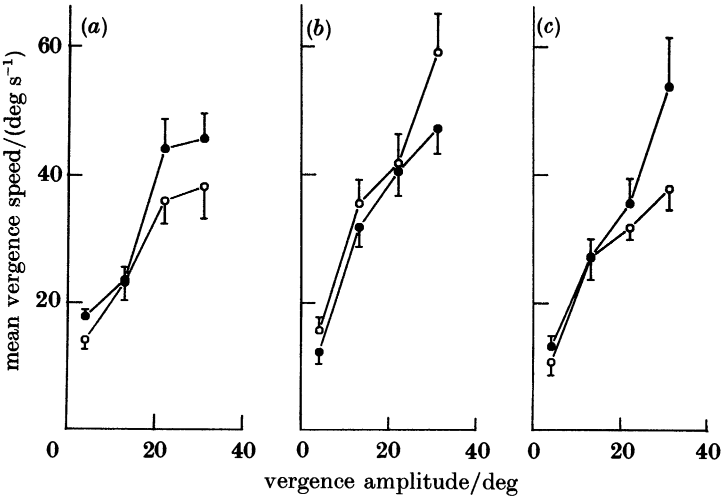

FIGURE 6. As figure 5, showing mean average vergence speeds for gaze shifts between targets in the median plane. (*a*) R.S.; (*b*) H.C.; (*c*) C.E.

50° s^{-1} for 5° vergence changes to values between 150 and 200° s^{-1} when vergence changes of 34° were made. These maxima represent, by and large, the smooth component of vergence. Inspection of the data revealed that unequal saccades only marginally increased the maximum vergence speeds when targets were located along the median plane. Mean vergence speeds were raised by about 10% by the contribution of unequal saccades when such saccades were present. Vergence was about equally fast in all three subjects, whose ages ranged from 36 (C.E.) to 60 (R.S.) years. Subject R.S.'s divergent responses were faster than his convergent responses; the reverse was true for H.C., whereas both kinds of C.E.'s vergence responses were about equally fast, at least when relatively small vergence changes were required. Such directional preferences cannot be accounted for by the contribution of small, unequal saccades, because H.C., as well as C.E., made saccades only while diverging, but H.C.'s convergence was faster than his divergence (figure 5). R.S. made saccades both during convergence and divergence; nevertheless, his divergence was much faster than his convergence. This shows, once again, that the saccadic contribution to the velocity of symmetrical vergence was relatively small. The extremely high vergence velocities we observed were produced primarily by smooth eye movements.

Neither age nor the direction of the required vergence response had systematic influences on performance. It is interesting to note that the briskness and accuracy of R.S.'s smooth vergence responses had persisted for many years after he no longer had any useful, unaided near vision. R.S.'s presbyopia has required him to wear $+2.75D$ spectacles for reading at normal distances for almost ten years; this correction was not worn during the present experiments. Clearly, avoiding diplopia, in itself, has been a sufficient reason for R.S. to maintain the competence of his vergence responses. Blur, which he could use to change accommodation when he was much younger, had not been required to keep his vergence responses functioning at youthful levels long after he had lost much of his capacity to focus his crystalline lenses for near objects. Later we will see that R.S.'s loss of accommodation through aging will influence the competence of his vergence responses when he was required to shift gaze while viewing targets monocularly, a condition during which binocular disparity was no longer available to stimulate and guide his vergence subsystem.

The effect of the size of the required vergence change on the maximum smooth-vergence speed observed was close to linear in all three subjects. Slopes were on the order of 4° s^{-1} per degree of vergence, but exact values varied considerably among directions and individuals.

The mean average vergence velocities, shown in figure 6, follow a pattern similar to the pattern of the maximum velocities, but, obviously, the values plotted are lower. They range only up to about 60° s^{-1}.

The predominantly smooth vergence responses made by each of the subjects were not only very fast, they were also very reproducible. This is illustrated for subject R.S. in figure 7. Each trace shows the mean and standard deviation of six consecutive vergence responses between the farthest LED (A) and each of the four progressively nearer LEDS (B, C, D and E).

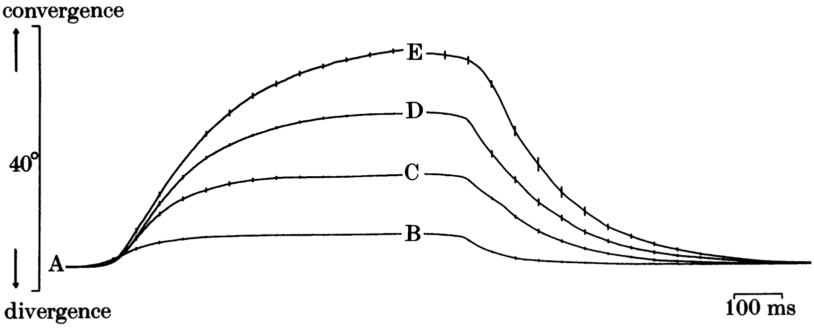

FIGURE 7. Mean position profiles of the smooth symmetrical vergence responses of subject R.S. to targets located at different distances along his median plane. The capital letters, A–E, indicate the positions of the targets (see text and figure 1 for their locations relative to the subject). The vertical bars in the traces show ±1 s.d.

Asymmetrical vergence responses during binocular viewing

Representative eye movements made by each of the subjects, when they shifted gaze between LEDs G and H (see figure 1), are reproduced in figure 8. Both of these LEDs were located off the median plane with LED G far from the subject whereas LED H was near. To shift gaze accurately between these targets, the right eye had to make a horizontal eye movement about 11° larger than the horizontal eye movement required of the left eye.

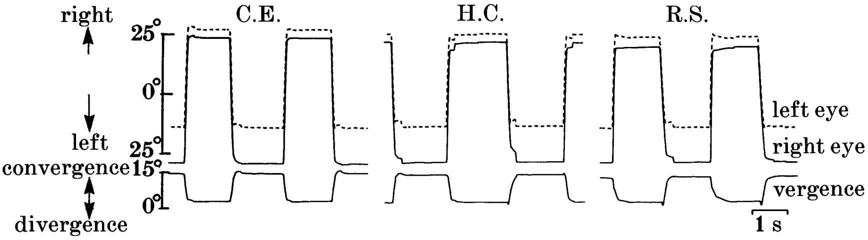

FIGURE 8. Representative eye movements of the three subjects (C.E., H.C. and R.S.) when they shifted gaze between LED G (located relatively far away and to the right of the subject's median plane) and LED H (located nearer and to the left of the subject's median plane). This target arrangement required asymmetrical vergence responses (see figure 1 for an illustration of the relative location of this target pair). Viewing, as well as eye movement recording, was binocular. The dashed trace shows the position of the left eye; the solid traces show the position of the right eye and the difference between the positions of each eye (vergence).

As summarized in table 2, about 99% of this required change in vergence was accomplished by all subjects when they shifted gaze. As expected from the results of the symmetrical experiment, small residual fixation disparities were present after gaze shifted to the far target, and slightly larger residual fixation disparities were present after gaze shifted to the near target (see figure 3, right panel).

Figure 9 illustrates the difference between these asymmetrical vergence

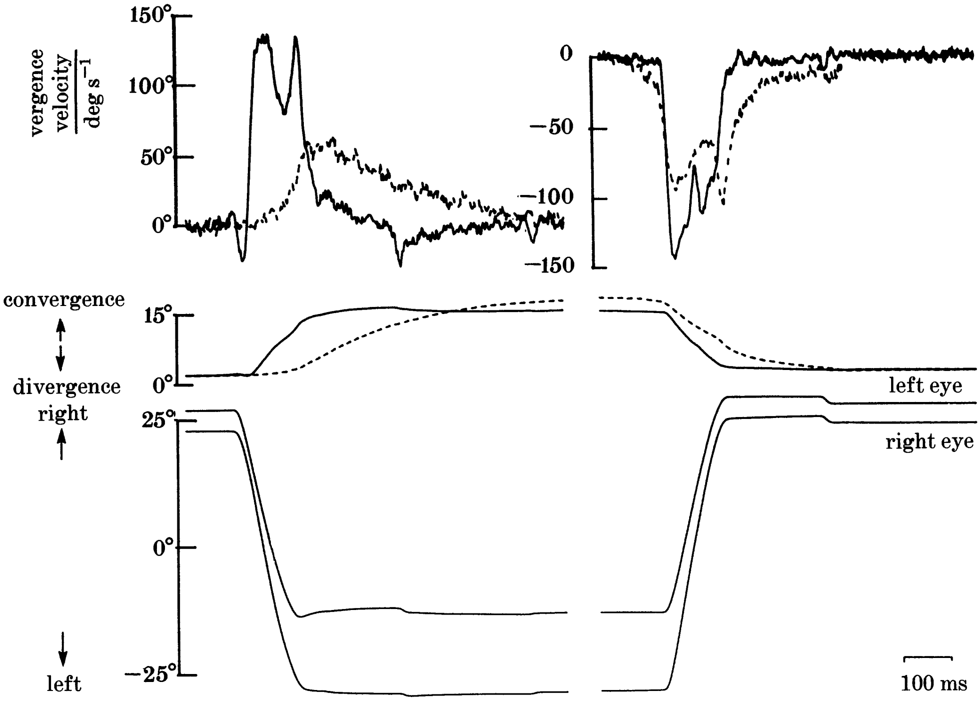

FIGURE 9. Representative position and velocity profiles of subject C.E. while he made symmetrical (dashed lines) and asymmetrical (solid lines) vergence responses of similar amplitude, that is, between LEDS A and C or between LEDS G and H in the symmetrical or asymmetrical conditions, respectively. The subject is shown converging at the left side of the graphs and diverging on the right side. The presence of a large saccade at the onset of the vergence response in the asymmetrical condition and the absence of such saccades in the symmetrical condition can be seen clearly in these profiles.

TABLE 2. PERCENTAGE OF DIFFERENCE IN TARGET VERGENCE, CORRECTED BY CHANGE IN OCULAR VERGENCE, DURING GAZE SHIFTS BETWEEN PAIRS OF LEDS DIFFERING IN DIRECTION (45°) AND TARGET VERGENCE (11°)

subject	total vergence (%)	vergence during saccade (%) divergent	vergence during saccade (%) convergent
C.E.	99	95	83
H.C.	99	95	76
R.S.	99	93	72

responses (solid traces) and the symmetrical vergence responses made in the first experiment when all targets lay along the median plane (dashed traces). This figure allows a comparison of subject C.E.'s typical asymmetrical position and velocity profiles when the required change of vergence was 11° with his typical symmetrical position and velocity profiles when the required change of vergence was 14°; the closest comparison possible with the target positions used in both experiments.

The asymmetrical experiment produced two important new results. First, asymmetrical vergence responses were mediated largely by saccades; and second, convergent and divergent responses had different characteristics.

The velocity profiles of the asymmetrical convergent responses illustrated in figure 9 contained two components. All gaze shifts started with an initial pair of saccades, seen as a short period of very high velocity that ended abruptly and was followed by a longer period of much lower velocity: the smooth vergence response. The saccadic component of asymmetrical convergence lasted about 150 ms and the smooth component lasted about 200 ms. The disjunctive component of the unequal saccades accomplished 72–83% of the convergence required (table 2).

The second, smooth component was either absent or very small during asymmetrical divergence. During divergence, the initial fast component, the pair of disjunctive saccades, lasted between 110 and 130 ms and the subsequent slow component, when it was present, lasted between 100 and 150 ms. About 95 % of the asymmetrical divergence response was accomplished within 120 ms (table 2) and all asymmetrical divergence responses were complete within 220 to 280 ms. The primarily smooth symmetrical divergence responses observed in the first experiment were slower. They required more than 500 ms for completion.

Asymmetrical *divergence* responses, which were accomplished primarily by unequal saccades, were extremely fast. Their maximum speeds ranged between 130 and 180° s^{-1}. These maximum asymmetrical saccadic vergence responses were much faster than the predominantly smooth, symmetrical divergence responses of *similar amplitude* (14° as opposed to 11°) observed in the first experiment. This can be seen in figure 5, where these maximum asymmetrical vergence speeds are plotted (asterisks) on the speed/amplitude graphs that summarize performance during symmetrical gaze shifts. Maximum asymmetrical *convergence* speeds were about 20% lower than asymmetrical divergence speeds, ranging only between 95 and 150° s^{-1}, but still higher than speeds observed in the first experiment.

Asymmetrical convergence, which, like divergence, was mediated in large part by saccades, started in the *wrong* direction (see the leftmost position and velocity traces in figure 9). After a brief period of about 20 ms, the response corrected itself, that is, the erroneous initial divergence response changed to the appropriate convergence response. The fast initial component of this, new correct, convergence response lasted between 90 and 160 ms and the subsequent slow component lasted between 190 and 250 ms.

We next asked whether the disjunctive saccades, which were very prominent during asymmetrical changes in vergence, had the same waveform as the binocular conjugate saccades that are used to shift gaze between targets which fall at different positions along the same isovergence circle. In other words, we asked whether saccadic gaze shifts that do not require changes in vergence have the same dynamic properties as the saccadic gaze shifts that do require changes in vergence. We found that they did not.

This was determined by using data from another series of experiments in which dynamic characteristics of conjugate saccades had been studied extensively (Collewijn *et al.* 1988). These data were obtained from the same subjects in the same eye-movement recording apparatus, and with the same LEDS mounted along the horizontal isovergence circle that passed through LED A (see figure 1). These data on conjugate saccades were collected within the same month as the data on vergence responses. We believe that the conditions were sufficiently similar to allow us to use the conjugate saccade data to evaluate their similarity to the disjunctive saccade data of similar amplitude now under consideration. The results of this comparison are illustrated in figure 10.

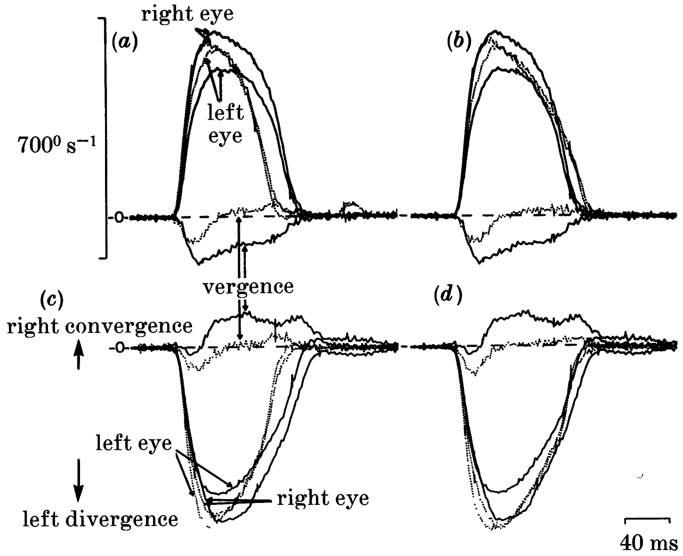

FIGURE 10. Comparison of velocity profiles of disjunctive saccades (this experiment) and conjugate saccades of the same subject, C. E., measured in the same apparatus (Collewijn *et al.* 1988). All traces are averages of four successive saccades; these were so reproducible that standard deviations (plotted as short vertical bars) are barely distinguishable. The solid traces represent gaze shifts from LED H to LED G ((*a*, *b*) rightward and divergent) or gaze shifts from LED G to LED H ((*c*, *d*) leftward and convergent). The solid traces in the right and left panels are identical; in (*a*) and (*c*) they are plotted together with conjugate saccades of 40°, and in (*b*) and (*d*) together with conjugate saccades of 50°. If the disjunctive saccades were similar in shape to conjugate saccades of comparable size, then the smaller, left-eye disjunctive saccades should be similar to the left-eye, 40° conjugate saccades, plotted as dotted traces in (*a*) and (*c*). Clearly, this is not the case. On the other hand, the larger, right-eye, disjunctive saccades should resemble the 50° conjugate, right-eye saccades plotted as dotted traces in (*b*) and (*d*). This outcome was realized rather well. See the text for further description.

In this figure, the continuous traces show typical examples (subject C. E.) of the movements of each eye during saccadic gaze shifts between LEDs H and G in the rightward, and convergent, direction (panels A and B) or in the leftward, and divergent, direction (panels C and D). The difference between the velocities of each eye, i.e. the vergence velocity, is also shown. Conjugate saccades of the left and right eye are shown separately (dotted traces) because the required size of the gaze change was about 50° for the right eye and 40° for the left eye. If the disjunctive saccadic waveforms were shaped like conjugate saccadic waveforms when these saccades had the same size in each eye, then the disjunctive saccade of the left eye, when the right eye made the 50° saccade, should have the same waveform as a conjugate saccade of 40°. This comparison can be made in the left panels (A and C) of figure 10. Similarly, the larger, disjunctive saccade made by the right eye should resemble a conjugate saccade of 50° (see figure 10, right panels, B and D). There was reasonable similarity between the waveform of conjugate saccades of 50° and the waveform of the larger, 50° member of the disjunctive pair. Only minor discrepancies can be seen, mainly during the deceleration phase. Note, however, that the smaller member of the disjunctive pair, whose size was about 40°, had a velocity waveform that was very different from the velocity waveform of a conjugate saccade of 40° (figure 10, left panels). Specifically, the peak velocity was lower and the duration was longer, as if a 'normal' conjugate saccade of 40° had been stretched in time so as to last as long as the larger saccade in the companion eye.

Disjunctive saccades, which mediated divergence, actually had virtually the same duration in each of the eyes (figure 10*a*, *b*). Saccades mediating convergence also reached, after deceleration, a plateau of low velocity at about the same time in each eye (figure 10*c*, *d*), but, because a smooth phase of convergence always followed the convergent saccades, this velocity plateau was not zero. This post-saccadic smooth vergence masked the exact end of the saccades, making it impossible to make exact comparisons of saccadic durations.

The dynamics of the asymmetrical vergence response, which is accomplished primarily by disjunctive saccades, is complicated by a well-known property of all horizontal saccades. Nasally and temporally directed saccades have different dynamic properties. The eye moving in the temporal direction always accelerates faster than the eye moving nasally. This is true even when saccades are made between targets, falling on an isovergence circle. As a consequence, all horizontal saccades show an initial phase of transient divergence, which can amount to several degrees (Collewijn *et al.* 1988). This initial divergence is clearly visible in the vergence traces (dotted) of the conjugate horizontal saccades in figure 10. Obviously, this inherent initial *divergence* would be beneficial when *divergent* disjunctive saccades are required. As can be seen in the upper panels of figure 10, this was indeed the case. As a result, almost all divergence (93–95%) had been completed by the time the saccades ended (table 2). Note, however, we used only a single combination of vergence and version. The effectiveness of unequal saccades with other combinations must still be examined.

The initial inherent *divergence* was detrimental when *convergent* disjunctive saccades were required. Its effect had not been completely overcome when the saccades ended, and, as a result, the net convergence achieved by the saccades was only 72–83% (table 2) of the convergence required. The remaining part of the requirement was accomplished by smooth eye movements following the saccades (figure 9).

These results strongly reinforce our earlier statement in the section on symmetrical vergence that binocular eye movements cannot be described as the linear sum of strictly conjugate saccades and disjunctive smooth vergence. Consider, for instance, the velocity profiles in figures 9 and 10. There is no way in which the velocities of the smooth vergence movements, associated with gaze shifts along the median plane (figure 9, dashed traces), could be increased by a yoked saccade to the much higher velocities of asymmetrical vergence shifts of comparable size (figure 9, solid traces). Even if some nonlinearity is allowed in the summation, the very different durations of symmetrical and asymmetrical vergence remain to be explained. Similarly, the saccades of the two eyes in the asymmetrical situation (figure 10, solid traces) show a velocity difference on the order of 100° s^{-1} about 40 ms after the gaze shift started. Smooth vergence velocities after 40 ms were never much higher than 10° s^{-1} (figures 4 and 9). The conclusion therefore is inescapable that the 'subsystems' controlling saccades and vergence are not independent.

In summary, asymmetrical vergence during binocular viewing was mediated largely by saccades in both the divergent and convergent directions. Asymmetrical vergence was somewhat more saccadic in the divergent than in the convergent direction, but both responses were faster for comparable target vergence than the predominantly smooth vergence responses observed in the first experiment where target placements were symmetrical. These differences were very consistent and were found in all three subjects.

Vergence responses during monocular viewing

The symmetrical and asymmetrical experiments were repeated while the subject viewed the target pairs with only a single eye (these data were actually collected during the same experimental sessions as the binocular data; blocks of monocular trials were interleaved with blocks of binocular trials). We included this condition for calibration purposes and also to determine how well monocular cues to depth (e.g. blur, size and linear perspective) could guide very fast and accurate smooth and saccadic vergence responses when binocular disparity is not present. This cue, of course, is only present when both eyes can see objects or frames in the visual scene. Motion parallax and optical flow are also potentially powerful monocular cues to depth but they were not available to the subject in these gaze shift experiments because the subject's head and the targets were stationary in space.

Binocular eye-movement recordings of a representative portion of each subject's performance, when he shifted his gaze between LEDS A and E along the median plane with the targets viewed only by his right eye, are reproduced in figure 11. Each subject performed consistently, but differently, when the target pairs were viewed with only a single eye. This contrasts with results obtained in both the

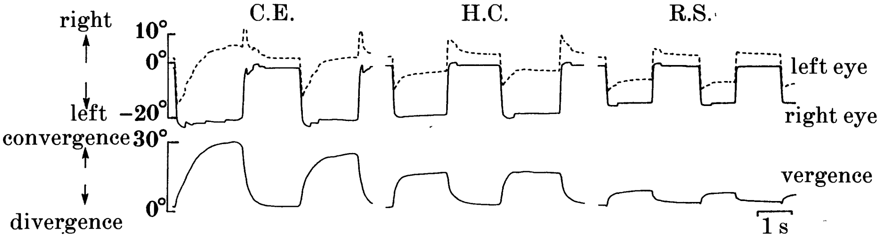

FIGURE 11. Representative eye movements of the three subjects when they shifted gaze between LEDS A and E, both of which were located along each subject's median plane (see figure 1 for their relative distances from the subject). Viewing was monocular with the right eye seeing the targets. See legend of figure 8 for additional details.

symmetrical and asymmetrical experiments during binocular viewing. In the binocular viewing experiments, individual differences were relatively modest; all subjects made very brisk, effective smooth or saccadic vergence responses, depending on the placement of the target pairs. In the monocular viewing symmetrical experiment, only subject C.E. made large, almost completely effective, vergence responses. Vergence responses were much smaller in H.C. and almost absent in subject R.S. The youngest subject, C. E., who still had a good deal of lens accommodation left, was able to make relatively effective vergence responses. H.C., who had lost most of his accommodation through aging, was only about half as successful, and R.S., who was well along into presbyopia, was half as successful again. When binocular disparity was no longer available for the control of vergence, the subjects' vergence responses were correlated positively with their remaining accommodative potential despite the presence of other monocular cues. Note, however, that these cues, such as linear perspective and size, would be blurred by the loss of lens power; they would only be effective for far targets for R.S. and for very near targets for H.C. (the emmetropic and myopic presbyope, respectively).

The percentage of the change in target vergence corrected by ocular vergence during monocular viewing is summarized in figure 12 (symbols connected by lines), which illustrates the points made above, namely the large individual differences among the subjects with only C.E. making relatively effective vergence responses,

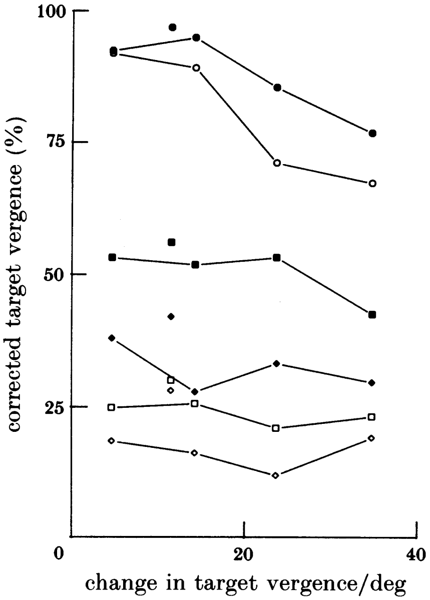

FIGURE 12. Percentage of change in target vergence corrected by ocular vergence when target pairs were viewed monocularly. The solid symbols signify viewing by the right eye and the open symbols signify viewing by the left eye. Subject C.E. is shown by circles, H.C. by squares, and R.S. by diamonds. The connected symbols represent the responses to the targets in the median plane; the single symbols refer to the asymmetric targets (change in target vergence 11°). The percentage of correction includes corrections made by both saccadic and smooth vergence responses.

while H.C. and R.S., the presbyopes, did only half or a quarter as well. Notice, however, that their responses corrected about the same fraction of target vergence over the whole distance range. (Absolute values of vergence are not given for the monocular situation, as they would be affected by phorias.) These results contrast markedly with the results of the binocular viewing experiment with the same symmetrical target placement where individual differences were modest; all subjects performed competently when disparity was present despite differences in their remaining capacity to focus for targets at different distances.

There was a second striking difference between the experiments with monocular and binocular viewing: the dynamics of vergence were very dissimilar. Whereas all subjects made primarily smooth vergence responses when they viewed the target pairs in the median plane with both eyes (figure 2), all responses in the monocular situation started with a saccade (figure 11). These saccades were disjunctive, and larger in the viewing eye; thus vergence was initiated rapidly. This was followed by a phase of smooth vergence, executed predominantly by the occluded eye. This smooth component was slow in comparison with the smooth-vergence response during binocular viewing. It was virtually absent in R.S., the longstanding presbyope, moderately developed in H.C., and prominent in C.E.

The asymmetrical experiment was also replicated with monocular viewing. Examples of each subject's binocular eye movements when they shifted gaze between LEDS G and H while they saw the target only with the right eye are reproduced in figure 13. This figure should be compared with figure 8, which shows performance with the same targets during binocular viewing. The eye that could see the target made a saccade to shift gaze. This saccade was followed by a post-saccadic drift in subject C.E. only. His covered eye made a saccade of smaller amplitude than the saccade made by his viewing eye, which was followed by considerable post-saccadic drift. This drift could be described as a smooth vergence response. The post-saccadic drifts of the covered eye of the other two subjects, H.C. and R.S., whose presbyopia was relatively far advanced, were very much smaller than C.E.'s. The total vergence response in the monocular, asymmetrical condition, as a percentage of the target vergence, amounted, on average, to 97% in C.E., 43% in H.C. and 35% in R.S. (see the unconnected symbols in figure 12).

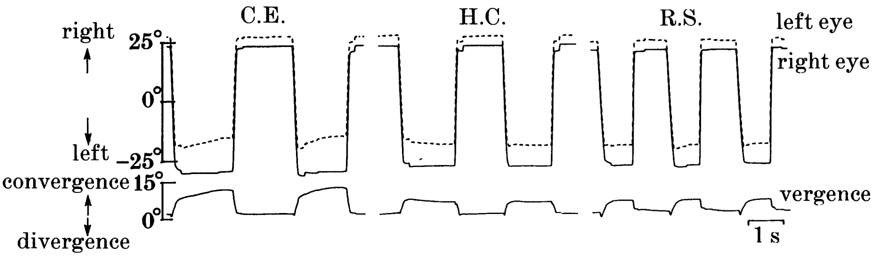

FIGURE 13. Representative eye movements of the three subjects when they shifted gaze between LED G (located relatively far away and to the right of the subject's median plane) and LED H (located nearer and to the left of the subject's median plane). This target arrangement required asymmetrical vergence responses (see figure 1 for an illustration of the relative location of this target pair). Viewing was monocular with the right eye seeing the target.

This degree of effectiveness of vergence was similar to the values observed when targets along the median plane were seen monocularly.

Gaze shifts to targets imagined in the dark

In the preceding paper (Erkelens *et al.* 1989), we reported that vergence responses, associated with attempted fixation of an *imagined* target changing distance along the median plane, could be made by only half of the subjects. The vergence responses these subjects could make were unreliable and poorly correlated with changes in the distance of the target imagined to be changing distance in the dark. Vergence responses in the dark could not be made by any subject when he moved his upper torso back and forth while imagining the target to be stationary. These results implied that visual cues to the distance and motion of a target were required to activate vergence-subsystem responses effectively. Imagined motion in depth, even when actively produced when the subject moved his arm or upper torso, yielded only very feeble changes in vergence.

We repeated this kind of experiment and found that shifting gaze in complete darkness between stationary targets imagined to be located at different distances along the median plane, was much more effective in activating vergence responses. All subjects made vergence responses in the dark. However, once again we found that fast, effective vergence responses required visual, rather than imagined, cues to the depth of the targets. Vergence responses in the dark to targets imagined to be located along the median plane were largely smooth, but smaller and slower than vergences responses to the same targets that had been seen shortly before. The timecourses of these vergence responses made in the dark were also very irregular. The ability to make vergence responses in the dark had another conspicuous feature: their size and speed declined over time. These features are illustrated for one of the subjects in figure 14. The vergence responses illustrated disappeared completely within 20 s.

No data were collected for the asymmetrical targets imagined in darkness because we did not anticipate that symmetrical and asymmetrical performance

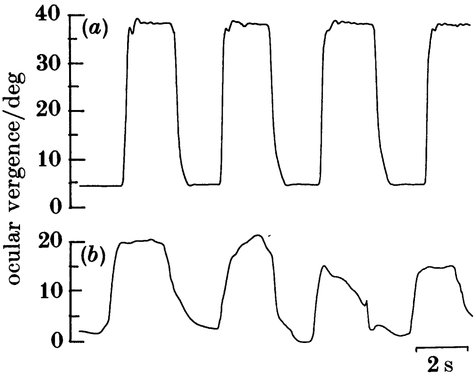

FIGURE 14. Ocular vergence responses of subject H.C. (*a*) when he shifted gaze between LEDS A and E visible along his median plane and (*b*) when he shifted gaze between imagined LEDS at the same locations while in complete darkness.

would be so different when we ran the experiments. We had no reason to suspect, when we collected the data, that saccades would be so prominent during vergence.

The results of the experiments with imagined targets, taken together with those described in the preceding paper, indicate that the memory for the perceived location of a target in depth is better than the ability to imagine a target changing its position in depth, at least with respect to its capacity to drive vergence-subsystem reflexes. We are emphasizing memory, rather than imagination, because the capacity of the mental process, unsupported by concurrent perceptions of motion or depth, faded out after a number of seconds at which time imagination could no longer be used to produce even feeble vergence responses. Note, however, that this can only be suggested for the memory of imagined distances but not for the memory of imagined directions because Skavenski & Steinman (1970) and Skavenski (1971) have already shown that there is excellent memory for the direction of previously seen targets, during many minutes spent in complete darkness, when eye movements are used as indicators of remembered directions.

Discussion

The velocity of vergence

Traditionally, vergence is described as a slow, as well as a smooth, oculomotor response. Our results do not support this view. Mean maximum smooth vergence speeds, observed when gaze was shifted voluntarily between targets located at different distances along the median plane, were higher by factors of five to ten than maximum smooth vergence speeds reported for step changes of disparity (Erkelens 1987). Our maximum smooth-vergence speed was also more than twice as high as the maximum smooth-vergence speed observed when subjects maintained binocular fixation of a target that made continuous backward and forward motions in depth. Even these speeds were much higher than traditional views would allow one to expect (see table 1 in Erkelens *et al.* (1989)). The maximum disjunctive, smooth vergence speeds our subjects attained when they shifted gaze were as high as the highest conjugate, smooth pursuit speed two of them (H. C. and R. S.) made when their smooth pursuit responses were recorded with the same eye-movement monitor (Collewijn *et al.* 1985). It is clear that *disjunctive*, smooth vergence responses are not slow relative to *conjugate*, smooth pursuit responses. Both vergence and smooth pursuit 'subsystems' are capable of smooth eye-movement speeds as high as $200^\circ\ s^{-1}$, providing stimulating conditions are right. We interpret these results to mean that the assumption of different vergence and smooth pursuit 'subsystems' is superfluous. These responses differ only in the coordination of the smooth response of each of the eyes and not in their speeds.

The smooth vergence velocities we observed are virtually unprecedented in the literature. Rashbass & Westheimer (1961) reported velocities not higher than about $20^\circ\ s^{-1}$ for 5° disparity steps. Erkelens (1987), also using pure disparity steps, observed maximum velocities that varied from $14^\circ\ s^{-1}$ to $40^\circ\ s^{-1}$ among his five subjects, with an average maximum of about $20^\circ\ s^{-1}$. Yarbus (1967) is not very explicit about vergence velocity but mentions a maximum of 'several tens of degrees per second' (Yarbus 1967, page 151). Unfortunately, he did not describe his stimulus conditions in detail beyond indicating that real targets were used. Stark (1983), in a recent textbook on vergence eye movements, made his only reference to vergence velocity in an introductory chapter, including a diagram relating peak vergence velocity to the magnitude of vergence. The relation illustrated amounts to 5° s^{-1} per degree of vergence over the entire range of vergence. The same relation was already reported by Bahill *et al.* (1975), but also without any supporting data. We have been unable to find data to support this relation. We do not know whether it was really measured, and if so, under what circumstances, or whether it is an extrapolation of data such as those published by Rashbass & Westheimer (1961). These authors found a somewhat similar relation, but it was based on measurements only of small disparities and small vergence eye movements. Erkelens (1987) showed recently that this relation should not be extrapolated to large disparities, because the velocity of vergence, controlled exclusively by disparity, reaches a maximum of 14° s^{-1} to 40° s^{-1} for disparities of about 4°, and is reduced almost to zero when disparity is only as large as 10°.

Thus we believe that our present data are the first to actually show that peak smooth vergence velocity is approximately linearly related to vergence amplitude with a slope of the order of 4° s^{-1} per degree of vergence (see figure 5). These fast, effective responses were obtained simply by providing the subject with a relatively natural visual environment that contained both monocular and binocular cues to the depth of the targets with respect to the subject and with respect to other objects and visual frames. All of these cues were static, that is the subject's head was fixed and the target pairs and their backgrounds remained stationary. In the preceding paper (Erkelens *et al.* 1989), we showed that dynamic cues to motion in depth were also more effective than could have been expected from earlier reports.

Vergence responses when gaze shifts in a structured visual environment

Vergence responses were very fast, accurate and reliable when gaze was shifted between targets located both along and off to the side of the median plane. These responses were primarily smooth when the target fell along the median plane and primarily saccadic when the targets fell off to the side of the median plane. The purpose of the present series of experiments was to explore the capacity of the vergence subsystem under relatively natural conditions. We had no idea when we ran these experiments that we would find performance under these relatively natural conditions departed from traditional beliefs about the nature and capacity of vergence under such conditions. Had we known, we would have included a number of additional target configurations. We do not yet know the function relating the proportion of smooth to saccadic components of the vergence response to the placement of the targets. At present we only know what happens along the median plane and when targets differ in direction by 45° and differ in vergence by 11°, while the targets were offset from the median plane by 20° to 25°. In this asymmetrical target condition, which was the only one tested, changes of vergence were achieved primarily by saccades of different sizes. Targets off the median plane are the most likely targets to be encountered in most natural viewing conditions. This means that the saccadic component of vergence is likely to be very significant in everyday life. Gaze movements exactly along the median plane would be very rare outside the laboratory. But even here we found a role for the saccadic component of vergence, despite the fact that vergence along the median plane was largely mediated by smooth eye movements. Any small saccades that did occur contained a disjunctive component that was effective in speeding vergence up. Even if subsequent research shows that the saccadic component of vergence only serves a substantial role in the vergence response when the objects of interest fall a few degrees off to the side of the median plane, our present results with asymmetrical targets clearly suggest that the traditional emphasis on the role of smooth eye movements in implementing changes in vergence is unwarranted.

There are a few earlier observations that support this view. They have usually been interpreted as curious exceptions to normal performance. Kenyon *et al.* (1980*a*, *b*) reported disjunctive saccades during symmetrical vergence in their normal controls for an experiment with strabismic and amblyopic patients. These authors reported that saccades tended to be more disjunctive in the early part of the vergence movement than later on. Our disjunctive saccades had similar properties (see figure 4). Kenyon *et al.* (1980*b*) ascribed their disjunctive saccades to a nonlinear interaction in the orbital plant that they simulated with a sixth-order linear-system model.

Disjunctive saccades during asymmetrical vergence that cannot be explained by a linear summation of conjugate saccades and ongoing smooth vergence have also been described previously. Ono & Nakamizo (1978) observed them first in a task in which two targets were in the line of sight of one eye (the Wheatstone–Panum limiting case). Ono *et al.* (1978) investigated them further. These authors attempted to explain them by referring to a possible nonlinear interaction of saccades and vergence at the muscular level. The occurrence of disjunctive saccades, mediating part of the vergence during gaze shifts between targets off the median plane, was also investigated by Enright (1984, 1986). He used a video system with severely limited temporal resolution to measure eye movements, but was able to demonstrate that saccades probably mediated a large fraction of a required change in asymmetrical vergence, even when the location of a new target was unpredictable and when subjects were inexperienced in the task. These findings are consistent with our view that saccades are very important for changing vergence in everyday life.

All these previous reports, however, described relatively small saccadic changes of vergence. We, on the other hand, found that vergence changes as large as 11° can be achieved almost completely by disjunctive saccades. This effect was so large, and the performance of our subjects so reliable, that we feel that the programming of saccades of unequal sizes must be an important basic capacity of the oculomotor system, and not an adventitious result of some peripheral nonlinearity.

Hering's law and the nature of version and vergence

There is a long tradition of discussing binocular eye movements in the light of Hering's law and its possible violations. The original formulation of the law (Hering 1868) was in terms of 'equal innervation' of both eyes, so that the two eyes would move with such perfect coordination that they could be considered as one 'double eye', aimed in direction and depth by coordinated vergence and version. Thus the basic tenet was that the lines of sight of both eyes cannot be directed independently. Rather, the eyes are controlled in such a manner that their lines of sight intersect at one and the same, selected target. Few people will argue against this view, which essentially states that we do not look at different objects with each of our eyes, unless our oculomotor system is disorganized by pathology.

The further elaborations of Hering's law are less obvious. Hering's next step was to describe all binocular eye movements as the sum of two processes: an equal innervation for version, causing a similar lateral deviation of both eyes, and an equal innervation for vergence, causing a symmetrical convergence. The crucial point here is the postulate of two different neuronal controllers. The statement that all binocular eye movements can be described as the sum of a symmetrical vergence response and an equal version response is, by itself, no more than a mathematical tautology. It is true under any circumstances and cannot be violated (Ono (1980) also pointed this out). Hering's preference for describing binocular eye movements in terms of separate version and vergence responses should be seen in the historical context of his time and his controversies with Helmholtz, who favoured the theory that each eye was controlled independently (see Bridgeman 1977). Neither Hering, nor anybody else in his time, had any direct knowledge of neuronal processes, muscular activities, or even the dynamics of eye movements. The first objective recordings and formal classification of eye movements were published 35 years after the formulation of Hering's law (Dodge 1903). Dodge described vergence as a separate, slow kind of eye movement (type 5). More or less by implication, it has been assumed ever since then that Dodge's other types of eye movements (currently called smooth pursuit, saccades and compensatory eye movements, such as the vestibulo-ocular response) are all basically conjugate. Thus it became customary to identify Hering's hypothetical processes with these apparently distinct categories of oculomotor output. These categories of eye movements seemed to show quite different dynamic properties, which suggested that they could be separated experimentally. This separation appeared to be particularly clear with respect to the saccade and the 'slow' vergence categories, which caused most recent discussions of the validity of Hering's law to concentrate on the hypothesis that gaze shifts between points in different directions and depths can be described as the linear sum of a disjunctive, smooth, slow vergence response and a conjugate, fast saccadic response (some contribution of conjugate smooth pursuit has also been suggested). Yarbus (1967) explicitly reported that he had confirmed this hypothesis. His schema (Yarbus 1967, figure 94) has been reprinted often, which has done much to popularize this view, despite the fact (discussed above) that exceptions to this schema have been reported (Kenyon *et al.* 1978, 1980*a*, *b*; Clark & Crane 1978; Enright 1984, 1986). Enright (1984) went so far as to point out that even Yarbus's (1967) own published recording, on which his schema was based, does not (on closer scrutiny) support the contention that saccades and vergence are independent. A marked acceleration of vergence can be seen to occur during the saccade in the published eye movement record. We noticed another discrepancy between our and Yarbus's (1967) results. In our experiments, gaze shifts between targets differing in distance and direction always started with disjunctive saccades, which were followed by smooth vergence if any correction was still required at saccade-offset. We never observed Yarbus's triphasic response consisting of an initial smooth vergence, followed by a saccade, followed by the continuance of smooth vergence.

It is doubtful that all these arguments really have much to do with the original ideas of Hering (1868), who never even made the distinction between saccadic and smooth movements. We propose, therefore, to avoid further discussion of this controversy and to concentrate on Hering's crucial insight, namely that the motions of the two eyes are coordinated to such an extent that the lines of sight of both eyes are always directed towards the single object that we wish to inspect. Hering never said that saccades should be conjugate; an assertion disproved by earlier, as well as by the present research. Instead, we propose to elaborate on Hering's original insight in the following manner.

Binocular eye movements are coordinated in such a way that a person can binocularly foveate any real object within his visual field. Furthermore, gaze can be shifted quickly between all stationary objects or moved continuously to track all objects moving relative to the person. The eye movement system uses two, and only two, subsystems to achieve this. The two subsystems participate synergistically in all oculomotor performance. They are distinguished only by the type of eye movements they produce: saccadic or smooth. These different modes of oculomotor behaviour have different acceleration characteristics, maximum speeds and continuity of output. We propose that both subsystems produce conjugate and disjunctive eye movements, as appropriate for binocular fixation of a particular stationary or moving object of interest in the real world. Most gaze shifts in the real world will be made between targets that differ in direction as well as in distance. In many cases the required changes in vergence will be relatively modest. For example, we print our books so that convergence does not exceed about 10° at normal reading distance. Our results, and those of Enright (1984, 1986) show that disjunctive saccades contribute markedly to changes of vergence at such distances. It is only on the very rare occasions that targets have exactly the same binocular direction, such as when they are located along the median plane, that the operation of the saccadic subsystem is not prominent. However, even here subjects often make some small disjunctive saccades. They use them to speed up their smooth vergence responses.

There is a great deal left to do now that we have shown that the control of vergence can be studied in the laboratory in ways that make sense with respect to the way vergence must operate in everyday life. We must now determine with our accurate, high-bandwidth instrumentation, how the saccadic and slow subsystems function, synergistically, when gaze shifts between stationary objects or tracks a moving object located anywhere within the three-dimensional visual field in which human beings locate, track and manipulate objects of interest to them. We must refine our techniques to allow the subject's head to be free while he interacts with objects within reach of his hands. Once this has been done, we will begin to have some idea of how cognitive, oculomotor and manual motor skills interact to guarantee our success as a species.

This research was supported partly by the Foundation for Medical Research MEDIGON (The Netherlands) (grant no. 900-550-092), partly by NIH-NEI grant no. EY-04647 (U.S.A.) and partly by the Department of Psychology, University of Maryland.

REFERENCES

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

Bridgeman, B. 1977 Introduction. In *The theory of binocular vision* (translation of Hering, E. *Die Lehre vom binokularen Sehen*), pp. 1–13. New York: Plenum.

Clark, M. R. & Crane, H. D. 1978 Dynamic interactions in binocular vision. In *Eye movements and the higher psychological functions* (ed. J. W. Senders, D. F. Fisher & R. A. Monty), pp. 77–88. Hillsdale, New Jersey: Erlbaum.

Collewijn, H., Erkelens, C. J. & Steinman, R. M. 1988 Binocular coordination of human horizontal saccadic eye movements. *J. Physiol., Lond.* **404**, 157–182.

Collewijn, H., Steinman, R. M. & Van der Steen, J. 1985 The performance of the smooth pursuit eye movements system during passive and self-generated stimulus motion. *J. Physiol., Lond.* **366**, 19*P*.

Dodge, R. 1903 Five types of eye movement in the horizontal meridian plane of the field of regard. *Am. J. Physiol.* **8**, 307–329.

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., Van der Steen, J., Steinman, R. M. & Collewijn, H. 1989 Ocular vergence under natural conditions. I. Continuous changes of target distance along the median plane. *Proc. R. Soc. Lond.* B **236**, 417–440. (Preceding paper.)

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.)

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

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

Kenyon, R. V., Ciuffreda, K. J. & Stark, L. 1980*b* Unequal saccades during vergence. *Am. J. Optom. physiol. Opt.* **57**, 586–594.

Ono, H. 1980 Hering's law of equal innervation and vergence eye movement. *Am. J. Optom. physiol. Opt.* **57**, 578–585.

Ono, H. & 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. & Steinbach, M. J. 1978 Nonadditivity of vergence and saccadic eye movement. *Vision Res.* **18**, 735–739.

Rashbass, C. 1981 Reflexions on the control of vergence. In *Models of oculomotor behavior and control* (ed. B. L. Zuber), pp. 139–148. Boca Raton: CRC Press.

Rashbass, C. & Westheimer, G. 1961 Disjunctive eye movements. *J. Physiol., Lond.* **159**, 339–360.

Skavenski, A. A. 1971 Extraretinal correction and memory for target position. *Vision Res.* **11**, 743–746.

Skavenski, A. A. & Steinman, R. M. 1970 Control of eye position in the dark. *Vision Res.* **10**, 193–203.

Stark, L. 1983 Normal and abnormal vergence. In *Vergence eye movements: basic and clinical aspects* (ed. C. M. Schor & K. J. Ciuffreda), pp. 3–13. Boston: Butterworths.

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