

CONVERGENCE DURING HUMAN VERTICAL SACCADES: PROBABLE CAUSES AND PERCEPTUAL CONSEQUENCES

BY J. T. ENRIGHT

From the Neurobiology Unit, A-002, Scripps Institution of Oceanography, La Jolla, CA 92093, USA

(Received 28 September 1987)

SUMMARY

1. When a downward saccade is made between equidistant targets, convergence consistently occurs during the saccade: about 1 deg overconvergence after an 8 deg saccade, with either binocular or monocular viewing, with either far (3 m) or near (30 cm) viewing distance.

2. During binocular viewing, this unnecessary convergence is corrected by divergence movement with a half-time of about 200 ms. During monocular viewing of far targets, similar post-saccadic divergence occurs, but for monocularly-seen near targets, recovery is considerably slower.

3. Vergence changes associated with upward saccades are much smaller and typically more variable among subjects.

4. The up-down asymmetry of intrasaccadic vergence changes can be accounted for by superposition of two plausible adventitious processes: co-contraction of the vertical recti, and tension increase (upward saccades) or tension release (downward saccades) in the superior oblique muscles.

5. During the 1000 ms after an upward saccade, constriction of the pupil consistently occurs; it apparently represents a near-triad response, for which concurrent convergence is masked. Such near-triad activation during upward gaze would presumably be necessary to counterbalance residual steady-state torques from the superior oblique muscles.

6. The up-down asymmetry of intrasaccadic vergence changes also arises when targets require both a vergence change and a vertical shift of gaze, thereby accelerating refixation for the typical natural spatial configuration, in which nearer objects are lower in the visual field.

7. During binocular viewing of equidistant targets, the convergence resulting from downward saccades produces large transient disparities, which can be expected to lead to biased evaluations of relative distances to targets. Several up-down illusions involving apparent distance may well be due to these disparities, including (a) backward tilt of the apparent vertical and of the vertical horopter, (b) the 'soup-bowl sky' illusion, and (c) the 'diverging sunbeams' illusion.

INTRODUCTION

Even the most elementary consideration of the arrangement of the extraocular muscles demonstrates the potential for 'cross-talk': the possibility, for example, that activation of the vertical recti, for an intended upward or downward movement of the eye, might also produce adventitious lateral and torsional rotations. Qualitative predictions about the nature of these effects during steady-state viewing were available more than a century ago, but many of the likely interactions, particularly the dynamic ones, have never been directly measured (Carpenter, 1977). Among these is the vergence component of vertical eye movements.

A strong basis for predicting that vertical eye movements might alter vergence is implicit in the eccentric manner in which the oblique muscles are attached to the globe; because of the configuration of forces involved, vergence changes *ought* to accompany activation of the vertical recti, unless the oblique muscles are simultaneously activated, to contract and relax by exactly appropriate amounts. Additional reason for suspecting that vertical saccades might involve vergence changes is provided by the fact that phoria varies with the vertical orientation of the eyes: when one eye is occluded, raising the direction of gaze is associated with increase in steady-state divergence (exophoria; Holland, 1958).

The evidence presented here demonstrates that there is indeed a vergence component to vertical saccades, but that these vergence changes involve an extreme up-down asymmetry. Immediately after downward saccades for equidistant targets, consistent overconvergence is present, but following upward saccades, overt vergence changes are much smaller and often negligible. The research described here explores possible explanations for that asymmetry, and considers its visual consequences, which probably contribute to several familiar perceptual phenomena.

METHODS

The two-camera video recording system used for monitoring eye movements has been described elsewhere (Enright, 1984*a*); its precision (reproducibility of replicate 'blind' readings of eye position) involves a standard deviation of about 6 min of arc for each eye, and hence is about 9 min of arc for an estimate of vergence state. Pupil size was also measured in many of the experiments; replicate 'blind' readings of pupil diameter have a standard deviation of about 50 μm . For monocular viewing tasks, an opaque black screen was placed about 5 cm in front of the non-dominant eye, at a vertical level that obstructed the subject's view of the target, but that permitted recording of eye position by the video camera, which was located about 10 deg below the line of sight.

Comparisons of vergence state between different vertical positions of the eyes are potentially subject to systematic errors. For example, the vertical axes of the two cameras might deviate slightly from parallelism. Potential biases of this sort were allowed for by assuming proper fixation by each eye, when averaged over many tests, during steady-state binocular viewing of each target. Hence, any apparent difference in mean vergence value between binocular fixation on upper and lower (equidistant) targets was subtracted out as a presumptive position-dependent systematic error, a correction that was particularly important for monocular tests conducted in the same session. In order to avoid any uncertainty associated with blurring of the video-recorded image during saccadic movements, net intrasaccadic changes in vergence were assessed by measuring eye position in the video frame just before onset of rapid eye movement, and in the frame 100 ms thereafter. One test series involved bidirectional video monitoring of ocular position in the horizontal plane (camera axes at 90 deg angle), in order to distinguish between normal rotation of the globe, and lateral ocular translation. Details of this procedure are described in Enright (1984*b*).

Eight subjects, ranging in age from 11 to 32 years, were tested. All have normal acuity without correction, and have no known oculomotor anomalies (normal appearing saccades; normal appearing pursuit movements in all quadrants; phoria, measured at 3 m, less than 2 deg). Several different sorts of fixation targets were used, including markers drawn in black ink on a white background, and, as described subsequently, the spherical heads of wire pins. When not otherwise indicated, the targets consisted of pairs of vertically oriented crosses, drawn with arms about 40 min of arc in length, and line width of 2–6 min of arc.

RESULTS

Vertical saccades for equidistant targets

An excerpt from a longer recording made during binocular viewing at 3 m distance, with targets demanding 8 deg vertical saccades, is shown in Fig. 1, based

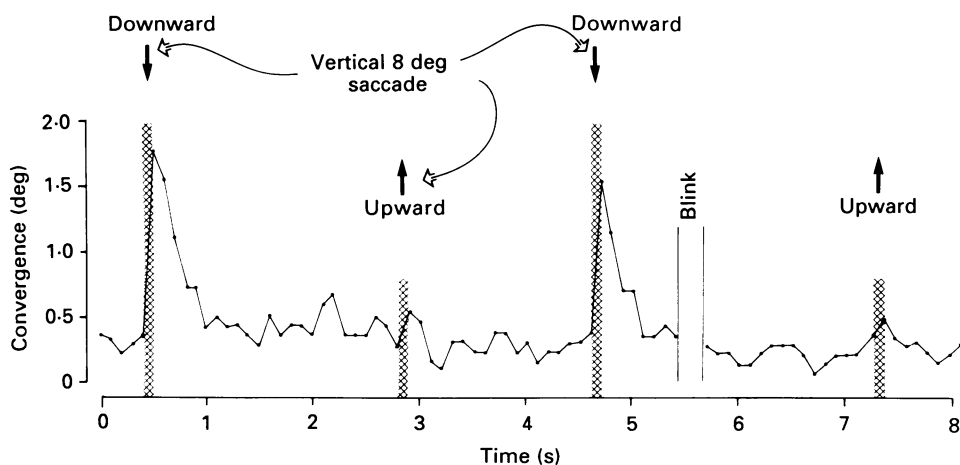


Fig. 1. Eight second excerpt from a longer recording, during which the subject alternated fixation, at about 2 s intervals, between two targets at 3 m distance, separated by 8 deg vertically. Vergence state was estimated every 100 ms (six video frames) synchronized with saccadic onsets; saccades indicated by cross-hatched vertical bars. Ordinate values, represent convergence, relative to an arbitrary zero.

on one measurement of vergence state every 100 ms. These data indicate that downward saccades were associated with a residual convergence of about a degree, a disparity that was gradually corrected over the ensuing second. Vergence changes, if any, following upward saccades, were much smaller. During the interval *between* saccades, the eyes remain at essentially the same vertical level; therefore, evaluations of vergence between saccades would not be contaminated by any systematic measurement errors dependent on vertical eye position. Hence, the gradual correction of vergence to its steady-state value in Fig. 1, following downward saccades, is indirect but persuasive evidence for convergence during the preceding saccade. The magnitude of post-saccadic divergence can thus serve as a convenient unbiased measure of intrasaccadic convergence; the only required assumption is that bin-

ocular fixation is accurate at steady state. Presented in the upper portion of Table 1 are estimates of intrasaccadic convergence based on post-saccadic divergence, measured from end of saccade to 1 s later, for all eight subjects, during 8 deg vertical saccades with targets at 3 m viewing distance, as in Fig. 1. These data indicate that

TABLE 1. Vergence and pupillary changes associated with vertical saccades: binocular viewing, crosses separated by 8 deg

Subject	Vergence change (min of arc)*		Pupillary constriction after upward saccades (μm)*
	Downward saccades	Upward saccades	
	3 m viewing distance		
1	62 \pm 7	27 \pm 6	348 \pm 39
2	53 \pm 6	19 \pm 4	225 \pm 42
3	66 \pm 3	26 \pm 8	268 \pm 29
4	47 \pm 5	7 \pm 6	140 \pm 29
5	53 \pm 5	7 \pm 4	219 \pm 81
6	49 \pm 3	1 \pm 4	10 \pm 55
7	54 \pm 5	12 \pm 2	209 \pm 64
8	60 \pm 7	15 \pm 6	115 \pm 23
Mean \pm s.d.	56 \pm 7	14 \pm 9	192 \pm 102
	30 cm viewing distance		
1	60 \pm 6	16 \pm 8	284 \pm 54
2	59 \pm 10	1 \pm 10	150 \pm 25
3	65 \pm 6	-5 \pm 10	157 \pm 26
4	56 \pm 7	17 \pm 2	80 \pm 22
5	54 \pm 4	13 \pm 3	183 \pm 65
6	51 \pm 4	2 \pm 3	93 \pm 25
7	57 \pm 5	22 \pm 3	129 \pm 41
8	46 \pm 4	8 \pm 4	168 \pm 35
Mean \pm s.d.	56 \pm 6	9 \pm 9	156 \pm 63

* Positive values represent convergence or pupillary constriction during vertical saccades. Perfect binocular fixation, on average, is assumed at 1 s after saccade, and tabulated values were determined by magnitude of the post-saccadic divergence. Pupillary constriction also evaluated at 1 s after upward saccades. Values from individual tests given as mean \pm standard error, based on n of 9 or 10; eight-subject averages given as mean \pm standard deviation. All values for convergence after downward saccades, as well as for difference in convergence between downward and upward saccades, are statistically significant at 0.01 level. With the exception of subject 6, for 3 m targets, all individual values for pupillary constriction are statistically significant at the 0.05 level, and most at the 0.01 level.

the phenomena shown in Fig. 1 can be generalized across subjects: downward saccades are associated with convergence of about a degree. After upward saccades, five of the eight subjects showed statistically significant convergence, but in all cases, it was of much smaller magnitude than after downward saccades.

In a paper submitted while this article was under review, qualitatively similar results have been reported for three subjects by Collewijn, Erkelens & Steinman (1988). In keeping with the the data of Table 1, their scleral-search-coil measurements show that vergence changes associated with downward saccades are con-

siderably larger than those for upward saccades; they demonstrated, as well, that maximum vergence changes arise *during* the saccade, and begin to decay well before the 100 ms 'end-of-saccade' measurements described here. (See, also, Oohira, Gota & Ozawa, 1983, for monocular measurements showing adduction during vertical saccades.)

TABLE 2. Vergence changes associated with vertical saccades

Data set	Target	Subject	Vergence change (min of arc)*		
			Downward saccades	Upward saccades	Steady-state difference
3 m viewing distance					
A	8 deg crosses, viewed monocularly	1	51 ± 13	28 ± 9	11 ± 9
		2	40 ± 8	10 ± 8	8 ± 10
		3	46 ± 7	8 ± 6	6 ± 6
	Mean ± s.d.		46 ± 6	15 ± 11	8 ± 3
30 cm viewing distance					
B	8 deg crosses, viewed monocularly	1	65 ± 12	17 ± 10	38 ± 12
		2	54 ± 10	-8 ± 12	14 ± 11
		3	71 ± 6	-20 ± 5	30 ± 9
	Mean ± s.d.		63 ± 9	-4 ± 19	27 ± 12
C	4 deg crosses, viewed binocularly	1	35 ± 6	5 ± 4	**
		2	31 ± 5	-2 ± 7	**
		3	24 ± 7	6 ± 6	**
	Mean ± s.d.		30 ± 6	3 ± 4	
D	4 deg crosses, viewed monocularly	1	33 ± 4	0 ± 6	35 ± 7
		2	35 ± 9	2 ± 9	10 ± 7
		3	26 ± 6	2 ± 6	12 ± 9
	Mean ± s.d.		31 ± 5	1 ± 1	19 ± 14
E	8 deg arc-pairs, viewed monocularly	1	67 ± 9	-3 ± 9	66 ± 13
		2	50 ± 11	27 ± 10	-9 ± 11
		3	87 ± 7	-29 ± 8	23 ± 9
	Mean ± s.d.		68 ± 19	-2 ± 28	27 ± 37

* Positive values for vergence change during saccades represent convergence; positive values for steady-state difference indicate greater convergence during downward position of the eyes. Values from individual tests given as mean ± standard error, based on *n* of 9 or 10; three-subject averages given as mean ± standard deviation. ** In binocular tests, perfect binocular fixation is assumed at 1 s after saccade; hence, no average steady-state difference in vergence can result. In each monocular test, the preceding binocular test was used as a basis of comparison; any residual apparent difference in mean vergence between the upper and lower steady-state values during binocular viewing was treated as a test-specific position-dependent measurement error, and subtracted from apparent vergence changes during monocular viewing (see Methods).

In his research on the influence of vertical eye position on phoria, Holland (1958) found that the effect of eye elevation on steady-state vergence during monocular viewing depended strongly on viewing distance: with targets at 30 cm, lowering the direction of gaze by 15 deg changed phoria by nearly twice as much as was measured for targets at 5 m. Hence, one might suspect that intrasaccadic vergence changes like

those shown in Fig. 1 would also vary markedly with target distance. This turns out, however, not to be the case. The data in the lower half of Table 1, for targets at 30 cm, are on average indistinguishable from those with targets at 3 m: convergence during downward saccades of about a degree, and much smaller vergence change, if any, observed following upward saccades.

One of the possible explanations for this up-down vergence asymmetry is that the eye-movement system may be miscalibrated in terms of retinal co-ordinates. If objects located vertically below the line of sight were to be interpreted by each eye as being displaced slightly in the nasal direction, this would represent crossed disparity, which could evoke convergence ('biased-disparity' hypothesis). In that case, the vergence component of vertical saccades should vanish during monocular viewing. (Any corresponding bias in perceived image location during monocular viewing would presumably indicate that the lower target is displaced obliquely from the upper one, downward and in the nasal direction, rather than vertically downward and nearer; and it might then evoke a conjugate oblique movement, but not a vergence change.) Data sets A and B in Table 2 demonstrate, however, that during downward saccades with monocular viewing, very similar intrasaccadic convergence arises. (See Methods section for the calculational procedure used for evaluating monocular-viewing data.) For all three subjects, the viewing eye's post-saccade orientation deviated in the convergence (nasal) direction by essentially the same amount as recorded during binocular viewing, and then gradually rotated in the temporal direction to its steady-state orientation.

The data in Table 1 indicate an intrasaccadic convergence during downward saccades that dissipated during the ensuing second. Data from three subjects are presented in Fig. 2, showing the average time course of this post-saccadic correction of intrasaccadic convergence after downward saccades, for targets at 3 m viewing distance. During binocular viewing (left side of Fig. 2) an exponential curve with half-time of 200 ms describes the recovery process for two of the subjects reasonably well, but the fit is somewhat less satisfactory for the data on subject 3. During monocular viewing (right side of Fig. 2), there was a recovery from intrasaccadic convergence that was roughly comparable with that during binocular viewing—even in the absence of binocular information about target disparity. Recovery was not, however, completed during monocular viewing; a small residual convergence persisted after the divergence movement had ended. In the data shown in Fig. 2, these persistent differences at steady state were not statistically significant, but it is noteworthy that this trend was consistent across subjects and that it corresponds in direction and approximate magnitude with the phoria to be expected from the measurements of Holland (1958): slight residual convergence during lowered direction of gaze.

While the intrasaccadic vergence changes during monocular viewing were not strongly dependent on viewing distance (data sets A and B in Table 2), the steady-state residual difference in vergence was of larger magnitude when viewing nearer targets—as Holland (1958) also noted (last column in Table 2). Furthermore, during monocular viewing of targets at 30 cm, the post-saccadic recovery process (divergence) following downward saccades was much slower than during binocular viewing; 1 s after the saccade, less than 40% recovery had been achieved (26, 35 and

38%, for subjects 1, 2 and 3, respectively: results from experiments of data set B of Table 2), and divergence then continued at roughly the same average rate during the ensuing second. This represents the most conspicuous effect of viewing distance on

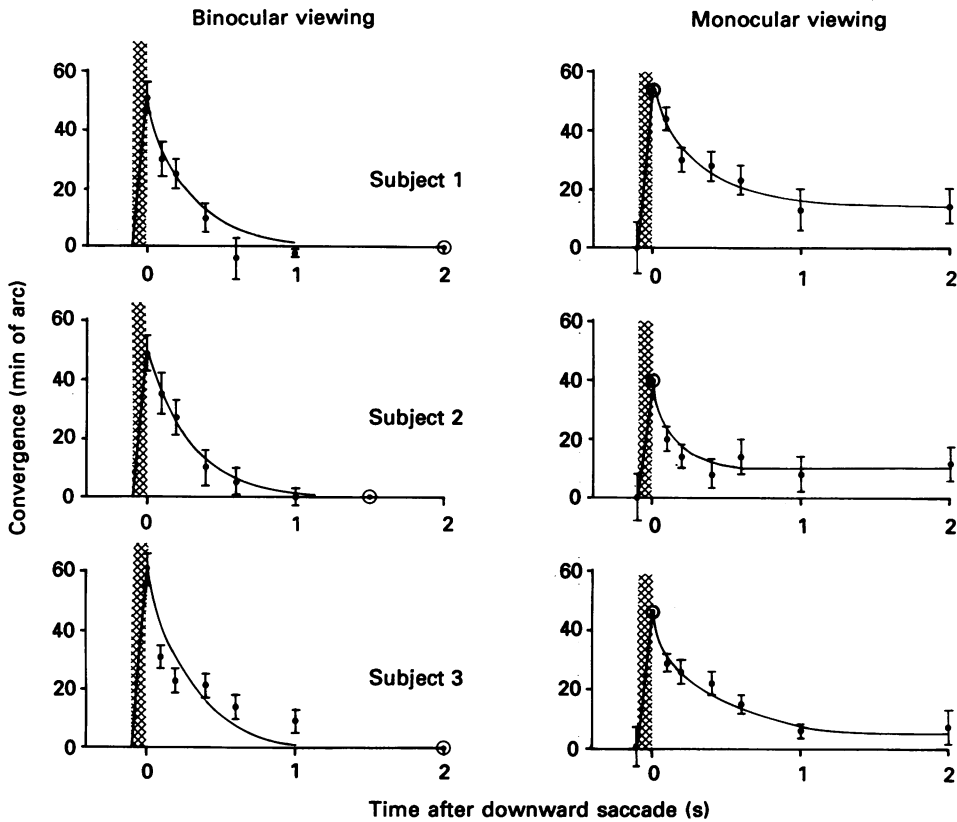


Fig. 2. Cross-trial mean values for vergence state during and after downward vertical saccades, with saccades (100 ms) indicated by cross-hatching; points with vertical bars represent ten-saccade mean, with associated standard errors. During binocular viewing, (graphs on left), vergence values were measured relative to the trial-specific 'steady-state' value at 2 (or 1.5) s after the saccade (O), and average pre-saccade values become identical with that final value, because of the assumption of perfect binocular fixation. During monocular viewing (graphs on right) vergence values were measured relative to the first post-saccade measurement (O), and the plotted pre-saccade value includes a correction (and its standard error) based on mean *apparent* vergence difference during steady-state binocular viewing of the same targets in the same recording session (see Methods). Superimposed curves through the binocular data represent exponential decay with half-time of 200 ms; curves through monocular data were fitted by eye.

the vergence changes associated with vertical saccades: for monocular viewing at 3 m distance, the post-saccadic recovery from intrasaccadic convergence qualitatively resembled that during binocular viewing (Fig. 2), and more than 75% of the intrasaccadic convergence had dissipated within 1 s—compared with less than 40% for monocular viewing at 30 cm viewing distance.

Three of the subjects were also tested with fixation targets that demanded 4 deg vertical saccades. The results of those tests are summarized in data sets C and D of Table 2. As shown there, the magnitude of intrasaccadic convergence during downward saccades was reduced when the saccades were smaller. The available data suggest that the relationship between amount of convergence and size of the saccade may involve simple proportionality, at least over the modest range of saccade sizes examined.

Control for accommodation stimuli

Another of the conceivable explanations for the observed intrasaccadic vergence changes is that targets below the line of sight might be interpreted, even monocularly, as being somewhat nearer because of an up-down bias in image-focus information ('biased-accommodation' hypothesis). In order to evaluate this possibility, fixation targets with no foveal stimuli were prepared. The illustration, for 30 cm viewing distance, consisted of pairs of 90 deg arcs (bounding the sectors, 45-135 deg and 225-315 deg, with 0 deg being the top) from two circles with diameter of 45 mm, with centres about 8 deg apart vertically. The arcs of each pair (line width about 6 min of arc) were drawn with their mid-points directly on the left and the right of an implied but unmarked fixation point, located at the centre of rotation for the arcs.

Any intrasaccadic vergence changes that might arise during monocular viewing due to biased perception of accommodation stimuli would require comparisons of image blur between initial and final fixation points. Images nearest the fovea are most important for perception of the blur that induces accommodation responses as well as the associated vergence changes (Semmlow & Tinor, 1978; Ciuffreda & Kenyon, 1983), and near-foveal stimuli were eliminated in the arc-pair targets. Hence, the 'biased-accommodation' hypothesis predicts that the convergence response should be reduced in magnitude, if not eliminated entirely by these targets. Data set E in Table 2 shows that it was not: for two of the three subjects, the up-down asymmetry in vergence change was even greater with the arc-pair targets than with crosses. On this basis, the biased-accommodation hypothesis can be rejected.

Control for ocular translation

When small vergence changes are assessed by a recording method like that used here, which depends on a single, frontal view of each eye, a legitimate source of concern is that the results might be contaminated by ocular translation. During large changes in vergence, systematic ocular translation does indeed arise, with consistent temporal displacement of the entire globe during convergence (Enright, 1984*b*). The possibility that similar phenomena might be involved during vertical saccades was, however, discounted by control experiments, based on bidirectional monitoring, in the horizontal plane, of the orientation of the left eye of subject 1, during the 1 s recovery interval following downward saccades. (See Enright (1984*b*) for details on this procedure.) No sign whatever for such translation was evident. Additional demonstration that the observed vergence changes are not an artifact of the video measurement technique is provided by the scleral-search-coil data of Collewijn, Erkelens & Steinman (1988).

Pupillary constriction

A conspicuous feature of the video recordings that led to the vergence data in Tables 1 and 2 is that the subjects' pupils quite consistently tended to constrict, immediately following upward saccades. The data summarized in Fig. 3 are a typical

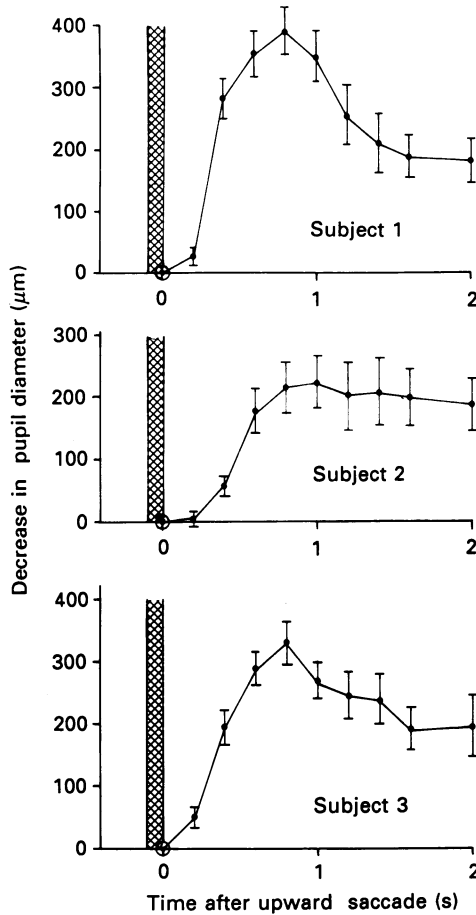


Fig. 3. Average changes in pupil diameter following upward saccades (indicated by cross-hatched vertical bars). Targets at 3 m distance, separated by 8 deg vertically, with binocular viewing. Points with vertical bars represent ten-saccade mean, \pm standard error, with each value measured relative to the trial-specific post-saccade diameter value (O).

demonstration of this phenomenon, as recorded following 8 deg vertical saccades at 3 m viewing distance; and additional data are presented in Table 1 (last column). Consistent constriction of similar magnitude, following upward saccades, was also measured during monocular viewing for all three subjects, for all three targets with 8 deg spacing (vergence changes given in data sets A, B and E in Table 2); in twenty-four of the twenty-five test sessions evaluated (end-of-saccade to 1 s thereafter) the

pupillary constriction was statistically significant at the 0.05 level, and in most cases at the 0.01 level. During the 1 s interval following downward saccades, modest dilatation of the pupil tended to occur, but it was far less consistent; only four of twenty-five test sessions gave evidence for pupillary dilatation that was statistically significant at the 0.05 level, and of those, only one reached the 0.01 level of significance. Evidence presented below (Discussion) indicates that pupillary constriction after upward saccades was probably not due to light intensity, but was instead the kind of response typically associated with convergence ('near-triad' constriction; Semmlow & Hung, 1983), despite the fact that very small to negligible overt changes in vergence state were measured after upward saccades.

Saccades with demand for vergence change

The opinion was long prevalent that the saccadic eye-movement system and the vergence-movement system operate independently, with their output being simply additive (Yarbus, 1957, 1965; Carpenter, 1977), but recent evidence (Enright, 1984*a*, 1986*a*) demonstrates that when an intended refixation requires both a horizontal saccade and a vergence change (tasks with combined vergence and version), the saccade greatly facilitates (i.e. accelerates) the overall vergence change. This interaction is then evident in the marked inequality of the horizontal saccadic excursions of the two eyes. Data from two subjects were also presented (Enright, 1984*a*) that indicated saccadic facilitation of vergence changes when the required conjugate eye movement involved only a vertical saccade; and those results, if substantiated, place strong constraints on the acceptable hypotheses for vergence-saccade interactions.

The data presented above, demonstrating vergence changes during vertical saccades for *equidistant* targets, suggest the need for a re-examination of the previously reported facilitation of vergence changes by vertical saccades. (It should be noted, however, that the target configuration described in Enright (1984*a*) involved a nearer target that was *above* the farther; hence, the asymmetry reported here would be expected to work against the reported saccadic facilitation of vergence changes.) In order to evaluate this issue quantitatively, a pinhead-target configuration was constructed. The three wire pins, with heads 2 mm in diameter, were mounted horizontally, with pinheads in a vertical plane. The upper and lower pinheads were about 26 cm from the subject's right eye, and separated by about 8 deg vertically. The middle pinhead was 5 cm farther away; it was seen by the right eye as collinear with the upper and lower targets, and located halfway between them. The refixation eye movements (top pinhead to middle, middle to bottom, bottom to middle and middle to top) therefore required vertical saccades of 4 deg excursion, either upward or downward, with simultaneous convergence or divergence of about 2 deg. The vergence change results from these tests are summarized in Fig. 4.

If the intrasaccadic vergence changes measured with equidistant targets (Tables 1 and 2 and 'coplanar targets' in Fig. 4) were to be additively superimposed upon those vergence changes due to target distance, one would expect convergence-downward targets to elicit stronger intrasaccadic vergence changes than convergence-upward targets; and divergence-downward targets to elicit weaker intrasaccadic vergence changes than divergence-upward. As can be seen in Fig. 4, that

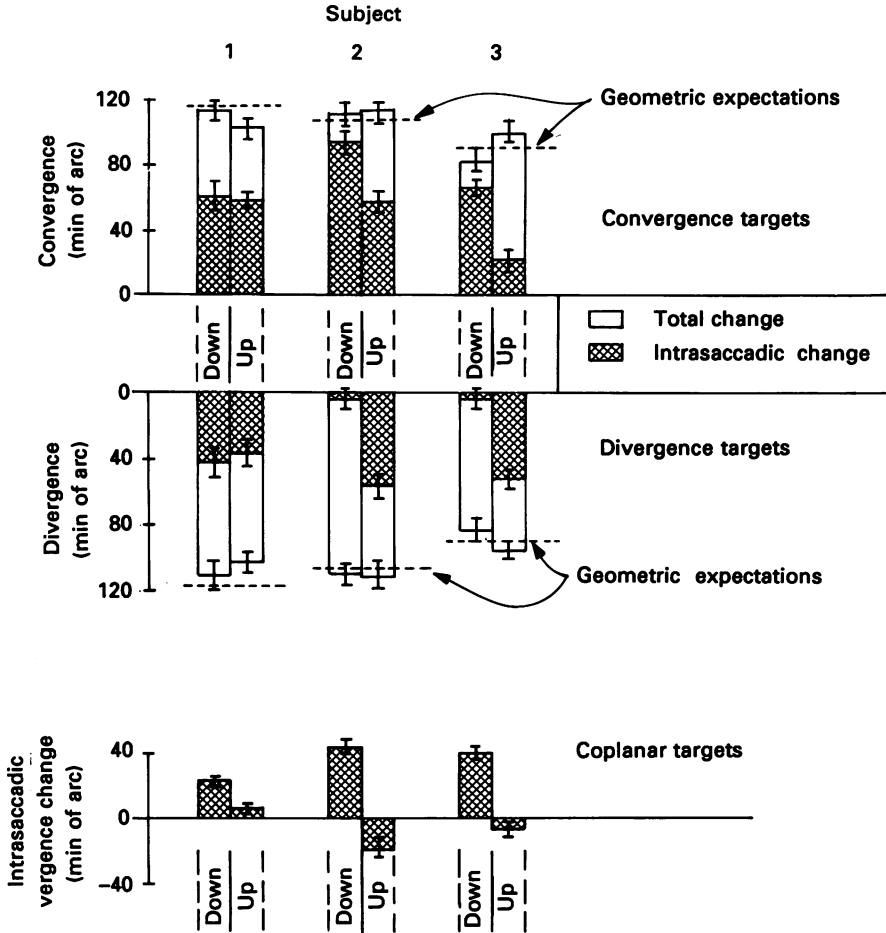


Fig. 4. Vergence changes for targets requiring a vertical saccade of 4 deg, either upward or downward, together with convergence (upper bar graphs), divergence (downward bar graphs) or no change in vergence (bottom bar graphs for 'coplanar targets'). For the upper graphs, each bar represents the ten-trial mean value (with standard error) corrected, when appropriate, for any apparent steady-state difference in mean value for fixation on the upper and lower (equidistant) targets (see Methods). Geometric expectations were calculated on the basis of measured target distances, interocular spacing and an assumed position of the nodal point 8 mm behind the cornea. 'Coplanar targets' were a set of three pinheads mounted at about 26 cm distance, and about 4 deg vertical separation, at heights comparable with the convergence-divergence targets; averages for 'coplanar targets' calculated for ten saccades between upper and middle pins and between middle and lower pins, leading to $n = 20$ for these estimated standard errors.

expectation is well fulfilled for subjects 2 and 3, but no such effect seems evident in the data from subject 1. A more quantitative examination of the additivity question is summarized in Table 3, where it is evident that the data from subject 1 do not represent statistically significant evidence against additivity of the two vergence components; his vergence changes for equidistant targets in these tests were suf-

ficiently similar, for upward and downward 4 deg saccades, that additivity cannot be rejected. The results for convergence by subject 2, however, represent evidence for modest departures from additivity (borderline statistical significance: $P = 0.04$).

The facilitation of vergence changes by vertical saccades, reported by Enright (1984*a*), thus turns out to be strongly dependent on the direction of the saccade. The extent of this asymmetry is summarized in Table 4, in terms of the percentage of the

TABLE 3. Tests of vergence additivity (intrasaccadic vergence changes in min of arc, mean \pm standard error)*

Subject	Vergence direction	Saccadic vergence change	Attributable to up-down	Residuum**	<i>t</i> test** (significance)
1	Converge-down	+61	+23	+38 \pm 10.1	1.16 (n.s.)
	Converge-up	+58	+6	+52 \pm 6.6	
1	Diverge-down	-42	+23	-65 \pm 9.7	1.72 (n.s.)
	Diverge-up	-36	+6	-42 \pm 9.2	
2	Converge-down	+93	+44	+49 \pm 8.2	2.14 ($P < 0.05$)
	Converge-up	+57	-18	+75 \pm 8.9	
2	Diverge-down	-3	+44	-47 \pm 7.2	0.73 (n.s.)
	Diverge-up	-56	-18	-38 \pm 10.0	
3	Converge-down	+65	+40	+25 \pm 5.9	0.19 (n.s.)
	Converge-up	+21	-6	+27 \pm 8.8	
3	Diverge-down	-3	+40	-43 \pm 7.0	-0.28 (n.s.)
	Diverge-up	-52	-6	-46 \pm 8.0	

* Positive values are convergence, negative are divergence. Standard errors for values in columns 3 and 4 are illustrated in Fig. 4. ** As a test of the additivity assumption, the mean calculated residual values for disparity- and accommodation-induced vergence were compared, for upward and downward saccades, by means of two-sample *t* tests. n.s.: $P > 0.05$.

TABLE 4. Intrasaccadic vergence change as portion (%) of total vergence change

Subject	Convergence targets		Divergence targets		Means
	Downward	Upward	Downward	Upward	
1	54	57	38	35	46
2	85	51	3	51	48
3	79	21	4	54	40
Mean		58		31	44

total vergence change that occurred during the saccade. The general average, for all subjects and target configurations (44%), is moderately less than the fraction of vergence changes that is typically mediated by horizontal saccades, when 4-6 deg version was combined with a vergence change of about 2 deg (Enright, 1984*a*, 1986*a*: range 41-70% for six subjects); but a comparison based only on overall averages conceals the important systematic dependence, for vertical saccades, on the direction of the saccade.

Vertical saccades with lateral gaze direction

If the convergence that arises during downward saccades were to be due to programmed input from the usual generators of other sorts of vergence movement, one might expect the total vergence change to consist of roughly equal contributions by each eye, associated with symmetrical changes in activation of the horizontal

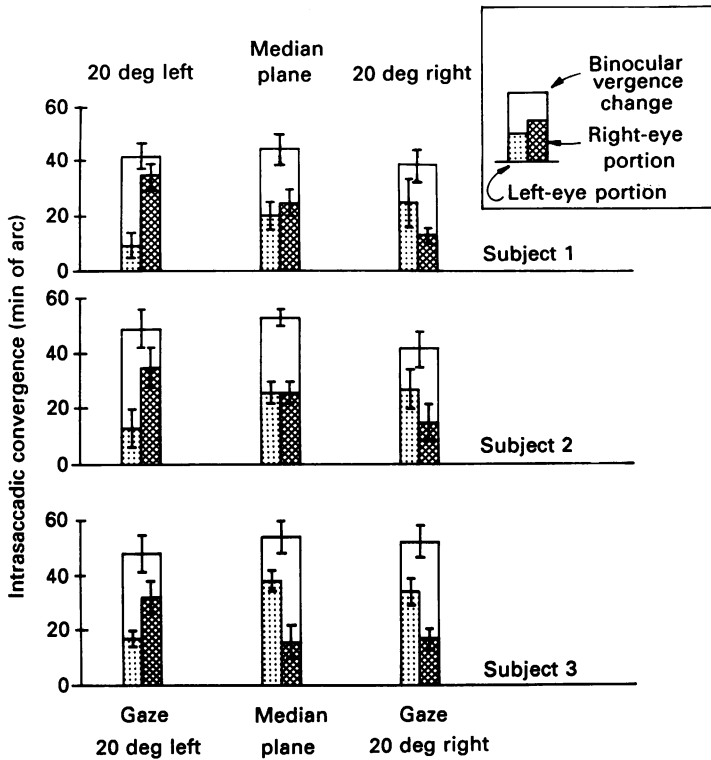


Fig. 5. Contribution by each eye to intrasaccadic vergence changes associated with downward saccades, for three different directions of gaze in the horizontal plane; bar-graphs represent ten-trial mean values and their standard errors. Binocular viewing, targets at 30 cm distance. Measurements represent the magnitude of divergence between the end of downward saccades, and the vergence value 1 s after the saccade; hence, perfect binocular fixation 1 s after the saccade is assumed.

recti, regardless of the direction of gaze. If, instead, the intrasaccadic vergence changes result from forces exerted by other muscles, then the contribution to vergence change by each eye might well depend importantly on the direction of gaze in the horizontal plane (see Discussion). This question was investigated by requiring three subjects to make 8 deg vertical saccades, with binocular viewing of targets at 30 cm distance, while gaze direction was either (a) 20 deg to the left, or (b) in the median plane (as in all previous tests), or (c) 20 deg to the right. The data on vergence changes resulting from downward saccades are summarized in Fig. 5. All three subjects showed somewhat greater values of total convergence for mid-line target

pairs, but those differences are of small magnitude. There was, however, a strong tendency for the right eye to make a smaller contribution to saccadic convergence during rightward gaze than during leftward; and for the left eye to show reciprocal behaviour: smaller vergence contribution during leftward gaze than during rightward (t test values = 10.0 and 17.8, with 2 d.f., for right-eye and left-eye data, respectively, both with $P < 0.01$).

There were no comparable trends evident in the data on vergence state following upward saccades (not illustrated). Total measured intrasaccadic changes ranged from 11 min of arc convergence to 14 min of arc divergence, and seven of the nine values (three gaze directions for three subjects) were not significantly different from zero; nor were there any consistent trends for the relative contributions of the two eyes to differ, as a function of direction of gaze.

DISCUSSION

Probable causal mechanisms

The most striking and conspicuous phenomenon described here is that excess convergence is consistently present after downward saccades: about 1 deg convergence for 8 deg saccades; in contrast, vergence changes following upward saccades are much smaller and less consistent. Typically these eye movements are binocularly symmetrical or nearly so, at least when the eyes are in primary orientation (Fig. 5): each eye makes a very rapid diagonal rotation, predominantly downward but with a nasal component. The fact that the vergence change is so rapid (completed and then reversed within less than 100 ms) represents *prima facie* evidence that extraordinary mechanisms are involved, since a vergence movement is typically a relatively slow exponential process (half-time of about 200 ms; Carpenter, 1977).

Several other lines of evidence also argue against ordinary near-triad vergence mechanisms: (1) vergence changes of similar magnitude also occur during monocular viewing (Table 2), demonstrating that disparity vergence, based on mismatch of retinal co-ordinates, is not involved ('biased-disparity hypothesis'); (2) convergence of undiminished magnitude arises with the arc-pair targets (Table 2) demonstrating that accommodation vergence, based on misperception of image-blur stimuli, is not involved ('biased-accommodation hypothesis'); (3) systematic changes in the contribution made by each eye were observed, dependent on the lateral direction of gaze (Fig. 5). None of these considerations can rigorously exclude the possibility that sudden brief contraction of both medial recti (a 'convergence saccade') occurs during downward saccades, but that suggestion would represent such an extreme departure from present understanding of the oculomotor system that other alternatives, based on 'cross-talk' among the other muscles, seem *a priori* more likely (see Introduction).

One potential source of such cross-talk lies in the temporal difference in action of agonist and antagonist muscles; the increase in tension of extraocular muscles due to an increase in motoneurone activation occurs within a few milliseconds, but the decrease in tension due to decreased activation is a much more gradual process. This asymmetry is evident in measurements of muscular tension during human horizontal saccades (Collins, O'Meara & Scott, 1975). The resulting forces that arise (agonist

initially exerting greater tension than the relaxation of the antagonist can match) represent 'co-contraction', leading to transient retraction of the globe during horizontal saccades, which decays with a half-time of about 100 ms (Enright, 1986*b*). Similar co-contraction of the vertical recti during vertical saccades should be expected to contribute to convergence, because when the eye is near its primary orientation, tension from the vertical recti includes a torque tending to rotate the eye in the nasal direction. Note, however, that this would be a fully symmetrical phenomenon, with similar co-contraction and hence, similar transient convergence expected during upward and during downward saccades.

The superior oblique muscles also contribute to eye orientation in the horizontal plane; and if the oblique muscles are not simultaneously and appropriately activated during upward and downward movement of the eye, vertical saccades would alter the tension in the superior oblique. Fuchs & Luschei (1971) have recorded relevant data from the macaque monkey on the activity of trochlear motoneurons associated with variations in the vertical orientation of the eye. For present purposes, the most important feature of their results involves the extent and rate of tonic activity of the neurons as a function of vertical position of the eye: (1) about 30% of the units were active, at a low rate, when the eyes were aimed 30 deg upward; (2) additional units were recruited into the active pool as gaze direction was lowered, at a rate of about 1.8% of the population per degree; (3) all active units showed linear increases in rate of tonic activity as direction of gaze was lowered; (4) for those units active when the eyes were aimed 30 deg upward, the typical slope of the rate-position line (regression of firing frequency *vs.* vertical eye position) was about 2.7 spikes s⁻¹ deg⁻¹; (5) for motoneurons recruited into the active pool at lower directions of gaze, the slope of the rate-position line was related to the unit's threshold, with an increase of about 0.16 spikes s⁻¹ deg⁻¹ (e.g. a motoneurone that first became active in the primary position typically had a rate-position slope of about 2.7 + (30 × 0.16) = 7.5 spikes s⁻¹ deg⁻¹.)

The consequence of this set of observations is that the mean *ensemble* behaviour (overall change in motoneurone activation per degree change in vertical orientation) would be highly non-linear; the ensemble slope would increase by about sixfold between gaze raised 30 deg and gaze lowered 10 deg. (Average slope would be

$$2.7(0.3 + 0.018D) + D^2(0.018 \times 0.16)/2,$$

where *D* is downward deviation from 30 deg raised gaze.) Assuming that observations from the monkey can be extrapolated, at least qualitatively, to the human, and that total motoneurone activation provides a reliable index of muscular tension, this result implies major change in the torque exerted by the superior oblique muscle, depending on the level of gaze. When the eyes are raised, the superior obliques would not relax sufficiently to compensate fully for the vertical rotation of the eyes. Since the inferior oblique muscle can contribute very little to vertical rotation of the eye, the superior rectus would have to exert greater force in order to raise the eyes than would be required of the inferior rectus in order to lower the eyes by an equivalent amount.

These considerations are also relevant for vergence changes because tension of the superior oblique muscle tends to turn the eye in the temporal direction. (The inferior

oblique, on the other hand, passes almost directly beneath the centre of the eye, so its tendency, if any, to produce rotations in the horizontal plane is much weaker.) If, as concluded above, the superior oblique is under greater tension when the eyes are raised, then a divergent torque is present, which would require compensatory convergence forces from the horizontal recti (near-triad activation). Probable evidence for this predicted sort of near-triad activation (without associated *overt* vergence changes) is contained in the pupillary constriction measured after upward saccades (Table 1 and Fig. 3). This phenomenon was nearly as consistent a component of the data as was convergence during downward saccades (twenty-four of the twenty-five cases evaluated, both with binocular and with monocular viewing).

TABLE 5. Constriction of pupil following convergence

Binocular (disparity) vergence changes*			
Subject	Decrease in diameter per degree of vergence, mean \pm s.e. (μ m)	Mean vergence change (deg)	
1	90 \pm 24	1.9	
2	123 \pm 19	1.8	
3	98 \pm 18	1.5	
Monocular (accommodative) vergence**			
Subject	Decrease in diameter per degree of vergence, mean \pm s.e. (μ m)	Mean vergence change (deg)	Range of vergence changes (deg)
3	94 \pm 17	5	3.9-7.1
4	41 \pm 2	12	9.9-13.9
5	101 \pm 7	12	7.8-14.9
6	56 \pm 6	14	12.7-15.1
7	36 \pm 7	10	7.5-12.6
8	58 \pm 11	7	4.7-10.4

* Mean of up-down and down-up convergences, from experiments with results illustrated in Fig. 4: vergence changes and pupil changes measured 1 s after saccade ($n = 20$). ** Asymmetrical accommodative vergence, with targets collinear for right eye; vergence changes and pupil changes measured 1 s after saccade ($n = 10$).

Because pupil size depends strongly on light intensity, it is tempting to dismiss these responses as perhaps due to the pupillary light reflex, rather than to near-triad activation. Several sorts of evidence, however, argue strongly against that interpretation. (1) The peripheral lighting field was dominated by the illumination used for video recording: two 25 W incandescent lamps aimed at the eyes from about 30 deg *below* the line of sight. (2) Measurements from the small field surrounding the fixation markers (Minolta digital luminance meter, 1 deg field of view) showed that reflected illumination from upper and lower targets typically did not differ by more than 5-10%. (3) Control experiments with five of the eight subjects were undertaken, in which the lower target was deliberately more brightly lit (45-70% greater reflected illumination); in four of those five tests, typical pupillary constriction followed upward saccades, with mean values between 115 and 240 μ m: constriction following fixation on the more *dimly* lit target.

TABLE 6. Postulated contributions by various muscles to vergence changes associated with vertical saccades

	Vertical recti			Superior oblique			Horizontal recti		
	Process	Consequence	Process	Consequence	Process	Consequence	Process	Consequence	
1. Upward saccade	Co-contraction	Convergence movement	Added tension	Divergence movement	—	—	—	—	
2. Post-saccade	Release co-contraction	Divergence movement	Hold tension	Divergence force	Near-triad activation (sustained)	Counterbalancing convergence force			
3. Downward saccade	Co-contraction	Convergence movement	Decreased tension	Convergence movement	—	—	—	—	
4. Post-saccade	Release co-contraction	Divergence movement	Hold tension	Convergence force	Near-triad de-activation	Counterbalancing divergence force			

If, as proposed here, pupillary constriction following upward saccades is due to near-triad activation, then it is of interest to estimate the magnitude of the convergence that would ordinarily accompany such constriction, and that is presumably counteracted by divergence forces from the superior oblique muscles. Data on nine subjects contained in Tables 4 and 5 of Enright (1987), for vergence changes of about 2 deg, indicate an average steady-state pupil constriction of $94 \mu\text{m}$ ($\pm 21 \mu\text{m}$, mean \pm s.D.) per degree of observed convergence; additional relevant data on the eight subjects studied here are presented in Table 5. None of those measurements can be considered as fully comparable with the pupil data of Table 1 (and the similar data for the monocular tests of Table 2); nevertheless, such results suggest that, as a conservative estimate, at least a degree or two of convergence 'should' have accompanied the observed pupillary constriction that followed upward saccades, an amount comparable with, if not larger than the intrasaccadic convergence measured during subsequent downward saccades. Since a downward saccade would release excess tension of the superior oblique muscle, that compensatory near-triad convergence force would suddenly be transformed into overt convergence.

The overall interpretation to which this leads, for the vergence changes associated with vertical saccades, is summarized in Table 6; the intrasaccadic convergence during downward saccades is regarded as being due to both co-contraction of the vertical recti and to the sudden overt expression of near-triad convergence, which had been activated when the eyes were raised. The lack of strong residual vergence changes immediately after upward saccades is regarded as being due to approximate balance between convergence forces from co-contraction of the vertical recti, and divergence forces arising from incomplete relaxation of the superior obliques. As the vertical-rectus force is gradually reduced in the ensuing post-saccadic interval, near-triad convergence compensates for the residual divergence force.

The proposals summarized in Table 6 provide an internally consistent framework, based on known properties of the oculomotor system, for the interpretation of the major features of the experimental results reported here. Furthermore, that framework offers a plausible explanation for the surprising result reported by Collewijn, Erkelens & Steinman (1988), that upward saccades have a consistent tendency to undershoot the target, and downward saccades to overshoot: the postulated action of the superior oblique would serve to brake upward movement and to facilitate downward movement.

The results shown in Fig. 5 were derived from experiments that were undertaken as an explicit test of a prediction implicit in Table 6: when gaze is turned to one side by 20 deg, the vertical recti of the ipsilateral eye will have negligible torque in the horizontal plane, but the nasalward torque in the contralateral eye would be nearly doubled. Hence, when gaze is directed to the side, the ipsilateral eye should – as observed – contribute less to total vergence changes. A further prediction inherent in Table 6, which deserves empirical testing, is that as an expression of near-triad activation, accommodation of the lens for nearer vision should arise following upward saccades – limited, of course, by the target's demand for clear focus.

In addition to the dynamic phenomena considered so far, Table 2 (last column) shows that during monocular viewing, steady-state convergence (esophoria) tends to accompany lowering the line of sight (eleven cases out of twelve, most of which were

not, however, statistically significant). Much more extensive data on this influence of the elevation of gaze on phoria were reported by Holland (1958). He found that lowering the line of sight increased esophoria in all subjects, with somewhat greater effects during near viewing. The intrasaccadic vergence changes reported here thus represent a dynamic phenomenon which, in the absence of binocular stimuli for fusion, has residual steady-state effects of the sort reported by Holland (1958). The steady-state effects are, however, considerably smaller than the dynamic ones; they apparently reflect incomplete compensation, during monocular viewing, for position-dependent tension in the superior oblique muscle. During binocular viewing, disparity-vergence responses can then correct this discrepancy.

Probable perceptual consequences

When vertically separated targets are equidistant, the binocular disparity that arises immediately after a downward saccade does not lead to the perception of image doubling (diplopia), probably because the disparity is of such short duration. Nevertheless, the disparity measured after an 8 deg saccade is more than two orders of magnitude greater than threshold values for stereopsis, even for targets that are presented very briefly; and it is also severalfold greater than the minimum disparities that can trigger vergence movements. Hence, the post-saccadic disparities might well be able to produce subtle but interesting consequences in subjective evaluations of target distance. Consider a comparable situation with targets in the horizontal plane: if one is fixating on an object 3 or 4 m away, and then makes a conjugate horizontal saccade to another target that is presumed to be equidistant, but that in fact is hundreds of metres away, the new target will initially be seen with overconvergence of about a degree; the resulting foveal binocular disparity will trigger divergence movement and the eventual recovery of fusion. In such a situation, the near-foveal retinal events – the binocular disparities – would be very similar to those associated with an 8 deg downward saccade: transient overconvergence followed by slow recovery. Both in the case of the postulated horizontal saccade, and with downward vertical saccades, one might well expect such post-saccadic disparities to lead to the perception that the newly fixated target is farther away than the initial fixation point.

With vertical saccades, however, the situation is more complex. If, after a downward saccade, the viewer then makes an upward saccade to the initial target, there would be negligible intrasaccadic vergence change, and the postulated initial impression that the lower target is more distant would not be confirmed. Nevertheless, repeated back-and-forth saccades might well produce some sort of compromise perception, with a residual bias toward the impression that objects lower in the visual field are farther away. The basic notion here, the critical assumption, is that during binocular viewing, decisions about distance of widely separated targets are apt to be made with an emphasis on foveal stimuli, utilizing a sort of 'sequential stereopsis', rather than on peripherally perceived target disparities.

The proposal that up-down saccades should result in an up-down bias in perceived distances (objects lower in the visual field apt to seem farther away) provides a novel explanation for laboratory data on the tilt of the apparent vertical (Amigo, 1974; Cogan, 1979), as well as for many past laboratory measurements, indicating a

conspicuous tilt to the vertical horopter (e.g. Helmholtz, 1910; Cogan, 1979; see, however, Nakayama, 1977, Owens, Kooi & Tyler, 1987). In addition, this predicted perceptual bias would be expected to contribute importantly to two familiar illusions involving apparent distance in an outdoor setting: the steep inclination of the near-horizon sky (Filehne 1895; Zoth, 1899; Zehender, 1900) and the seeming divergence of sunbeams, shining through a series of gaps in the clouds (Enright, 1988). Recent experiments, which permit variations in vergence so that near-horizon and above-horizon targets are made to seem equidistant, offer clear evidence in support of these postulated perceptual consequences of up-down saccades (unpublished observations).

This research was supported by Grant BNS 85-19616 from the National Science Foundation. Valuable suggestions for the experimental programme were offered by Drs R. H. S. Carpenter and C. Erkelens. Revision of the manuscript was assisted by an anonymous referee. Many of the experiments described here were undertaken in the Abteilung für Medizinische Optik, Eye Clinic of the University of Hamburg, where Professor B. Rassow generously provided space and facilities.

REFERENCES

- AMIGO, G. (1974). A vertical horopter. *Optica Acta* **21**, 277-292.
- CARPENTER, R. H. S. (1977). *Movement of the Eyes*. London: Pion Press.
- COGAN, A. I. (1979). The relationship between the apparent vertical and the vertical horopter. *Vision Research* **19**, 655-665.
- COLLEWIJN, H., ERKELENS, C. J. & STEINMAN, R. M. (1988). Binocular co-ordination of human vertical saccadic eye movements. *Journal of Physiology*, **404**, 157-182
- COLLINS, C. C., O'MEARA, D. & SCOTT, A. B. (1975). Muscular tension during unrestrained human eye movements. *Journal of Physiology* **245**, 351-369.
- CIUFFREDA, K. J. & KENYON, R. V. (1983). Accommodative vergence and accommodation in normals, amblyopes, and strabismic. *Vergence Eye Movements: Basic and Clinical Aspects*, ed. SCHOR, C. M. & CIUFFREDA, K. J., pp. 101-173. Boston: Butterworths.
- ENRIGHT, J. T. (1984a). Changes in vergence mediated by saccades. *Journal of Physiology* **350**, 9-31.
- ENRIGHT, J. T. (1984b). Saccadic anomalies: vergence induces large departures from ball-and-socket behavior. *Vision Research* **24**, 301-308.
- ENRIGHT, J. T. (1986a). Facilitation of vergence changes by saccades: influences of misfocused images and of disparity stimuli in man. *Journal of Physiology* **371**, 69-87.
- ENRIGHT, J. T. (1986b). The aftermath of horizontal saccades: saccadic retraction and cyclotorsion. *Vision Research* **26**, 1807-1844.
- ENRIGHT, J. T. (1987). Perspective vergence: oculomotor responses to line drawings. *Vision Research* **27**, 1513-1526.
- ENRIGHT, J. T. (1988). Up-down saccades and up-down illusions. *Investigative Ophthalmology and Visual Science* **29**, suppl., 166.
- FILEHNE, W. (1895). Die Form des Himmelgewölbes. *Pflügers Archiv* **59**, 279-308.
- FUCHS, A. F. & LUSCHEI, E. S. (1971). The activity of single trochlear nerve fibers during eye movements in the alert monkey. *Experimental Brain Research* **13**, 78-89.
- HELMHOLTZ, H. v. (1910). *Handbuch der Physiologischen Optik, Dritte Auflage, Band 3*, Hamburg, Leipzig: Leopold Voss.
- HOLLAND, G. (1958). Untersuchung über den Einfluss der Fixationsentfernung und der Blickrichtung auf die horizontale Heterophorie (Exo- und Eso-Phorie). *Albrecht von Graefes Archiv für Ophthalmologie*, **160**, 144-160.
- NAKAYAMA, K. (1977). Geometrical and physiological aspects of depth perception. In *3-D Image Processing*, ed. BENTON, S.: *Proceedings of the Society of Photo-Optical Instrumentation Engineers* **120**, 2-9.

- OHIRA, A., GOTO, K. & OZAWA, T. (1983). Vertical and oblique saccadic eye movements. *Japanese Journal of Ophthalmology* **27**, 631–646.
- OWENS, L. R., KOOL, F. L. & TYLER, C. W. (1987). A new twist on the vertical horopter. *Investigative Ophthalmology and Visual Science* **28**, suppl., 295.
- SEMMLOW, J. L. & HUNG, G. K. (1983). The near response: theories of control. *Vergence Eye Movements: Basic and Clinical Aspects*, ed. SCHOR, C. M. & CIUFFREDA, K. J., pp. 175–195. Boston: Butterworths.
- SEMMLOW, J. L. & TINOR, T. (1978). Accommodative convergence response to off-foveal retinal images. *Journal of the Optical Society of America* **68**, 1497–1501.
- YARBUS, A. L. (1957). Eye movements during changes of the stationary point of fixation. *Biophysics* **2**, 679–683. (Translated from *Biofizika* **2**, 698–702.)
- YARBUS, A. L. (1967). *Eye Movements and Vision*. New York: Plenum Press.
- ZEHENDER, W. V. (1900). Die Form des Himmelgewölbes und das Grösser-Erscheinung der Gestirne am Horizont. *Zeitschrift für psychologie* **24**, 218–284.
- ZOTH, O. (1899). Über den Einfluss der Blickrichtung auf die scheinbare Grösse der Gestirne und die scheinbare Form des Himmelgewölbes. *Pflügers Archiv* **78**, 363–401.