CHANGES IN VERGENCE MEDIATED BY SACCADES

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SUMMARY

1. When binocular fixation is shifted between two targets which require change in vergence as well as an equivalent or greater alteration in the mean visual direction, the observed eye motions do not – as asserted by Yarbus (1957) and widely accepted today – consist of slow symmetrical change in vergence, upon which a conjugate (binocularly balanced) saccade is additively superimposed.

2. In all tested target configurations, an unexpectedly large fraction of the total change in vergence occurred during the saccades; observed values ranged from about 40 % in certain tasks, to essentially 100 % when large version (4°) was combined with small vergence change (less than 1°). In these latter situations, binocular congruence can be restored within about 50 ms by appropriately unbalanced saccades, rather than about 500 ms, as expected if slow fusional vergence movement were required.

3. When larger vergence changes are demanded, additivity between vergence movement and conjugate saccade is also violated in that the rate of vergence change during the saccades is several-fold larger than the rate before the saccade or during subsequent completion of the required change in vergence. Furthermore, the residual fusional vergence movement observed in these tests was usually strongly asymmetrical, and often almost entirely monocular.

4. Vertical saccades are nearly as effective as horizontal saccades in mediating a large fraction of an intended change in vergence.

5. In saccades, which contributed strongly to (or fully mediated) an intended vergence change, target-specific binocular differences in saccadic excursion of as much as 40–50 % were observed; hence, these eye movements are not fully yoked, as the term 'conjugate' implies. Instead, the eyes behave in such situations as though visual information from each eye is processed separately prior to the saccade, in order to generate the neural signals which control open-loop saccadic movement of the eye.

INTRODUCTION

During binocular vision in a natural environment, we commonly shift our attention among targets which differ in both direction and in distance from the eyes. If the difference in distance between successive points of fixation is large enough to permit stereopsis, there is detectable difference in the images upon the two retinas ('disparity'); and this difference not only permits stereopsis, but also provides the

eye-movement system with a potential stimulus for vergence change, so that the angle between the visual axes can be appropriately altered during the shift in fixation.

The dynamics of the eye movements which occur, when fixation is changed in such a situation, were extensively investigated by Yarbus (1957), who used the results of
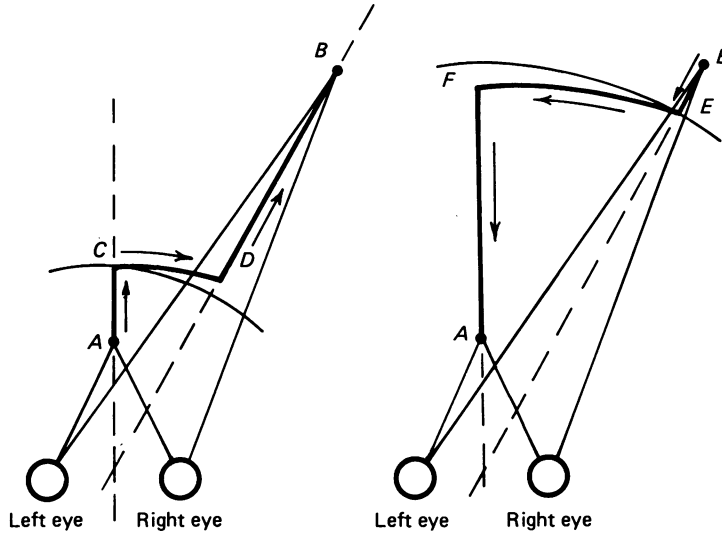

Fig. 1. Eye movements according to Yarbus (1957), during change of fixation between two targets which are located in different directions and at different distances. Left diagram, for change from A to B, involves divergence movement; right diagram, for change from B to A, involves convergence movement. The heavy lines trace the progressive movement of the point at which the visual axes intersect. This scheme indicates an initial phase of slow, symmetrical vergence change (AC or BE); a rapid conjugate saccade, during which slow vergence change continues (CD or EF); and a final prolonged phase of slow symmetrical vergence movement, to the new point of fixation (DB or FA).

'numerous records' in formulating the schematic diagram shown in Fig. 1 (Yarbus, 1957; Fig. 6). This illustration has been widely accepted as a convenient summary of current views about how the eyes deal with this composite viewing task (Alpern, 1962, 1969; Yarbus, 1967; Carpenter, 1977). According to Fig. 1 (hereafter referred to as the Yarbus interpretation), the motion can be divided into three phases, involving two independent components: a first, brief phase during which slow vergence movement begins; a rapid conjugate saccade, with excursion equal to the difference in mean direction between fixation points, during which slow vergence movement continues; and subsequent gradual completion of the symmetrical vergence change demanded by the targets. This sort of compound motion was described by Yarbus (1957, 1967) as representing arithmetic summation of two independent kinds of movement which have been extensively studied in simpler situations: ordinary, symmetrical fusional change in vergence, upon which is superimposed, in mid flow, a conjugate saccade of the sort which occurs between a pair of equidistant targets. The essence of the Yarbus interpretation is the additivity of version and vergence movements.

Additivity was also subsequently reported for combinations of vergence and

smooth pursuit movements (Rashbass & Westheimer, 1961 *a*), and this latter interpretation has been reasonably well borne out by more recent work (Miller, Ono & Steinbach, 1980). Nevertheless, data from another recent study (Ono, Nakamizo & Steinbach, 1978; see also Ono & Nakamizo, 1978) suggest that Yarbus's claim for additivity of saccades and vergence movement deserves re-examination. That research involved Johannes–Müller-type targets, in which only one eye undergoes net displacement at steady state (i.e. the two fixation targets were not laterally displaced, as are *A* and *B* in Fig. 1, but instead were both on the same line of sight for one of the eyes). In principle, only one eye needs to move during this manoeuvre, but in fact a binocular saccade consistently also occurs (Alpern & Ellen, 1956), and this seemingly superfluous saccade has, as in the Yarbus interpretation, also been interpreted as due to superposition of version and vergence movement. Ono *et al.* (1978) reported, however, that the saccades in such situations involve statistically reliable binocular differences in magnitude and velocity, 'which were too large to be understood by an additivity hypothesis' (Ono *et al.*, p. 735; see also, Ono & Nakamizo, 1978, p. 518 for a similar conclusion based on results from an identical stimulus configuration). Furthermore, Kenyon, Ciuffreda & Stark (1980) have examined the adventitious saccades which are occasionally observed during a simple symmetrical vergence task (i.e. no net version), and found that these unexpected saccades tend to be markedly asymmetrical in excursion in a way which 'cannot be explained by linear summation of saccadic amplitude onto the ongoing vergence' (Kenyon *et al.*, p. 586). Since version and vergence movements were found to be non-additive in these situations, a careful re-study of the eye movements which arise with the more commonly encountered target configuration investigated by Yarbus seems warranted.

Results which are in superficial agreement with Fig. 1 are reported here for vergence change of about 2·3° combined with 5° version, but detailed analysis of those data reveals serious discrepancies. The results are qualitatively similar to those reported for Johannes–Müller-type targets (Ono & Nakamizo, 1978), but quantitatively more extreme, with 60 % of the vergence change arising during the saccade, compared with about 15–30 % in the collinear target configuration. Further data demonstrate that when the demand for change in vergence is much smaller than the demand for version (less than 1°; and 4° respectively), the interpretive scheme proposed by Yarbus (1957) is completely inapplicable: the expected slow-motion components of vergence change, preceding and following the saccade, become negligible, and the required change in vergence is mediated entirely or almost entirely by saccades which are binocularly unequal in excursion. This phenomenon, which represents a striking departure from long-standing concepts about the dichotomy between conjugate and disjunctive eye movements, can reduce by an order of magnitude the time required for those shifts of fixation which require only small changes in vergence.

<div align="center">METHODS</div>

The tips of vertically oriented needles, located at distances of about 25 cm from the eyes, served as fixation points, except where otherwise specified. The two needles of a pair were continuously visible in front of a featureless white background in a well-lit room; they were inserted into a frame which had several potential target positions, and the five positions used most often are shown in Fig. 2. Prior to a measurement session, the subject entered the bite board, which included a plastic

custom-fitted impression of the subject's upper teeth, and, with left eye occluded and right eye oriented straight ahead, carefully aligned two needles placed in the right-hand column of target positions. The target frame was fastened in this position, and alternating shifts of binocular fixation were then undertaken between the left-hand needle (L in Fig. 2) and a second needle placed in one of the four right-hand positions (R_1, R_2, R_3 or R_4). The expected steady-state displacement of the right eye was therefore the same (about 4°) for all these tasks. Positions L and R_3 demanded version with unchanged vergence; position L together with R_1, R_2 or R_4 demanded change in vergence of about 2·3°, about 1/2° or about 3/4°, respectively, with small inter-subject differences dependent upon inter-ocular spacing.
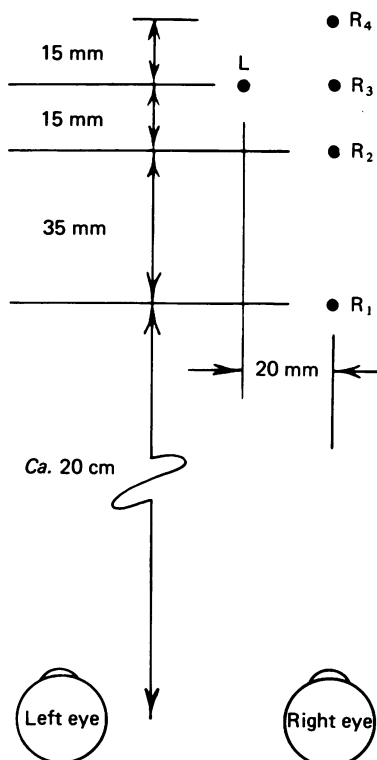

Fig. 2. Schematic illustration of the sorts of target configuration used in the experiments. One needle was in position L, and a second needle was in one of the four alternative positions in the right column. The right column of positions was aligned with the visual axis of the observer's right eye, which was oriented straight forward.

The motion of each eye was monitored by a video camera (Sony model AVC 3250) equipped with extension tube and zoom lens. The two cameras were about 10° below the plane of eye movement, and were firmly mounted to the forehead-rest-and-bite-board assembly. The resulting video pictures were combined with an image splitter (Sony model SEG-1), which produced a high-contrast vertical discontinuity in mid-screen between the images of the two eyes; magnification was about 7-fold on the video monitor (Sony model CVM-131, 33 cm diagonal). Brightness of the monitor was greatly reduced to enhance sharpness of the images of the iris margins, and the position of each eye was then measured separately in single frames of the video recording, using a procedure which takes advantage of vernier acuity. The zero line of a transparent ruler was aligned with the sharp mid-screen discontinuity produced by the image splitter, and an opaque vertical straight edge was then slowly brought to a point of tangency on the iris. While re-checking the zero alignment, the position of the straight edge was then read on the ruler, interpolating to 0·1 mm. All measurements were made monocularly, and parallax has no residual effect on the readings because the images

of both the iris and the discontinuity are coplanar and equidistant from the ruler. Each estimate of eye position was based on three to five such measurements.

Replicate blind evaluations of several sequences of video frames indicate that after practice with the method, the measurement error for a single reading typically has a s.d. of about 0·14 mm, implying that 95 % of the time an interpolated reading from the video monitor would be within about ±1/4 mm of its true value. A s.d. of 0·14 mm on the monitor corresponds to about 20 μm at the eye, representing about 6 arcmin of rotation, as an estimate of the precision of single readings. Averages based on replicate measurements, as used here, will of course be more precise; but even without replication, the video method compares favourably in precision with standard photo-electric recording methods (e.g. Biometrics SGH/V-2), where the resolution is reported to be about 15 arcmin. Temporal resolution of a video recording, however, is limited by the sampling rate of 60 frames/s, meaning that estimates of eye velocity represent averages over many milliseconds.

A strongly attenuated stroboscopic flash signalled the subjects to change fixation; the faint corneal reflexion of this signal served as a time marker to identify individual frames of the video record. In most experiments, full sequences of the recordings were not completely evaluated; instead, four single frames were chosen for each change in fixation, selected as follows. During a preliminary frame-by-frame scan of the recording, the time was identified at which rapid saccadic eye movement began, relative to the signal marker. Measurements were then made of: (1) the video frame in which the strobe signal appeared; (2) the frame just preceding onset of the saccade; (3) the frame 83 ms (five frames) later, an interval sufficiently long to include the entire saccade; and (4) the frame 500 ms after saccadic onset, an interval chosen to be long enough for completion of all expected vergence movement (Bahill & Stark, 1979), as well as for small corrective saccades which might be necessary to re-adjust for perceived errors of fixation. Measurements from these four frames serve to define the temporal distribution of vergence change, as illustrated in Fig. 3, in which the expected eye motions in Fig. 1 are presented in a form in which time is made explicit, together with similar expectations for the mirror-image target configuration. The four video frames selected as described above provide estimates of the distances designated D_1, D_2, D_3 and D_4 in Fig. 3. Given these estimates, one of the important expectations for all four viewing situations, according to the Yarbus interpretation, can be summarized as follows: $|D_4 - D_3| \gg |D_2 - D_1| > |D_3 - D_2|$.

Measurements of version alone, which served both as a calibration task and as an indication of variability in performance for a non-vergence task, were conducted either in a single block of twelve alternating shifts of fixation, or in two blocks of six shifts. Other measurements were made in blocks of six tests, either in alternation with pure version (e.g. positions L–R$_3$, L–R$_1$, L–R$_3$ and L–R$_1$) or with alternation of different directions of vergence change (L–R$_2$, L–R$_4$, L–R$_2$ and L–R$_4$) for a total of twenty-four observations to a test situation. Within a block of tests, each fixation was held for about 6 s, and was terminated on command given via the strobe-flash signal, at an irregular time within an announced 1·5 s temporal window, a procedure which prevented anticipatory eye movements. Changeover to a new target position between blocks of six tests required about 30 s, leading to a total test session of about 4 min.

None of the experimental subjects had any known visual anomaly, and all had uncorrected normal acuity. They ranged in age from 23 to 26 years, and their inter-ocular spacings ranged from 53·5 to 67·5 mm. Two subjects, both right-eye dominant, participated in essentially all test situations; for the most extreme component of the results (Figs. 8 and 9), two additional subjects were tested, both left-eye dominant. None of the subjects had prior experience in similar tests of oculomotor performance.

<div align="center">RESULTS</div>

Modest changes in vergence with version

Two subjects were tested with a demand for change in vergence of about 2·3° combined with about 5° version (target positions L–R$_1$ in Fig. 2); results are summarized in Fig. 4, in terms of the time, relative to saccadic onset, at which vergence movement occurred. (See Appendix for consideration of the absolute accuracy of such average values.) The data resemble expectations based on the Yarbus interpretation in two features: prior to the saccade, a small amount of

vergence movement was evident, and for one of the subjects, the mean value of this change, though small, was significantly greater than zero (t test, $P < 0.01$); in addition, as expected, a major fraction of the total change in vergence occurred after the saccade. It is unexpected, however, to find that more than half the total required change in vergence occurred during the saccade itself. The Yarbus interpretation (Fig. 1) indicates that this should be the smallest rather than the largest of the three components of total vergence movement.
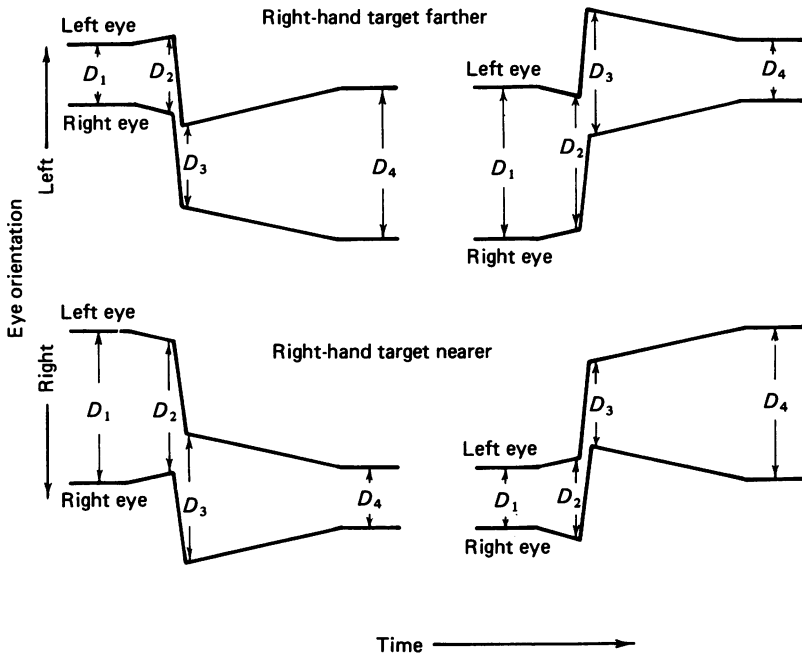

Fig. 3. Schematic plot of eye orientation (rotational position) as a function of time, to be expected according to Yarbus (1957) during change of fixation between two targets which are located in different directions and at different distances. The upper illustrations apply to the target configurations shown in Fig. 1; the lower illustrations apply to the mirror-image arrangement, in which the more distant target (B in Fig. 1) is located to the left of the nearer. In the present experiments, D_1 was measured at the time the signal was given to initiate a change of fixation; D_2 was measured in the video frame just before saccadic onset; D_3 was measured 83 ms later; and D_4 was measured 500 ms after saccadic onset. By dealing with absolute value of differences between values of D, observations for convergence and divergence movements can be combined.

A closely related anomaly in these experiments is that the changes in vergence which occurred during the saccades had a very high mean velocity; based on the data in Fig. 4, average values over the 83 ms interval were $16.4°$ vergence/s for subject 1 and $18.5°$ vergence/s for subject 2. The 83 ms 'saccadic interval' of the analyses of Fig. 4 was appreciably longer than the actual duration of saccadic movement, meaning that the true intrasaccadic velocity of vergence change could in fact be much greater. Therefore, these recordings were re-analysed with only 50 ms allocated to the saccade (taken as that 3-video-frame interval during which most version movement occurred). Fig. 5A and B presents the average vergence data, together

with standard errors, from these finer-grain analyses of the 200 ms intervals surrounding the saccades. As is evident there, the rate of vergence change during the saccades was much greater than that measured before or afterward ($P < 0.01$, F test); furthermore, these average intrasaccadic vergence rates are larger by several fold than literature values would lead one to expect as maximum velocity for pure vergence movement of this size (see Bahill & Stark, 1979, for summary). In order to determine whether comparison with literature values is appropriate for these subjects, both of
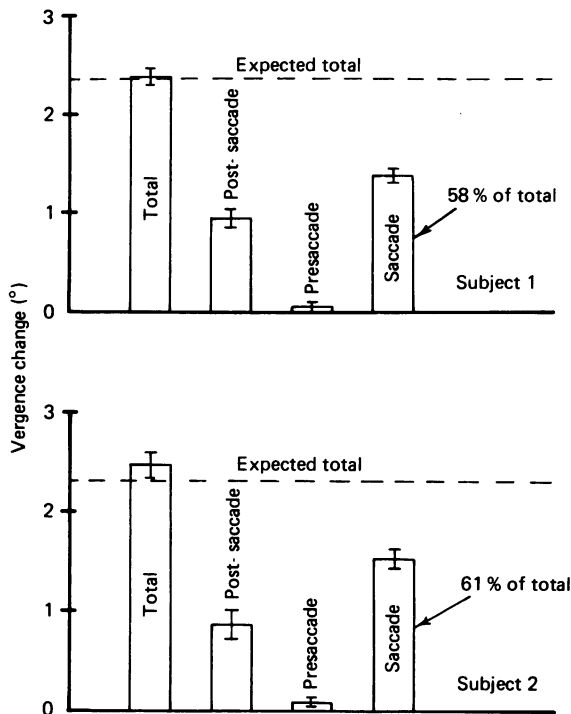

Fig. 4. Mean vergence changes, presented in terms of the phase at which movement occurred, for twelve changes in fixation between target positions L and R_1 of Fig. 2, for two subjects. 'Post-saccade' corresponds to $|D_4-D_3|$ in Fig. 3; 'Presaccade' corresponds to $|D_2-D_1|$, and 'saccade' to $|D_3-D_2|$. Vertical lines at the top of columns correspond to ± 1 s.e. of mean.

them were subsequently tested with targets which required $2.7°$ of symmetrical fusional vergence movement. Each of those video recordings (twelve tests with each subject) was measured on a frame-by-frame basis for the full 60 s following the strobe signal. From these data, the maximum observed value for velocity of vergence change over a 50 ms interval was determined, regardless of when it occurred relative to onset of eye movement. For subject 2, all twelve of those maximum values were less than the mean (or the median) of the intrasaccadic velocities shown in Fig. 5B; for subject 1, eleven of the twelve maximum values were less than the mean (or the median) shown in Fig. 5A. Hence, the data shown in Fig. 5 involve not only a remarkable temporal coincidence of rapid vergence change and occurrence of the
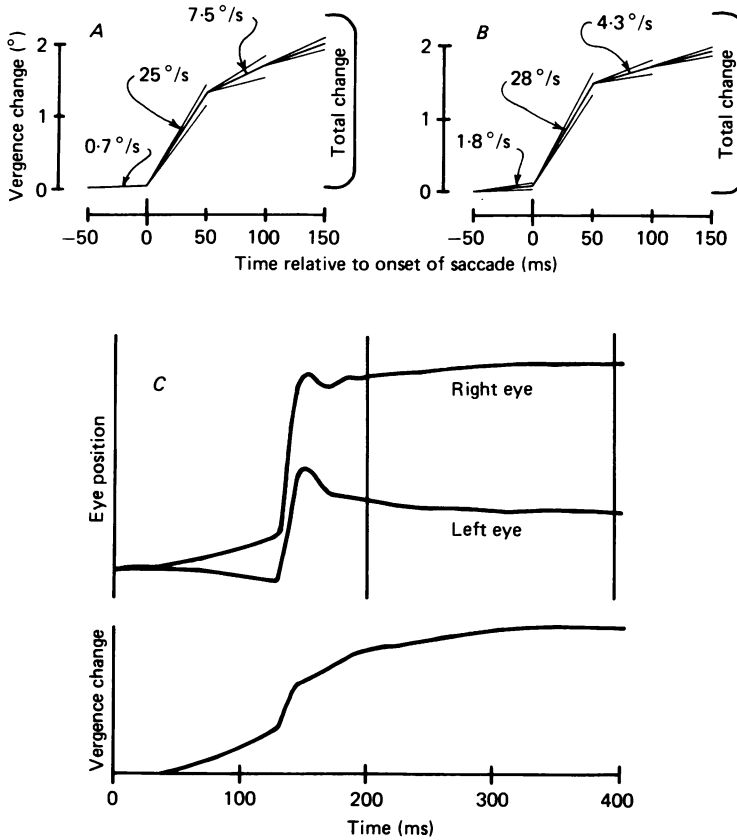
Fig. 5. Vergence as a function of time. A (subject 1) and B (subject 2): data from tests summarized in Fig. 4, but based on re-measurement at 50 ms intervals surrounding saccade. The interconnected lines, with values indicated for slope, represent mean values over twelve changes in fixation; the diverging pairs of lines represent ±1 s.E. of mean for vergence change during each 50 ms segment. The brackets labelled 'total change' represent mean amount of vergence change measured from signal to 500 ms after saccadic onset. C, upper graph: tracing of eye position record from Yarbus (1957, Fig. 4) for task combining version and vergence change. Lower graph: vergence as a function of time, derived as difference between eye positions in upper graph. Ordinate values are only relative scale in this illustration, because original Figure has no ordinate scale in degrees.

saccade, but also exceptionally large velocities of vergence movement compared with pure vergence-change tasks.

In the article in which Yarbus (1957) proposed the interpretation shown here as Fig. 1, only a single eye-movement recording was illustrated for a combined version and vergence-change task. Tracings from that recording are shown in the upper panel of Fig. 5C; the lower panel of Fig. 5C contains a plot of vergence derived from those tracings. The discontinuity in slope of this curve, during the most rapid saccadic motion, resembles the results shown in parts A and B of Fig. 5; and the short duration of the spurt in vergence movement in Fig. 5C suggests that the 50 ms sampling interval, which underlies the analyses of Fig. 5A and 5B, may lead to underestimates of the true maximal velocities of intrasaccadic vergence change.
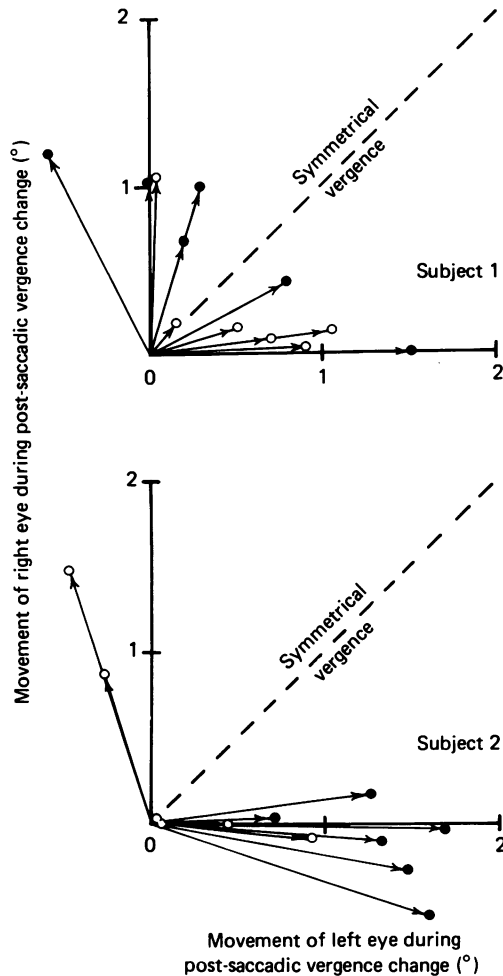
Fig. 6. Contribution of each eye to post-saccadic vergence movement, for the tests illustrated in Fig. 4. Filled circles represent convergence movement, open circles, divergence. Points to the left of the ordinate indicate that both eyes after the saccade had overshot target location; points below the abscissa indicate that both eyes had undershot target location during saccade.

Still another unexpected aspect of the detailed data from these tests is illustrated in Fig. 6, in which the *post-saccadic* vergence changes are resolved into the contribution from each eye. In nearly all trials, this vergence movement was strongly asymmetrical, rather than symmetrical, as illustrated in the schematic summary of Yarbus (Fig. 1). In seven of the twelve tests with subject 2, the right (dominant) eye contributed less than 0·1° to the resulting post-saccadic vergence movement; in those tests, that eye had essentially reached its steady-state orientation at the end of the saccade. Similarly, in seven of the twelve tests with subject 1, one eye or the other had reached its final orientation at the end of the saccade, to within 0·15°, while the other eye undertook the post-saccadic vergence movement essentially alone; in five of these seven cases, it was again the dominant eye which was on target after the saccade.

As is implicit in the fact that the saccades in these experiments contributed so strongly to vergence change, the two eyes moved by quite different amounts during the saccades. The extent of this saccadic imbalance is shown in Fig. 7, in terms of the ratio of left-eye movement to right-eye movement; on average, the left eye moved some 30–40 % more during the saccades than the right eye, as was appropriate for the target configuration.
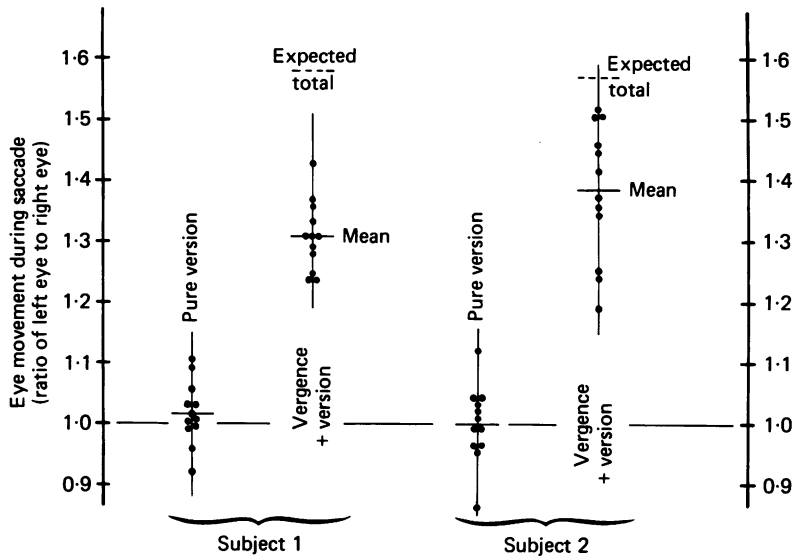

Fig. 7. Ratios of movement of left eye to movement of right during the saccadic phase of eye motion (83 ms) in the tests of Fig. 4 ('vergence + version') as well as in the preceding and intervening blocks of tests with pure version (target positions L–R$_1$ and L–R$_3$, respectively, in Fig. 2). Horizontal lines through data columns represent averages of twelve tests; dashed horizontal lines show expected ratio if all vergence movement had occurred during saccade.

In summary of these modest vergence-change experiments, the data show superficial resemblances with the Yarbus interpretation, but quantitative aspects of the data disagree strikingly with the conclusion that the over-all eye movements can be adequately described as simple summation of ordinary fusional vergence motion and a conjugate saccade. Experiments with smaller demand for vergence change, described below, reveal even more extreme departures from the Yarbus interpretation.

Vergence change much smaller than version

In these tests, the required change in vergence was less than 1°, combined with demand for version of about 4°; the data for all four subjects are presented in Fig. 8, in terms of the phase at which vergence change occurred. On average, over all subjects, more than 90 % of the vergence change took place during the saccade; in most test series, the data are compatible with the hypothesis that the full vergence change was mediated by the saccades ($P > 0.10$). Only one data set (subject 2 at 0.72°)
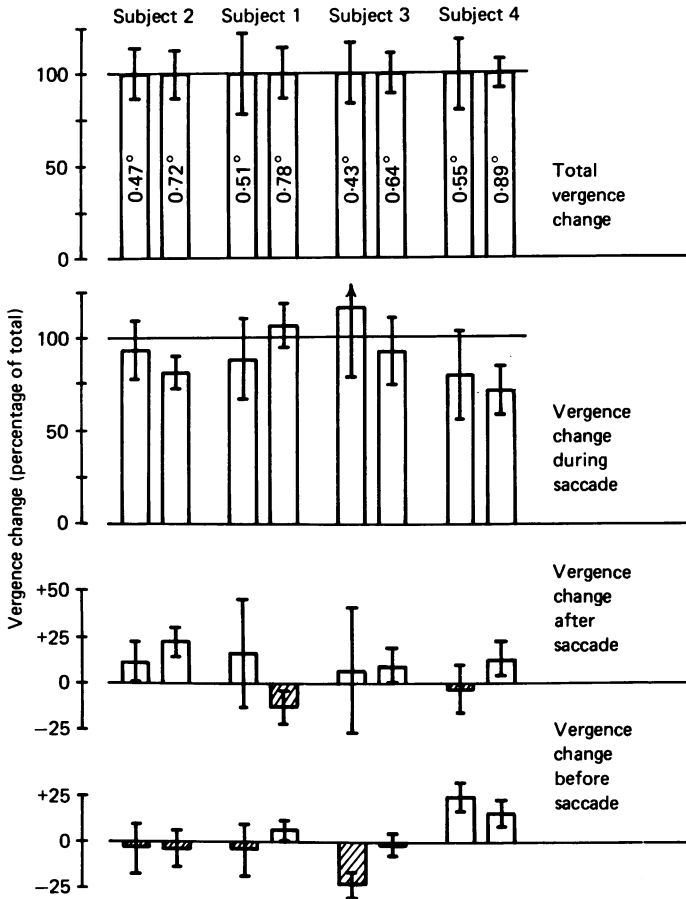
Fig. 8. Vergence changes categorized by the phase at which movement occurred, for the four subjects in tests with targets in positions L–R$_2$ and L–R$_4$ of Fig. 2 (left and right columns, respectively, for each subject). Average total vergence change, from signal to 500 ms after saccadic onset, was set equal to 100 %, with corresponding value in degrees shown within the columns for 'total vergence change'; vertical lines at the top of columns represent ±1 s.e. of mean ($n = 12$). The four rows of data, from top to bottom, correspond with $|D_4 - D_1|$, $|D_3 - D_2|$, $|D_4 - D_3|$ and $|D_2 - D_1|$ in Fig. 3. Hatched areas represent negative contribution to finally achieved vergence change.

showed statistically significant evidence for slight but consistent post-saccadic vergence change, although the Yarbus interpretation indicates that nearly all vergence change should occur then. The eye-movement ratios during these saccades are presented in Fig. 9, and document clear binocular asymmetry in excursion, although the binocular imbalance was less extreme than with larger vergence change (Fig. 7). For all subjects, the results demonstrate that the left eye usually performed larger saccades than the right eye when these were appropriate for the targets, and smaller when those were appropriate. (See Appendix for evidence that changes in the axis of ocular rotation did not contribute significantly to the saccadic imbalance shown in Fig. 9.)

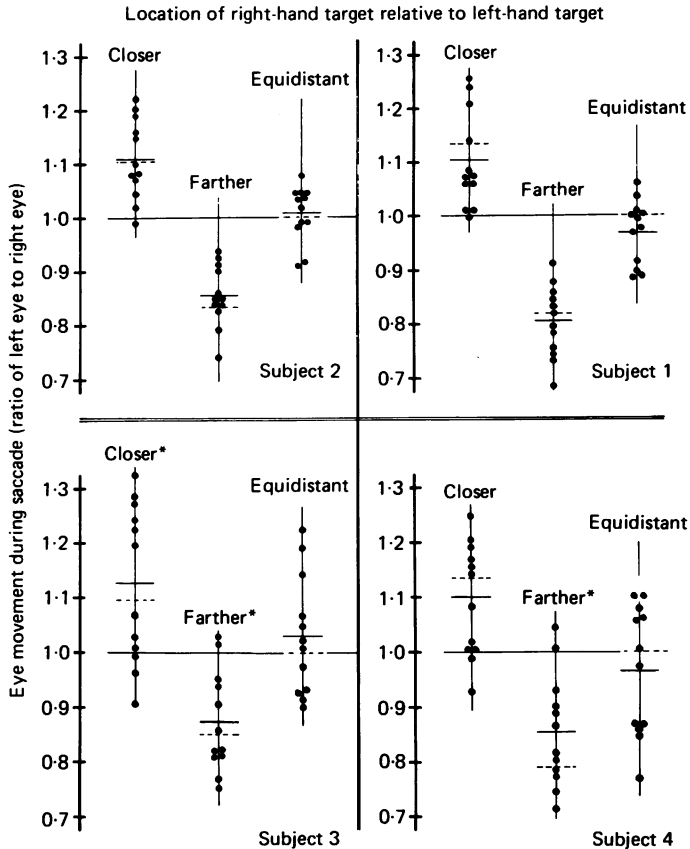Location of right-hand target relative to left-hand target

Fig. 9. Ratios of the movement of the left eye during the saccade to that of the right eye, in the tests summarized in Fig. 8 ('closer' and 'farther'), as well as during preceding or following tests with pure version movement ('equidistant'). 'Closer', 'farther' and 'equidistant' correspond to target positions L–R$_2$, L–R$_4$ and L–R$_3$, respectively, in Fig. 2. Continuous horizontal lines through the columns of data points represent calculated average of each set; dashed lines represent the average of the corresponding set of ratios observed for total eye movement (signal to 500 ms after saccade). Asterisks indicate those data sets in which the variance of the ratios after the saccade was significantly greater ($P < 0.05$, F test) than the variance of the ratios achieved during total eye movement.

The experimental protocol used here involved repeated alternations of fixation between continuously visible pairs of targets at 6 s intervals, and the suspicion therefore arises that practice during a test series might have contributed to the results. If repetition of the same task contributed to greater saccadic vergence change, the first saccades within a block of six tests should be less asymmetrical than the last ones. In Fig. 10, the saccadic eye-movement ratios of the four subjects are presented for the two target configurations which resulted in the data of Fig. 9, with data segregated by order within the blocks of six tests. There is no evidence here that the saccades became progressively more unbalanced, suggesting that target-specific practice was unimportant in these experiments.

By dealing only with the absolute value of vergence change, the preceding analyses

(except for Fig. 6) have treated convergence and divergence movements as equivalent, mirror-image processes, as did Yarbus (1957; see Fig. 1), but there are indications in the data that this is an over-simplification. Zuber & Stark (1968) have concluded that convergence movement is more rapid than divergence; consistent with that conclusion, the rate of vergence change during the saccade was, on average, greater during convergence movements than during divergence, in seven of the eight test series of Fig. 8. In several instances, these differences within the data sets were statistically significant, and contributed appreciably to the inter-test variability shown in Fig. 9. This trend was not evident in the experiments with 2·3° demand for vergence change which led to Figs. 4, 5 and 7.
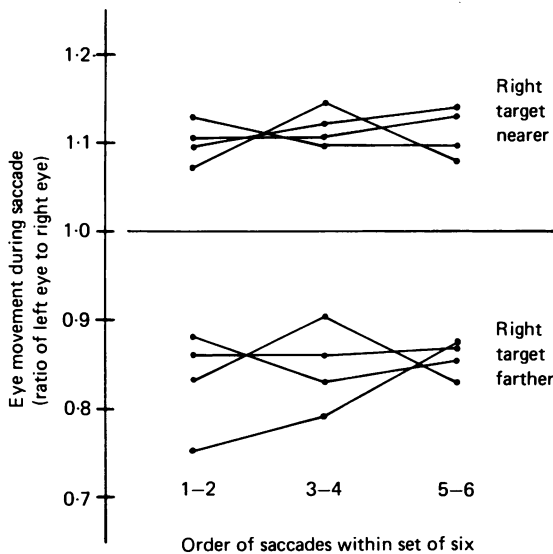

Fig. 10. Ratios of movement of left eye during saccade to movement of right eye, in the tests illustrated in Figs. 8 and 9, segregated by order of the test within the blocks of six changes in fixation. Each point represents the average of four tests (one convergence movement, one divergence, from each of two blocks of six tests); points for each subject connected by lines.

Other combinations of version and vergence change

A: small version and small change in vergence. In these tests, one needle was located in position R_4 and the other was 6 mm to the left of position R_3 (rather than position L; see Fig. 2), requiring version of about 0·9° and vergence change of about 0·7°. The results are summarized in the first two lines of Table 1, where it can be seen that 40–60 % of the total vergence change occurred during the saccade, as compared with nearly 100 % when similar vergence change was demanded in conjunction with version of about 4° (Fig. 8). Nevertheless, the saccades in these tests were extremely unbalanced in excursion (last column in Table 1), with binocular asymmetry far greater than that shown in Fig. 9 for similar vergence change and a larger saccade.

B: larger version and modest change in vergence. In these tests, one needle was located in position R_1 and the other was 40 mm to the left of position R_3 (rather than

20 mm as for position L; see Fig. 2), requiring version of about 9° and vergence change of about 2·3°. The results, summarized in lines three and four of Table 1, indicate that about 80 % of the required change in vergence occurred during the saccade: an appreciably larger fraction than when the same vergence change was required with version of only 5° (60 %; see Fig. 4), although the saccades were less unbalanced in excursion (compare last column of Table 1 with Fig. 7). In these tests, post-saccadic vergence change was also usually markedly asymmetrical; results were qualitatively comparable with those shown in Fig. 6, except that intervening corrective saccades (versional movements) were more common.

TABLE 1. Saccadic vergence change as a function of versional magnitude

			Percentage of total vergence change during:			Ratio of movement during saccade: left eye:right eye
Subject	Vergence change (°)	Version (°)	Saccade (83 ms)	Presaccadic interval	Post-saccadic interval	
1	0·74	0·88	61 ± 12	9 ± 8	30 ± 13	0·668 ± 0·058
2	0·70	0·95	42 ± 8	19 ± 8	40 ± 6	0·628 ± 0·075
1	2·29	9·35	81 ± 7	−2 ± 1	21 ± 6	1·243 ± 0·020
2	2·32	9·13	78 ± 5	1 ± 2	21 ± 6	1·234 ± 0·025

Vertical saccades in conjunction with change in vergence

For these tests, the fixation targets consisted of the spherical heads (2 mm diameter) of pins, which were mounted horizontally. The large pinheads facilitated fixation; when needles are mounted horizontally, their tips do not provide clearly defined alternative points of fixation for vergence change. The lower target was about 28 cm from the eyes, and the upper target (requiring a vertical saccade of about 4°) was either 50 mm or 15 mm closer. (These target configurations are comparable with positions L–R$_1$ and L–R$_2$ in Fig. 2, except that the entire mounting board would be rotated around the line of sight.)

The results of these tests (corrected for slight apparent vergence changes associated with vertical saccades between equidistant targets) are summarized in Table 2. These data show obvious similarities with those from tests in which horizontal saccades rather than vertical saccades were demanded: much of the vergence change took place during the saccade; and that fraction was larger when the ratio of saccade to vergence change was greater. In all four data sets, however, the fraction of vergence change mediated by the saccades was on average somewhat less than when horizontal saccades of comparable excursion were involved (cf. Figs. 4 and 8).

DISCUSSION

The experiments with 2·3° change in vergence with 5° version (Figs. 4–7) were undertaken as an attempt to confirm the basic results underlying the Yarbus interpretation, since there are apparently no subsequent data in the literature which deal with a fully comparable target configuration. There are two striking ways in which those results depart from expectation: a majority of the vergence change occurred during the saccade (Fig. 4); and the velocity of vergence change during the saccade was much greater than during the presaccadic and post-saccadic phases of

vergence movement (Fig. 5*A* and *B*). As shown in Fig. 5*C*, similar anomalies are also evident in the single original recording presented by Yarbus (1957) which deals with this sort of task. In that case also, much of the vergence change took place during the saccade, and velocity of intrasaccadic vergence change was about 5-fold that which prevailed before and afterward. Since these discrepancies with the Yarbus interpretation are evident in his own data, there is no basis for attributing the unexpected results described here to some peculiarity of the experimental subjects or the targets used in the present study, or to differences in experimental protocol or monitoring methods.

TABLE 2. Vergence change during vertical saccades

Subject	Vergence change (°)	Vertical saccade (°)	Percentage of total vergence change during saccade	Nature of vergence change
1	2·56	3·62	45±5	Asymmetrical
1	0·67	3·62	72±9	Asymmetrical
2	2·54	3·89	45±5	Symmetrical
2	0·66	3·89	87±8	Symmetrical

The finding that such a large fraction of the realized vergence change can occur during the saccade (Fig. 4) could perhaps be regarded as a relatively unimportant over-simplification in Yarbus's schematic diagram, if this were the only discrepancy; the unexpectedly large *rates* of vergence change during the saccade (Fig. 5), however, are crucial. The central point of the Yarbus interpretation is that version and vergence movement are independent processes which are additive during combined viewing tasks, meaning that the velocity of vergence change during the saccade should be fully comparable with that observed before and afterward. The large observed velocities of vergence movement during the saccades are therefore critical evidence against the additivity which is the essence of the Yarbus interpretation. Comparable failure of additivity between saccades and vergence movement has also been recently documented in two other situations: Johannes–Müller-type vergence (Ono *et al.* 1978); and the adventitious saccades which occasionally occur during symmetrical change in vergence (Kenyon *et al.* 1980).

The consistent asymmetry observed of the post-saccadic vergence movement in these experiments (Fig. 6) is a further conspicuous departure from the idealization defined by Yarbus (1957). It has, however, clear if indirect precedent in other binocular viewing tasks (Pickwell, 1972); the finding here that one eye or the other so frequently contributes nearly 100 % to the post-saccadic vergence movement is reminiscent of the monocular vergence movement of the occluded eye which arises during accommodation vergence (Alpern & Ellen, 1956).

Given that the Yarbus interpretation is inadequate for his own data, as well as for the data illustrated in Figs. 4–7, the results with small demand for vergence change combined with large version (Figs. 8 and 9) are somewhat less surprising. Nevertheless, in these tasks the departures from expectation are extreme: on average, essentially all the finally achieved change in vergence occurred during the saccades. The difference between these results with small vergence change and those with 2·3°

vergence change (Fig. 4) suggests the interpretation that while small change in vergence can be fully mediated by a saccade, larger changes cannot. The data in Table 1, however, indicate that this is an over-simplification. Instead, the decisive factor is apparently the relationship between size of the saccades and the amount of the required vergence change. As shown in Fig. 11 *A*, the over-all data are consistent with the notion that the larger this ratio, the greater the fraction of vergence change which can be achieved during saccades. The extent of saccadic imbalance, however, expressed as the ratio of larger eye movement to smaller, shows a converse relationship (Fig. 11 *B*): saccades are binocularly more similar to each other in excursion when large version is coupled with small demand for vergence change.

The Johannes–Müller target configuration is distinctly different from those investigated here, because one eye eventually returns to its initial alignment, and the saccade performed by that eye is thus, in principle, superfluous. Nevertheless, this unique target configuration can be treated as a more extreme case in the continuum of the present experiments, with the specification that net version is half the required vergence change. Based on that interpretation, the data obtained with this target arrangement by Ono & Nakamizo (1978, table 3) and Ono *et al.* (1978, table 1) are also plotted in Fig. 11. Those data points appear to conform satisfactorily with an extrapolation of the trends in the present experiments, even though distinctly different kinds of targets, measurement methods and protocols were involved.

While the classical view, due to Hering (1868), is that both eyes move by equal amounts during a saccade, as the term 'conjugate' (i.e. yoked together) implies, a conspicuous departure from this ideal arises with Johannes–Müller-type targets, in which the non-aligned eye performs an appreciably larger saccade than the aligned eye (Alpern & Ellen, 1956). The binocular inequality in those saccades has, as in the Yarbus interpretation of other visual tasks, traditionally been attributed to the superposition of ongoing vergence motion upon an otherwise balanced saccade, but that interpretation has been shown to be quantitatively wrong by Ono & Nakamizo (1978) and Ono *et al.* (1978): the saccades are more unequal in excursion than can be accounted for by simple additivity. Still more recently, Kenyon *et al.* (1980) have established that the adventitious saccades, which sometimes occur during symmetrical vergence, can be strikingly unequal in excursion, also to an extent which cannot be explained by simple additivity of vergence movement upon a binocularly balanced saccade. The results reported here (Figs. 7 and 9; Table 1) thus supplement those of others, in indicating that the dichotomy between conjugate and disjunctive eye movement is one which the eyes do not always properly respect: conspicuously unbalanced saccades are also the norm for the more natural target configurations considered by Yarbus (1957), and in these cases as well, additivity of version and symmetrical vergence motion cannot adequately account for the extent of imbalance.

The nature of this saccadic imbalance, as observed with Johannes–Müller targets, symmetrical vergence and the tasks described here, is such as to be clearly useful, in that it accelerates an ongoing vergence movement, permitting more rapid recovery of binocular congruence to within the limits of Panum's areas of fusion. The achievement of essentially all vergence change by means of saccades, when large version is coupled with small vergence change, is simply the extreme case in this continuum, but here, the contribution to visual efficiency is even more conspicuous.
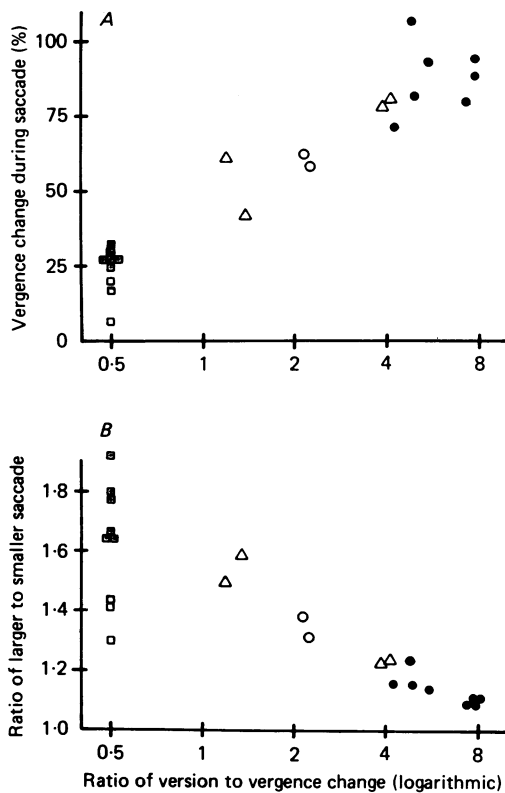
Fig. 11. Summary of percentage of vergence change mediated by saccades (*A*), and saccadic imbalance (*B*) as functions of the ratio between version and vergence change: one average value plotted for each subject and target configuration. Open circles: experiments of Fig. 4; filled circles: experiments of Fig. 8; triangles: experiments of Table 1; squares: data for Johannes–Müller-type targets, from Ono & Nakamizo (1978) and Ono *et al.* (1978). Squares with dot involved near targets at apparent distance of 28·7 cm, i.e. comparable with other data; open squares involved targets at greater apparent distances (68·7 and 313·7 cm).

A minimum of about 500 ms is required to complete an ordinary symmetrical vergence change in the range from 0·1 to 10° (Bahill & Stark, 1979). The data in Fig. 8 indicate, however, that when a shift in fixation requires only small change in vergence, combined with larger version, both eyes can be brought to bear on the new target within the roughly 50 ms required for a saccade, thereby eliminating as much as a half-second of potential diplopia. Since much of our visual behaviour in a natural environment involves situations like those which led to the data of Fig. 8 (saccade much larger than required vergence change), the capacity of saccades, even vertical saccades (Table 2), to mediate vergence change must play an important functional role in the human eye-movement system.

The first detailed evidence that unbalanced saccades could contribute usefully to visual function was reported by Krauskopf, Cornsweet & Riggs (1960), from a study of the miniature eye movements (less than 0·1°) which occur during steady fixation.

The binocularly unequal saccades which they measured helped to maintain an existing state of vergence, since on average, the saccades tended to correct for binocular differences in preceding drift motion. In order to explain such data, Krauskopf *et al.* (1960) proposed that as soon as either eye detects drift from the intended target, that eye by itself can initiate a binocular saccade, in which larger excursion would be achieved by the initiating eye, with the other eye being 'dragged along' because of the binocular coupling of saccadic command signals. This hypothesis suggests that unbalanced saccades might be peculiar to miniature eye movements, but the present data, as well as those of Ono & Nakamizo (1978), Ono *et al.* (1978), and Kenyon *et al.* (1980) indicate that the phenomenon is more general, extending also to macrosaccades. Since the amount of saccadic inequality in the present experiments varied appropriately with the demand for vergence change, the notion that the eye making the smaller saccade was a 'passive partner' in the motion, as suggested by Krauskopf *et al.* (1960) for their data, is insufficient for these macro-saccades; instead, the visual input of each eye influences saccadic excursion.

A qualitative and formal way of summarizing the present results, as well as those of others, is the statement that 'saccades and vergence movements interact when they occur together' (Ono *et al.* 1978, p. 738). Vergence movement during the saccade is accelerated, and a saccade thereby facilitates an intended change in vergence. In considering what the nature of this facilitation might be, the results with vertical saccades (Table 2) deserve special attention. The primary eye motion in those saccades was due to activation of the vertical recti, and nevertheless, vergence change, which involves the horizontal recti, was facilitated nearly as effectively as when only the horizontal recti were responsible for all eye movement. That result serves as a strong constraint on speculation about mechanisms of facilitation; it indicates, for example, that an interaction based upon different mechanical responses of slow and fast fibres within the horizontal recti, as proposed by Ono *et al.* (1978), is an insufficient explanation.

As emphasized by Krauskopf *et al.* (1960), and is evident in all subsequent studies on the topic, unbalanced saccades involve complete binocular coincidence in timing, to within the limits of resolution of the measurement method; and, with negligible exceptions, the saccades are consistently in the same direction. Nevertheless, the eyes move by different amounts. Because of these features, Ditchburn (1973, p. 353), in his consideration of the micro-saccade data, has made an interesting suggestion: it appears as though 'the decision to make a saccade is controlled by one centre (which accepts information from both eyes) and the decision concerning the magnitude is made by another (which depends, wholly or mainly, on information from the eye which is to move).'

In the tasks with large version and small vergence change (Figs. 8 and 9), each eye moved during the saccade by an average amount which matches its expected movement, had that eye alone seen the target configuration in a monocular viewing situation. This result is consistent with Ditchburn's (1973) suggestion that visual input from each eye might be processed completely independently, so as to determine the magnitude of the saccade for that eye. There is a similar tendency in the large-vergence-change experiments as well. The data in Fig. 6 indicate that in a majority of the tests, one of the eyes, usually the dominant one, moved during the

saccade by an amount corresponding fully to that expected, had that eye seen the target configuration alone, monocularly. Nevertheless, the residual post-saccadic vergence movement also indicates that in nearly every trial, one eye or the other (and sometimes both eyes) departed during the saccade from the performance expected had each eye viewed the targets separately. Hence, partial interdependence in saccadic excursion is evident in the responses to such target configurations.

Unbalanced saccades thus show a peculiar mixture in extent of co-ordination: complete simultaneity in onset of saccadic motion; complete agreement in direction of motion; but partial, or, in some cases, seemingly complete binocular independence in excursion of the resulting motion. Note, however, that strong co-ordination is associated with *onset* of saccadic motion, and that binocular differences in excursion refer to *termination* of the saccades. The neural events underlying saccadic motion involve a similar dichotomy: an intense burst of discharge by the motorneurones which initiates the eye motion and which lasts roughly half as long as the saccade itself (the 'pulse' component); and a change in the tonic levels of nerve input, so that the eye, once it slows down, is attracted to and held in its new orientation (the 'step' component). Systematic, target-specific binocular inequality in saccadic excursion does not necessarily imply binocular inequality of the pulse component; it indicates, instead, that visual information from each eye contributes to generation of the 'step' component, the configuration of tonic impulses which determine position of that eye at the end of the saccade. Let us consider, therefore, a modification of the two-centre hypothesis of Ditchburn (1973): that the pulse component of saccadic control signals might arise from full integration of binocular visual input, processed so as to produce fully identical, 'yoked' signals to the muscles of both eyes; but that the step component might be determined independently for each eye, on the basis of evaluations of that eye's own visual input.

Several consequences of this interpretation are in agreement with the experimental data. If the centre responsible for the pulse component were to perform binocular averaging of visual input, one would of course expect initial movement of both eyes in the same direction, as well as simultaneity in saccadic onset. In an ordinary version task, balanced saccades would be expected because of complete matching between visual inputs for both the pulse and the step components. When change in vergence is demanded, however, simultaneously with version, there would be a mismatch between pulse and step components. If small change in vergence is required with large version, the mismatch would be slight, so the tonic, step component of the saccade, based on monocular evaluation of each eye's visual input, including vergence change, might be strong enough to attract and hold both eyes, after slightly unequal excursions: vergence change mediated fully by saccades. If the demanded change in vergence is large relative to version, the step component might be able to attract the eyes, particularly during their deceleration phase; but the pulse component would nevertheless push the eyes beyond the 'catch-and-hold' zone of the step component, so that subsequent slow fusional vergence change would ensue. The monocular dominance which was typical of post-saccadic vergence movement in the experiments with larger change in vergence (Fig. 6) might reflect a binocularly balanced phasic impulse given to the eyes, of magnitude such that one eye or the other often arrived sufficiently close to its tonically determined goal as to be within 'catching' distance,

with the other eye then overshooting or undershooting its own goal, meaning that subsequent (monocular) fusional vergence movement would be required.

The primary viable alternative to the interpretative scheme proposed here is that central, non-linear processing of visual information leads to the generation of binocularly unbalanced pulse signals, which are then synchronized by some sort of temporal gating. Difficulties with that alternative arise, however, when vergence change is mediated by vertical saccades (Table 2), since the required pulse signals to the horizontal recti would have to drive the eyes in opposite directions: a phenomenon rarely if ever observed in other contexts. The central point of the two-centre hypothesis is that facilitation of vergence change by a saccade may arise, instead, due to non-linearities in the responses of the globe as a mechanical system. To that extent, at least, there are similarities between this proposal and the non-linear, sixth-order model for the globe and the horizontal recti, which was invoked by Kenyon *et al.* (1980), to account for the unbalanced saccades which occasionally occur during a symmetrical vergence task. They postulate that the step component of saccadic command signals is added algebraically to that of the ongoing vergence motion. Translated to the present context, that suggestion would be formally identical with the hypothesis that the total tonic change in muscle activation is determined independently for each eye, on the basis of its own visual input. Simulations with this mathematical model have demonstrated that it can generate saccades which are markedly unequal in excursion (Kenyon *et al.* 1980). Those simulations did not lead to acutely asymmetrical post-saccadic vergence change, such as reported here, but it is conceivable that modest changes in assumptions or parameters could lead to a fit for the present data. Since that model considers only horizontal eye motion, it cannot, of course, account for facilitation of vergence change by vertical saccades without further elaboration. Those observations, however, represent the strongest evidence available for suggesting that saccadic facilitation of vergence change arises at a peripheral, mechanical level.

The suggestion that the phasic (pulse) component and the tonic (step) component of saccades arise due to distinctly different processing of visual information, one based on binocular averaging, the other on separate monocular evaluations, is not, to date, supported by any independent physiological evidence, in spite of the many studies which have been undertaken to explore the brain mechanisms by which visual information is translated into saccadic movements. There is, of course, no assurance that all brain areas relevant to saccadic motion have been explored; but there is an obvious test of the hypothesis proposed here, which side-steps that uncertainty. The phasic input to the extraocular muscles of both eyes could be explored with electromyogram techniques, in viewing situations like those described here, in which there is marked binocular difference in saccadic excursion. Independent generation of phasic and tonic components of a saccade, in the manner hypothesized, implies that saccades of varying excursion can arise from the same magnitude of phasic input, depending upon the nature of the respective monocular visual inputs, and the resulting arrays of tonically generated muscle forces.

It has been suggested that the information-processing system which underlies stereopsis may be closely related to that which controls vergence movements (Marr & Poggio, 1979). Clearly, both phenomena require the assessment of similar kinds

of binocular differences in visual information. The demonstration here, that the demand for change in vergence can be acted upon by each eye separately and simultaneously, using the open-loop saccadic-movement system, and not just using the binocularly balanced, closed-loop fusional vergence system, makes the possibility of a close relationship with stereopsis more plausible, since it indicates the simultaneous availability, to the eye-movement system, of information about the magnitude of binocular disparity.

<div align="center">APPENDIX</div>

Vergence change and ocular translation

The study of vergence movements has a long history of reported discrepancies between measured eye position and expectations based on target geometry (e.g. Westheimer & Mitchell, 1956; Tani, Ogle, Weaver & Martens, 1956; and many earlier reports). Rashbass & Westheimer (1961), however, established that no such anomalies are evident, when a complex measurement technique is used, by which possible contamination of the data by ocular translation is eliminated. That landmark result tended to confirm the suggestion by Tani *et al.* (1956) that ocular translation is probably an important problem in any measurements of vergence change which are based upon single-view monitoring of the front surfaces of the eyes. Another, more recent study (Enright, 1984) has demonstrated that systematic ocular translation, large enough to be mistaken for as much as a full degree of rotation, does indeed arise during large vergence changes (*ca.* 20°). Hence, there are legitimate grounds for concern about the interpretation of any study of vergence changes (present experiments, as well as Ono & Nakamizo, 1978; Ono *et al.* 1978; Kenyon *et al.* 1980; and many others) in which the monitoring methods allow possible contamination of the data by ocular translation.

Because of this concern, most of the analyses of data described here are based upon the temporal distribution of total measured vergence change. Possible inaccuracies in estimates of the magnitude of steady-state vergence change would not, in themselves, influence the question of what *fraction* of the total vergence change occurs, at what time. Nevertheless, it is of some interest to know whether the averaging of results over a series of similar eye movements, as done here, can reduce or obviate anomalies which arise due to ocular translation. For assessing this issue, fourteen data sets which involve changes in vergence together with version are available; each data set consists of twelve changes in fixation. Many of these single-case measurements indicate appreciable deviations between geometric expectations and total measured vergence change at steady state, such as have been noted by previous workers (e.g. Westheimer & Mitchell, 1956): discrepancies which sometimes greatly exceeded measurement error.

In spite of these single-case anomalies, the average values of steady-state vergence change, calculated over sets of twelve changes in fixation (six convergence, six divergence movements) consistently showed satisfactory agreement with expectation. In the four measurement series with 2·3° demand for vergence change, average departures from geometric expectations were 1 arcmin, 3 arcmin, 8 arcmin and 10 arcmin. In the ten data sets based on change in vergence of less than 1°, the average

values for total vergence change departed from expectation by amounts in the range between 1 and 6 arcmin, with a mean deviation across all tests (absolute value) of 3·5 arcmin. This sort of agreement suggests that the larger anomalies in apparent eye orientation, which arose in single eye-movement tests, did not represent *systematic* ocular translation associated with vergence (of the sort which does indeed occur during much larger vergence changes; Enright, 1984), but were instead irregular case-to-case variations in performance which can be satisfactorily dealt with by averaging data over a balanced experimental design. Somewhat larger discrepancies in apparent vergence change were, however, evident in the four data sets involving vertical saccades (mean deviation between observed and expected vergence change at steady state of 8 arcmin; maximum 12 arcmin). The origin of these unexplained anomalies with vertical saccades is presently under investigation.

Even when steady-state vergence changes conform satisfactorily with expectation, it remains possible that the measured values for the proportion of vergence change mediated by saccades might be contaminated by another form of ocular translation; the axis of ocular rotation during the saccades might vary appreciably in its location within the globe as a function of target position. Forward displacement of the axis of saccadic rotation, if it were to occur, would mean that a given rotation of the visual axis in the horizontal plane is associated with lesser movement of the frontal surface of the eye, and backward displacement of the axis with greater movement. Such displacements of the axis of rotation for saccades, by as much as 1 mm, have been recently documented as a consequence of convergence by about 20° (Enright, 1984).

In order to investigate this possibility, eye movements during combined version and small change in vergence were monitored with two video cameras mounted at right angles to each other; one camera viewed the eye from a frontal position (as in the preceding binocular data) and the other camera monitored movement of the same eye in the sagittal plane from the temporal side of the eye. In frontal view, the position of the temporal margin of the iris was measured as before, relative to the vertical line on the monitor screen produced by the image splitter; in side view, the position of the same point (temporal margin of the iris) was measured relative to the front of the cornea. The results were evaluated in terms of the ratio of movement of the eye in frontal plane during the saccade, to its simultaneous movement in the sagittal plane; changes in this ratio have proven to be a sensitive indicator of the location of the axis of saccadic rotation in other situations (Enright, 1984). Differences in this ratio on the order of 30 % would be required to explain the extent of saccadic imbalance shown in Fig. 9, and much larger differences for other target configurations.

Subject 2 was tested using the two small-vergence-change target positions ($L-R_2$ and $L-R_4$ of Fig. 2). Each eye was monitored separately, in a sequence of about twenty saccades for each target position. The resulting data showed no significant difference between target positions, for either eye, in the average ratio of frontal to sagittal movement. For the left eye, the mean ratio was $2·185 \pm 0·068$ (s.e. of mean) for target position $L-R_2$, and $2·149 \pm 0·062$ for target position $L-R_4$ ($P > 0·20$, t test). For the right eye (with slightly different orientations of the cameras relative to the visual axis), the mean ratio was $1·736 \pm 0·039$ for target position $L-R_2$ and $1·831 \pm 0·039$ for target position $L-R_4$ ($P > 0·10$, t test). Furthermore, there was no significant

evidence, within the data for a given eye and target position, for change in the ratio as a function of whether convergence or divergence movement was involved (all four probability values > 0.10, t test). These data do not, of course, rigorously exclude change in the location of the axis of rotation for saccades in the experiments which led to the data in Figs. 8 and 9, but they indicate that if this factor contaminates the data, its contribution is on average quite small.

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