

## UNEXPECTED ROLE OF THE OBLIQUE MUSCLES IN THE HUMAN VERTICAL FUSIONAL REFLEX

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### SUMMARY

1. If a weak vertically oriented prism is inserted before one eye, binocular single vision is restored by vertically divergent eye movements (one eye turning upward, the other downward); and it is usually assumed that the vertical rectus muscles mediate that fusional reflex.

2. When vertically divergent eye movements occur, both eyes also systematically rotate in parallel *around* their lines of sight (conjugate cyclotorsion). The direction of these unexpected eye movements demonstrates that they must be due to the oblique muscles, not the vertical recti.

3. The magnitude of these conjugate torsional movements is large enough to imply that the oblique muscles, in producing such torsion, would simultaneously effect all the divergent vertical re-orientation of the eyes required by the targets.

4. The cyclotorsion is accompanied by systematic translation of the eye along a nasal–temporal axis; the direction and extent of that non-rotational displacement indicate that the eye movements of the fusional reflex may well be mediated exclusively by the superior oblique muscles, acting against fixed tone in the inferior oblique muscles.

5. This revised understanding of the oculomotor co-ordination involved in the vertical fusional reflex has significant implications for both neurophysiology and oculomotor surgery.

### INTRODUCTION

Useful binocular vision requires that the two retinal images of a target remain in nearly perfect register with each other; if complete congruence in the central visual field fails by more than a few minutes of arc ('Panum's fusional region'), single vision cannot be sustained (Tyler, 1983). In order to bring retinal images into this narrow zone of tolerance, both eyes must be well aimed towards the target; and the required fine control of eye orientation is achieved by an involuntary response known as the fusional reflex (Grisham, 1983; Fry, 1983). A failure of this reflex leads to persistent diplopia ('double vision'), one of the most common clinical symptoms of oculomotor malfunction.

The images of a target can be out of register either horizontally or vertically or rotationally, directions that correspond to the primary actions of the three pairs of

extraocular muscles. Horizontal failures of image congruence ('disparities') arise whenever the object of attention is nearer or farther away than the fixation point; that situation, however, is less than ideal for study of the fusional reflex (Fry, 1983). Horizontal disparities underlie stereopsis (Tyler, 1983), and they also induce an integrated motor response to differences in target distance known as the 'near triad' (Semmlow & Hung, 1983), which includes ordinary horizontal convergence-divergence eye movements. The fusional reflex is thought to represent only a small part of horizontal vergence movements (Fry, 1983), with a scope of a few degrees compared with tens of degrees for convergence. Furthermore, the 'near' response system is mediated by specialized regions of the brain (Fry, 1983), which respond to several stimuli other than those involved in the fusional reflex, including image misfocus and 'knowledge of nearness'; and horizontal vergence movements are often under voluntary control, indicating that more than a simple reflex is involved.

Images that are vertically non-congruent, however, do not activate the 'near' response; therefore, the fusional reflex can be more easily studied, in isolation, by providing images that are out of register vertically: for example, by placing a vertically oriented prism before one eye (Fry, 1983). The resulting vertically divergent eye movements are relatively slow and are usually of small excursion: sudden imposition of vertical image disparity greater than 2–3 deg typically results in persistent double vision (Ellerbrock, 1949; Perlmutter & Kertesz, 1978; Kertesz, 1983).

Ordinary up-down rotations of the eyes are mediated primarily by the vertical rectus muscles, applying forces to the top and bottom surfaces of the eye; and it has therefore been tacitly assumed – without direct evidence – that when diverging eye movements in the up-down direction are required by the fusional reflex, they would also be mediated by the vertical rectus muscles. The evidence presented here demonstrates, however, that vertical fusional eye movements are achieved by an exotic and previously unsuspected effector mechanism: co-ordinated activity of only the *oblique* muscles, which are also responsible for those fusional movements that counteract rotational image disparities (cyclofusional rotations).

## METHODS

### *Production of vertical image disparities*

In the experiments reported here, vertical image disparities were either introduced stepwise by inserting a vertically oriented prism before one eye, or produced gradually by what is here called an 'overconvergence protocol'. In this latter method, a pair of identical targets – here, circles with 2 mm line width, 4 cm in diameter (*ca* 4 deg) – were presented with lateral separation of 15 cm at about 50 cm distance, affixed to a support bar that pivots on a horizontal mid-sagittal axis, located midway between the targets; rotation of the bar raises one target and lowers the other. With the support bar level (targets separated horizontally), the observer is instructed to overconverge (as in 'free-fusion' of stereo targets), so as to achieve inappropriate target superposition: the right eye fixates the left-hand target, while the left eye fixates the right-hand target. A single, fused image is then seen straight ahead, flanked on either side by a 'ghost' image (seen by only one eye). Modest rotation of the target support, so as to raise one target and lower the other, produces vertical image disparity between the components of the fused midline target, which can be compensated by laterally tilting the head; but when head movement is prevented, only small rotation of the support bar can be tolerated before the fusional reflex has been pushed beyond its capabilities: the fused midline image segregates into its two components, separated vertically. (In this situation,

horizontal eye orientation is sustained by non-fusional convergence; the 'double' images do *not* appreciably drift apart laterally.) Imposed change in image disparity is calculated as:

$$\tan^{-1}((y/d)(\tan r)),$$

where  $y$  is the lateral separation of the targets,  $d$  is the distance from the eye to its fixated target, and  $r$  is the angle through which target support has been rotated in the frontal plane. The subject's head was held fixed during the experiments by forehead rests and a custom-fitted bite-board; and

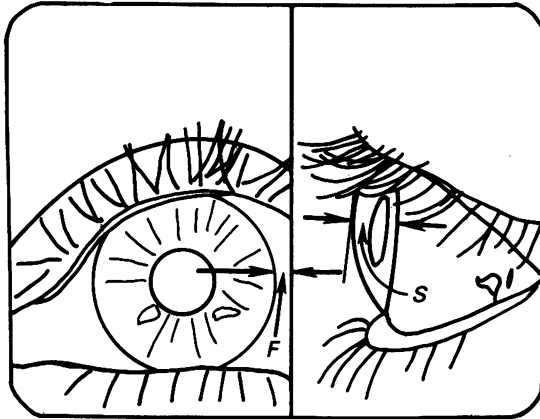


Fig. 1. Tracing from video-screen view during bidirectional monitoring of eye orientation, with  $F$  being distance, in frontal view, between temporal margin of the cornea and electronically imposed image-splitting line; and  $S$  being distance in side view between corneal margin and front surface of cornea.

after overconverged fusion of the targets had been achieved, the target-support bar was then slowly rotated about its axis, until the subject signalled by depressing a key that diplopia had arisen. Slight reverse target rotation, which restored single vision, then produced the final target configuration, near one of the fusional limits.

#### *Monitoring of eye position*

Eye orientations, either with and without prism, or near the two extremes of single vision (overconvergence protocol), were evaluated using a video-recording system (Enright, 1984*a*, 1990), with measurements starting after about 10 s of steady fixation on the fused targets. In that monitoring system, the pictures from two video cameras, equipped with close-up lenses, are combined by an image splitter, providing about 7-fold magnification of the iris of each eye on the monitor screen. Cyclotorsion is measured by superimposing a transparent straightedge on radially oriented pigment markers in the iris; those evaluations have a single-measurement precision of 10–15 min of arc (standard deviation, based on replicated 'blind' readings). Horizontal eye position is measured between iris margin and the electronically superimposed image-splitting line, with a resulting precision of about 6 min of arc or 20  $\mu\text{m}$ . All estimates reported here are mean values calculated from replicated changes in stimulus, with at least two measurements per presentation, thereby greatly reducing the impact of measurement error on reliability of the estimates. Reported  $N$  values refer to number of pairs of stimulus presentations compared.

In some of the experiments, lateral translation of the eye was estimated by a technique described in Enright (1984*b*), which involves two video cameras, oriented at right angles to each other, both aimed at one of the subject's eyes. For the measurements here, the upper and lower limits of vertical fusion were achieved by rotation of the target-support bar in the overconvergence protocol. Locations of the outer corneal margin at mid-eye height in both frontal view (relative to the image-splitting line) and in side view (relative to the anterior surface of the cornea) were measured ( $F$  and  $S$  in Fig. 1) after about 10 s of steady-state viewing, and changes in  $F$  and in  $S$  were determined between sequentially measured opposite extremes of vertical divergence. The

expected ratio,  $R$ , of displacement in the frontal plane to that in the sagittal plane for normal horizontal ocular rotation was derived from control experiments involving 4 deg conjugate horizontal eye movements during overconvergence. For each comparison between sequential pairs of up-down measurements, the apparent translation,  $\Delta F$ , was corrected for that component attributable to simple rotational changes in the direction of gaze:  $Tr = \Delta F + R\Delta S$  (where  $Tr$  is translation; and  $\Delta F$  and  $\Delta S$  will have opposite signs for normal rotation). Conversion of displacement in millimetres on the monitor screen to translation of the eye itself was based on video calibration using a ruler placed beside the cornea.

#### *Estimating non-motor contributions to single vision*

Estimates of the 'central' (i.e. non-motor) contribution towards overcoming image disparities were obtained using Nonius lines. In this procedure, a horizontal line, 3 mm in width and 2 cm long, was superimposed upon each of the 4 cm circles used in the overconvergence protocol. The lines were placed at midheight of the circle, one crossing its circle on the right side, the other crossing the other circle on the left side, each ending about 4 mm from centre of the circle. When the two circles are fused during overconvergence, each eye sees only one of these line segments; if the circles are seen with perfect retinal correspondence, the two line segments will be perceived as fully aligned with each other, on opposite sides of the circle. The non-motor component of vertical fusion within Panum's fusional regions (as it affects perception of the circle) is then indicated by the extent to which these Nonius lines are perceived as being misaligned, while the circles remain fused. The subjects were required to estimate the magnitude of misalignment, as a fraction of the 3 mm width of the lines, and those estimates, for both extreme limits of vertical fusion, were summed and expressed in units of angular subtense.

#### *The subjects*

Subject 2, 48 years old, is somewhat presbyopic; the other four subjects, aged 15–28, have normal acuity without corrective lenses, and all have qualitatively normal oculomotor performance (saccades, pursuit in all quadrants, and vergence movements apparently normal). Subjects were selected for presence of clear pigment patterns in the irises of both eyes, which are essential for reliable measurement of torsion. These experiments met with local Ethical Committee approval.

## RESULTS

### *Torsional responses to vertical image disparity*

When oppositely directed vertical re-orientation of the eyes was demanded in order to maintain fused single vision, the most significant component of the eye movement responses measured here was a systematic rotation *around* the visual axis that consistently arises in both eyes: cyclotorsion with magnitude typically greater than the required vertical re-orientation of the eye (i.e. greater than half the imposed disparity). Both eyes rotate in the same directions: clockwise (as seen by the video cameras) when the right eye should turn downward relative to the left eye, and counter-clockwise, when the right eye should turn upward. Data showing this effect, in response to insertion and removal of a 1.5 diopter prism (0.86 deg image deflection), are summarized for two subjects in Fig. 2. Additional data, derived from the overconvergence protocol, are contained in Table 1A.

### *Control for target rotation itself*

While the results from insertion of a prism (Fig. 2) involve the traditional method of producing vertical image disparity, the overconvergence protocol has apparently not been previously utilized, and it leads here to a potential complication: rotation of targets in the frontal plane is required, and it is conceivable that the observed

torsional changes (Table 1A) might in part be a response to target rotation itself. (Note, however, that torsional responses of this magnitude to small target rotations would be unprecedented.) To examine this possibility, three targets like those in the overconvergence protocol (circles 4 cm in diameter, separated laterally by 15 cm)

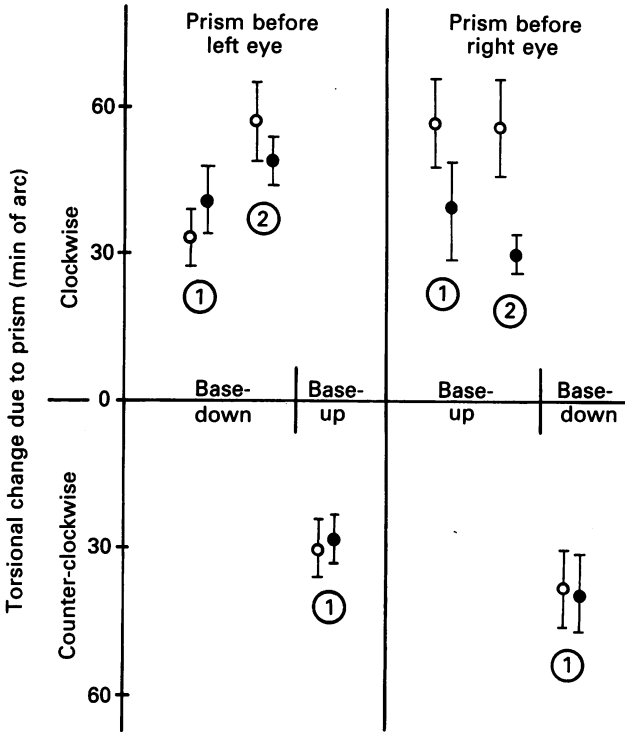


Fig. 2. Torsional changes due to insertion of 1.5 diopter prism before one eye (image deflection of 0.86 deg), during fixation on 4 deg circle at 3 m distance: changes in orientation between steady-state position with prism and position without prism, with clockwise/counter-clockwise distinction based on direction of change seen by video camera. ○, right eye values; ●, left eye values, with vertical bars showing standard errors derived from comparisons of sequential pairs of estimates (seven to ten pairs of values per point). Large circles with enclosed number, subject identification. Subject 2 was unable to achieve fusion with prism base-up before left eye, or with prism base-down before right eye.

were affixed symmetrically to the target-support bar. The subject fixated on the middle of those three circles with *normal* convergence, and torsional orientation of the eyes was measured while that set of circles was rotated by an amount comparable with that imposed on the set of three circles (one seen binocularly fused, the other two seen monocularly as unpaired 'ghost' images) during the overconvergence protocol. These resulting control measurements of changes in torsion are summarized in Table 1B; they clearly demonstrate that torsional changes comparable with those in Table 1A do not accompany rotation of similar target sets by themselves, provided that vertical disparity is not also imposed. The torsional results from the

TABLE 1. Eye movement responses in the 'overconvergence' protocol  
(A) Changes in torsion resulting from vertical disparity produced by target rotation

| Subject | Average target rotation (deg) | Imposed change in disparity (min of arc) | Torsional re-orientation* (min of arc $\pm$ s.e.m.) |              | N |
|---------|-------------------------------|--|---|--------------|---|
|         |                               |  | Right eye   | Left eye     |   |
| 1       | 3.7                           | 65                                       | 60 $\pm$ 7  | 40 $\pm$ 11  | 6 |
| 2       | 5.1                           | 90                                       | 71 $\pm$ 7  | 63 $\pm$ 10  | 7 |
| 3       | 5.7                           | 104                                      | 51 $\pm$ 13   | 103 $\pm$ 13 | 5 |
| 4       | 6.2                           | 109                                      | 88 $\pm$ 9  | 87 $\pm$ 7   | 6 |
| 5       | 6.0                           | 107                                      | 112 $\pm$ 12  | 118 $\pm$ 12 | 8 |

(B) Control tests: Changes in torsion when targets are rotated without induced change in disparity

| Subject | Target rotation (deg) | Torsional re-orientation† (min of arc $\pm$ s.e.m.) |            | N |
|---------|-----------------------|---|------------|---|
|         |                       | Right eye   | Left eye   |   |
| 1       | 4.9                   | 7 $\pm$ 7   | 4 $\pm$ 11 | 5 |
| 2       | 4.9                   | 3 $\pm$ 9   | 7 $\pm$ 4  | 6 |
| 3       | 5.7                   | 0 $\pm$ 7   | 13 $\pm$ 7 | 8 |
| 4       | 6.4                   | 6 $\pm$ 7   | 5 $\pm$ 5  | 6 |
| 5       | 6.3                   | 14 $\pm$ 10   | 20 $\pm$ 9 | 7 |

(C) Lateral translation resulting from vertical image disparity produced by target rotation

| Subject | Imposed change in disparity (min of arc) | Eye measured | Conversion factor† ( $\pm$ s.e.m.) | Lateral translation§ ( $\mu$ m $\pm$ s.e.m.) | $N_1; N_2$ |
|---------|--|--------------|------------------------------------|--|------------|
| 1       | 70                                       | Right        | 1.836 $\pm$ 0.063                  | 92 $\pm$ 22                                  | 8; 9       |
| 2       | 78                                       | Left         | 1.669 $\pm$ 0.060                  | 100 $\pm$ 18                                 | 10; 10     |
| 3       | 84                                       | Right        | 1.650 $\pm$ 0.051                  | 79 $\pm$ 24                                  | 9; 9       |
| 3       | 70                                       | Left         | Assumed 1.65†                      | 78 $\pm$ 30                                  | —; 7       |
| 4       | 112                                      | Right        | 1.734 $\pm$ 0.046                  | 216 $\pm$ 26                                 | 8; 9       |
| 5       | 98                                       | Right        | 1.647 $\pm$ 0.057                  | 139 $\pm$ 40                                 | 8; 8       |

\* Positive values for torsional change represent clockwise rotation (as seen by video camera) when left target was at lowest position at which fusion was still maintained, relative to torsional orientation when left target was at its highest position. This represents clockwise change in orientation when right eye was required to diverge downward relative to left eye.  $N$  values, used for calculation of standard errors, represent numbers of *pairs* of estimates compared, each estimate based on at least two measurements.

† Positive values of torsional change use convention of part A: clockwise rotation of eye when left end of target-support bar was at its lower position, relative to orientation when left end was at its higher position.

‡ Conversion factor,  $R$ , that was used for correcting apparent translation for any shifts in direction of gaze: determined as absolute value of the ratio between frontal and side view changes measured in a sequence of horizontal shifts of fixation between sides of 4 deg target, during overconvergence (see Methods). Conversion factor was not measured for left eye of subject 3, but in this case, nearly identical mean value of translation would be estimated with any reasonable value of  $R$ .

§ Positive values of translation represent nasal displacement when that eye was required by target configuration to rotate downward relative to its partner, and was showing 'intorsion' (dorsal margin of cornea moving nasally relative to ventral margin).

||  $N_1$  and  $N_2$  are number of pairs of estimates compared for conversion factor and for translation, respectively.

overconvergence protocol – which reproduced those from insertion of a vertically oriented prism – were thus apparently due only to vertical image disparities, and were not appreciably contaminated by a response to target rotation itself.

*Ocular translation due to vertical image disparity*

The torsion rotations documented in Fig. 2 and Table 1 A, which accompany that vertical divergence of the eyes which was demanded by the target configurations, was so unexpected that it seemed worthwhile to search for other unusual accompanying eye movements. Unexpected translation of the eye along the nasal-temporal axis has been previously found to accompany torsional rotations during vergence eye movements arising from *horizontal* image disparities (Enright, 1981, 1984*b*), suggesting that measurements of possible translation, during the vertical fusional reflex, might be informative. Estimates of translation can be obtained by simultaneously monitoring position of the outer corneal margin from both frontal and side views (Enright, 1984*b*; see Methods and Fig. 1); such measurements were undertaken during the overconvergence protocol. The results (Table 1C) demonstrate that translation of the eye along the nasal-temporal axis consistently occurred during the vertical fusional reflex: nasal displacement of the entire eye, when it was required to rotate downward, relative to its partner. The implications of this translation about the muscular activity producing vertically divergent eye movements will be considered below (Discussion).

*Non-motor contributions to single vision*

While the data in Fig. 2 and Tables 1 (A and C) include information about the magnitude of the *imposed* vertical target disparities, it is to be expected that the resulting vertically divergent eye movements would be somewhat smaller in magnitude; achievement of single vision can be expected to include a central, non-motor component, by which images that are slightly out of register on the retinas, but within Panum's fusional region, are not perceived as double images (Tyler, 1983). In previous studies, the eye movement component of vertical fusion has typically been reported to be about 80–85% of the imposed disparity (Perlmutter & Kertesz, 1978; Kertesz, 1983, and references there). The video eye-monitoring system used in the experiments here is poorly suited for directly evaluating vertically divergent eye movements, but indirect estimates of their magnitude can be obtained using horizontal Nonius lines (see Methods). Most subjects initially reported that during fusion of the circles with overconvergence, the two horizontal line segments (one seen by each eye) were aligned even at the extreme limits of fusion; but when encouraged to look for even small misalignments, all reported discrepancies – usually slight ones – for at least one of the fusional limits. The direction of those discrepancies indicates that central, non-motor processes make a consistent contribution to maintaining single vision in this sort of experiment, albeit usually a small one. Estimates for the five subjects ranged from 6 to 33 min of arc (median 10 min of arc), values that can be interpreted as being twice the width of Panum's fusional region for such targets. The approximate magnitude of the divergent vertical eye movements during the overconvergence protocol would represent the difference between the imposed target disparities (Table 1A, column 3) and these Nonius-line estimates of non-motor

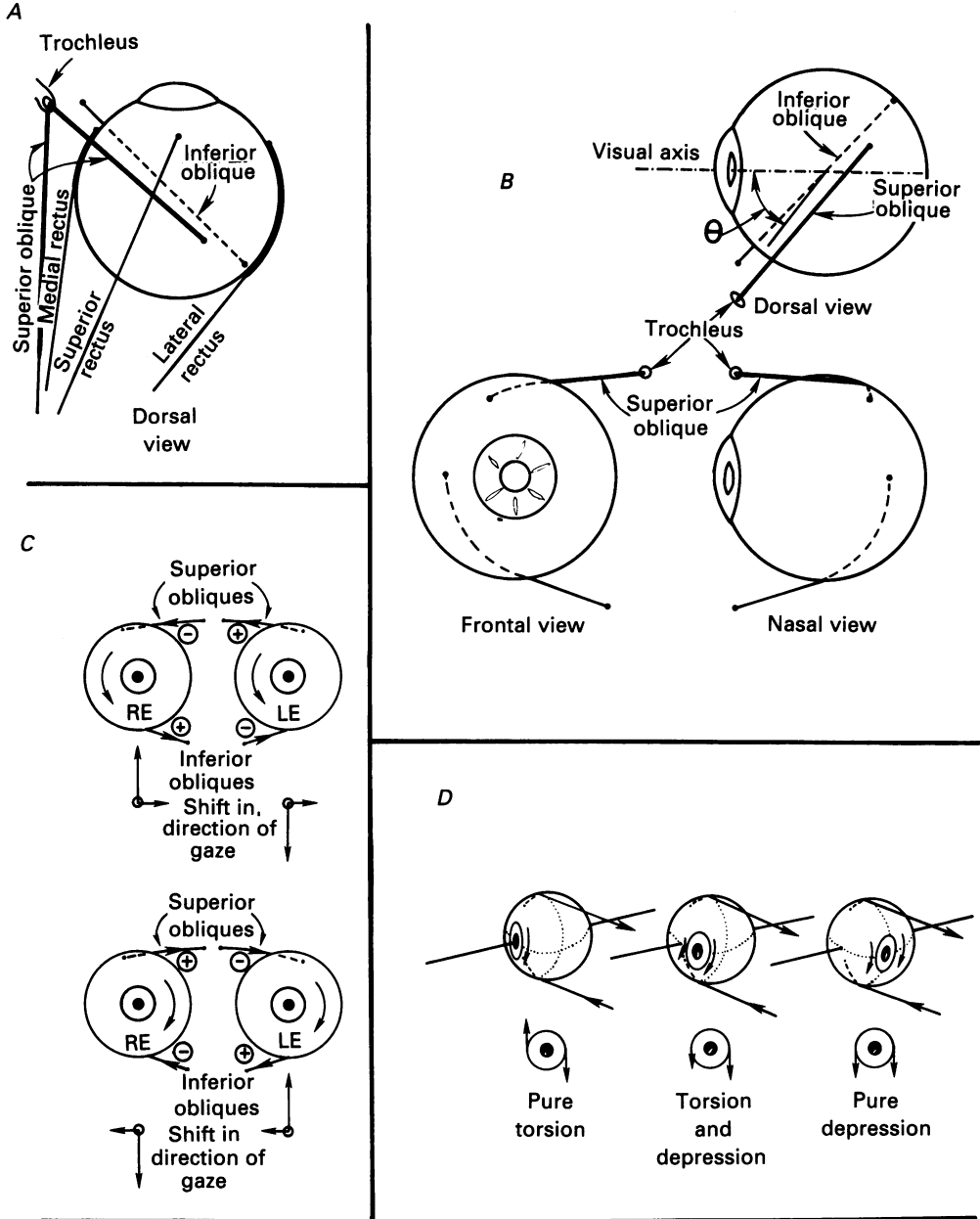


Fig. 3. *A*, schematic diagram indicating points of insertion and direction of action of extraocular muscles of right eye (with inferior vertical rectus, not shown, being directly beneath superior vertical rectus). *B*, schematic diagram of right eye in plan view, side view and front view, emphasizing path of superior oblique muscle from attachment up to trochleus; and path of inferior oblique muscle. (*A* and *B* based on data in Volkman, 1869). *C*, schematic diagrams of both eyes in frontal view (RE = right eye, LE = left eye), with oblique muscles producing parallel changes in torsional orientation; encircled '+' sign indicates increase in tension of the adjacent oblique muscle, and '-' sign indicates decrease in tension; vector diagrams (beneath) show resultant eye-specific shifts in direction of gaze. Note that in both cases, binocularly parallel torsional rotation is accompanied by vertically divergent shifts of gaze, one eye turning upward and the other



contributions. It has been reported that Nonius lines are sometimes unreliable indicators of vertical eye orientation (Kertesz, Hampton & Sabrin, 1983), but discrepancies of the magnitude that they encountered do not materially affect the present use of Nonius-line estimates.

#### DISCUSSION

##### *Involvement of the oblique muscles*

Although torsional rotation is usually ascribed to the oblique muscles, the vertical rectus muscles also produce some torsion, because they are not fully aligned with the visual axes (Fig. 3A); and since the targets presented here required vertical readjustments in the lines of sight, the suspicion naturally arises that the torsional rotations in Fig. 2 and Table 1A might be incidental byproducts of divergence produced by the vertical rectus muscles. That interpretation, however, is contradicted by the evidence. Lowering the direction of gaze by the vertical recti would be associated with modest counter-clockwise torsional rotation of the right eye, and clockwise rotation of the left eye ('extorsion' in both cases: see Carpenter, 1988, pp. 156–165). Hence, not only are the observed torsional rotations far too large to be attributed to the anticipated forces from the vertical recti, but they are also consistently in the *wrong direction*: clockwise when counter-clockwise should be expected on the basis of the required vertical eye movements, and counter-clockwise when clockwise is expected.

The alternative possibility is that the oblique muscles were responsible for the observed torsions; and this interpretation has noteworthy implications. Torsional rotation itself would do nothing to counteract vertical image disparities, but the oblique muscles do considerably more than simply produce torsion. Changes in their tension also include vertical and horizontal torques, producing vertical rotation because the muscles are not oriented perpendicular to the line of sight (Fig. 3A and B); and modest horizontal rotation because the tendon of the superior oblique passes on the nasal side of the upper pole of the eye. Those components of action by the obliques have, of course, long been recognized, but have traditionally been regarded as subsidiary consequences of the role of the obliques in producing cyclotorsion (Alpern, 1962; Carpenter, 1988); in the present context, however, those 'incidental' torques assume critical significance. When both eyes rotate in parallel around their visual axes, as documented in Fig. 2 and Table 1, the expected consequence would be a small lateral rotation of both eyes, moving in parallel; and a considerably larger divergent movement in the vertical direction, one eye turning upward while the other turns downward (Fig. 3C). and, most interestingly, the observed torsional rotations are consistently in that direction which implies that the oblique muscles would contribute appropriately to the vertical reorientation of the eyes demanded by

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downward. *D*, schematic diagrams of right eye illustrating dependence of vertical rotation and torsion upon angle between visual axis (implied by position of pupil) and plane of action of oblique muscles (i.e. angle shown as  $\theta$  in part *B*); near-horizontal diagonal lines indicate axis of ocular rotation. For small displacements, torsion is proportional to sine of that angle (maximal at 90 deg, as on left; zero at 0 deg, as on right); and vertical rotation ('depression') is proportional to cosine of that angle (zero at 90 deg, as on left; maximal at 0 deg, as on right).

the target configurations. Is the magnitude of the implied vertical divergence also appropriate?

*Quantitative relationships between vertical divergence and cyclotorsion*

In order to calculate the expected relationship between the torsion and the vertical rotation of the eye produced by action of the oblique muscles, let the eye be

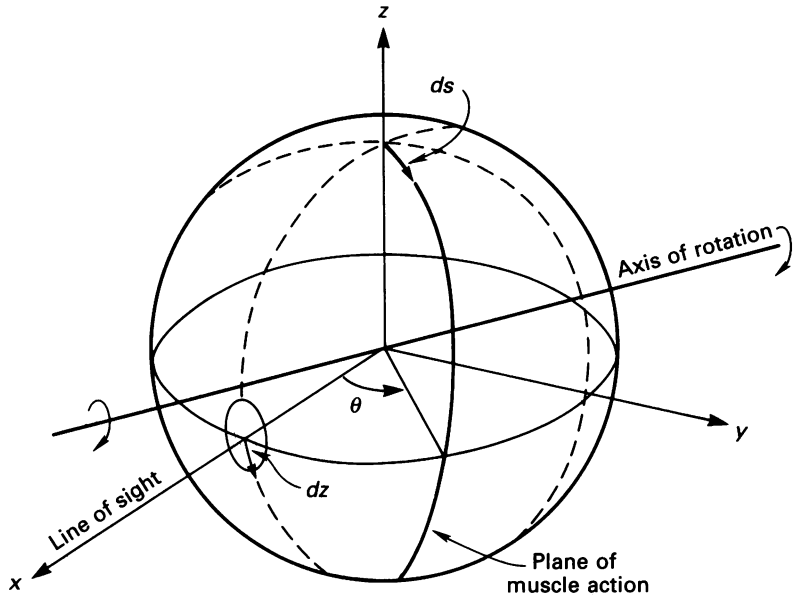


Fig. 4. Schematic diagram of the right eye as a sphere in a Cartesian co-ordinate system, showing the plane of action of the oblique muscles, which is assumed to be vertical and which makes an angle  $\theta$  with the  $x$ - $z$  plane.  $ds$  represents a small rotation of the eye produced by the oblique muscles, around an axis which is perpendicular to their plane of action and which passes through the centre of the eye; and  $dz$  represents the resulting downward displacement of the pupil.

approximated by a sphere of radius  $R$  in a co-ordinate system with origin at its centre, with the  $x$ -axis being the line of sight (positive outward) and  $z$  positive upward (Fig. 4). Now let us make several oversimplifications (to be reconsidered below): first, assume that the inferior oblique muscle and the tendon of the superior oblique muscle exert their forces in a vertical plane, a plane that passes through the centre of the eye and makes an angle  $\theta$  with the  $x$ - $z$  plane (Figs 3A and 4). Assume, further, that the oblique muscles co-operatively turn the eye by some small amount (one contracting, its antagonist relaxing), around an axis that is perpendicular to their plane of action and that passes through the centre of the eye (because of orbital constraints). If the upper pole of the eye is thus turned by the oblique muscles through an arc  $ds$ , the vertical rotation of any point that is on the surface of the sphere and in the horizontal (i.e.  $x$ - $y$ ) plane ( $dz$  in Fig. 4) can be readily shown to be equal to:

$$(x \cos \theta + y \sin \theta) ds/R.$$

The vertical displacement of the centre of the pupil would be  $dz$  evaluated at  $x = R$ ,

$y = z = 0$ , or  $ds \cos \theta$ ; and the angular rotation of the visual axis in the vertical ( $x$ - $z$ ) plane would be  $dz/R$ , which is equal to  $(ds \cos \theta)/R$ . Torsional rotation is the partial derivative of  $dz$  with respect to  $y$ , which, evaluated at the centre of the pupil, is  $(ds \sin \theta)/R$ . These calculations predict that the ratio of vertical rotation to torsional rotation would be

$$r = (\cos \theta / \sin \theta). \quad (1)$$

(See Fig. 3D for a qualitative demonstration of how these relationships arise.)

In the prism experiments, with the target 3 m away, the eyes were aimed nearly straight ahead. In this situation, torque from the superior oblique muscle typically is applied at an angle,  $\theta$ , of about 50–55 deg to the line of sight (Volkman, 1869; Alpern, 1962; Carpenter, 1988); and the inferior oblique acts at a slightly smaller angle to the visual axis. Equation (1), evaluated for a  $\theta$  of 50 deg, indicates that the ratio,  $r$  (vertical rotation to torsional rotation), should be about 0.84. In other words, with quasi-parallel binocular torsional rotation, as documented in Fig. 2, the oblique muscles would be expected – according to this calculation – to produce vertical divergence of the visual axes by about 84% of the summed torsional rotation of both eyes. In the overconvergence experiments (data in Table 1A), with each eye turned nasally by about 12 deg, the angle,  $\theta$ , between oblique muscles and the line of sight would be smaller by about 7 deg (as can be derived graphically from the measurements of Volkman, 1869), in which case the expected vertical divergence would be slightly greater than the summed cyclotorsion ( $\cos 43 \text{ deg} / \sin 43 \text{ deg} = 1.07$ ).

How do such values compare with observation? For the six experiments of Fig. 2 (insertion of 0.86 deg prism, with eyes near primary orientation), the average value of the ratio of imposed disparity to summed cyclotorsion was 0.66 (range 0.53–0.89), compared with expectation of 0.84. For the five sets of values in Table 1A, the average ratio of imposed disparity to summed cyclotorsion was 0.62 (range 0.46–0.68), compared with expectation of 1.07. In both data sets, then, the observed cyclotorsion was somewhat greater than calculated expectation. Hence, if the sorts of approximation in the above calculations can be relied on, the observed torsional rotations are large enough – in most cases, even more than sufficient – as to imply that the entire fusional reflex re-orientation of the eyes would be mediated by forces of the oblique muscles alone; no divergent changes in tension from the vertical rectus muscles would be required.

#### *Assumptions of the calculations*

A quantitative comparison between imposed target disparity and calculations of expected torsion due to the oblique muscles involves several assumptions that are known to be oversimplifications: (1) that the realized vertical eye movements fully compensate for all imposed image disparity; (2) that the oblique muscles act in a vertical plane; (3) that angles of 50 deg (or 43 deg) between the muscles and the visual axis – averages from literature values for many individuals – can be used for these subjects; and (4) that the eye movement is simple unresisted rotation around an axis perpendicular to the lines of force of the obliques and passing through the centre of the globe.

Assumption (1) ignores the contribution of central (non-motor) factors to the

achievement of fused single vision, within Panum's fusional region. The Nonius line estimates described here, as well as prior reports in the literature (Kertesz, 1983), indicate that with vertical image disparities, vertically divergent eye movements usually overcome most – but not all – of an imposed disparity. The implication, then, is that realized divergent eye movements were presumably somewhat smaller than the imposed changes in disparity, somewhat reducing the magnitude of predicted torsional rotation.

Assumption (2), that the oblique muscles act in a vertical plane, is not precisely correct, as can be seen in Fig. 3A and B; instead, the tendon of the superior oblique passes on the nasal side of the centre of the eye. That deviation, however, is sufficiently small as to have a quite minor influence on the expected ratio of vertical divergence to cyclotorsion. Probable violations of assumption (3) (that when the eye is aimed straight ahead, the plane of action of the oblique muscles deviates from the line of sight by 50 deg) has a considerably larger impact on the reliability of the calculations. Volkman (1869), in his anatomical studies (thirty-one cadavers), found large variation among individuals in this angle, with the observed range for the superior oblique being from 40 to 61 deg. This variability means that the factors calculated above (0.84 and 1.07) are subject to an uncertainty of at least 35–40% due to individual variation in anatomy.

In addition to that problem, other aspects of the fusional eye movements measured here demonstrate that the observed torsional changes are not, as proposed by assumption (4), ordinary rotations involving contraction by one oblique muscle while the other lengthens a corresponding amount. The data in Table 1C document the occurrence of systematic nasal–temporal translation of the eye during reflex fusional movements, and thereby indicate that 'co-contraction' and 'co-relaxation' occur; simultaneous increases or decreases in net tension from *both* oblique muscles of the same eye produced displacement of the entire globe along the nasal–temporal axis.

#### *Implications of ocular translation*

The observed translational movements can be interpreted as follows: Table 1A indicates that clockwise torsional rotation occurs in both eyes when the right eye diverges downward, relative to the left; clockwise torsion of the right eye ('intorsion') involves contraction of its superior oblique, and/or relaxation of its inferior oblique (Fig. 3C); and the positive values in Table 1C indicate a nasal translation of the right eye in this situation – meaning that the superior oblique (which pulls nasally) has shortened to a greater extent than the inferior oblique has lengthened. By similar reasoning, positive values in Table 1C for left eye measurement also imply a dominance of changed forces from the superior oblique muscle.

Furthermore, these nasal–temporal displacements were sufficiently large as to suggest that the torsion may be due *only* to action of the superior obliques. If the superior oblique muscle were to produce a 1 deg torsional rotation of the eye, while the inferior oblique served only as an unyielding passive restraint, and if the eye were completely unconstrained by its surrounding tissues, the expected total translation of the centre of the globe in the nasal direction would be about 200  $\mu\text{m}$ . (Picture the eye, seen in frontal view, rotating by 1 deg around its lower pole; the pupil as well as the centre of the globe would be displaced by the radius of the globe multiplied

by  $\tan 1$  deg.) This  $200 \mu\text{m}$  would be about twice the typically measured displacement. Allowance for orbital constraints (elastic resistance from the fatty tissue around the eye) can be expected to reduce such a potential displacement; and reduction to the levels actually measured (Table 1C) does not seem unreasonable. In brief, then, the magnitude of the observed translation indicates that the bulk, and perhaps all of the cyclotorsion that occurs during reflex vertical fusional movements, is due only to the superior oblique muscle; *if* contraction-relaxation by the inferior oblique muscle makes an additional contribution, it must be a minor one.

If torque from the superior oblique muscle were to rotate the eye while the inferior oblique simply restrains it, and if there were no other constraints from the orbit, the resulting movement would represent rotation of the eye around its lower pole. The question of how this would affect the expected ratio of vertically divergent rotation to torsional rotation can be evaluated by geometric calculations similar to those described above. Those calculations demonstrate that for a given value of  $ds$ , both vertical rotation of the visual axis and torsional rotation would be half as large as derived above, meaning that the expected ratio would still be  $\cos \theta / \sin \theta$ , as derived above (i.e. 0.84 or 1.07).

It is by no means self-evident, however, how those ratios might be modified by distributed orbital resistance to translation. Furthermore, torque applied by the superior oblique muscle, contracting alone, would be opposed not only by the inferior oblique muscle (producing lateral translation like that documented in Table 1C), but also by the superior rectus and the medial rectus muscles (but not by the inferior rectus or the lateral rectus). Because of such complications, in addition to probable interindividual variations in anatomy, the calculated expected ratios (0.84 and 1.07) could easily be wrong by as much as a factor of 2.

### *General conclusions*

Despite the extent of uncertainty in the quantitative geometric calculations, several conclusions from the experimental results deserve emphasis: (1) the observed direction of torsional rotation (Fig. 2 and Table 1A) implicates the oblique muscles, and not the vertical recti; (2) rotation of the eye *around* the visual axis would do nothing to compensate for the imposed vertical image disparities, and, in the overconvergence protocol, it does not arise due to target rotation alone (Table 1B); (3) action by the obliques, necessary to produce the observed torsional changes, must be expected to produce vertical divergence of the visual axes, in the direction appropriate to compensate for the imposed vertical image disparities; (4) the summed torsional re-orientations documented in Fig. 2 and Table 1A are impressively large, in both cases averaging somewhat more than 160% of the imposed disparity, although a first approximation indicates that only 120% (Fig. 2) or 93% (Table 1A) would be enough to account for all the required vertical divergence; and (5) if the vertical recti were *also* to contribute to the demanded vertical divergence, that difference between observation and calculation would be even larger; one would expect not only that the oblique muscles would produce lesser torsion but also that the vertical recti would produce torsion in the opposite direction. The evidence, therefore, strongly supports the interpretation that the oblique muscles, and they alone, are responsible for the eye movements of the vertical fusional reflex. Furthermore, the translation documented in Table 1C

suggests that only changes in tension of the superior oblique muscles may be involved, working against fixed tone in the inferior obliques. If the inferior oblique contributes actively rather than passively, its role must be a minor one.

### *Broader implications*

The superior oblique muscles may well be the most remarkable and least understood components of the human oculomotor system. Their peculiar anatomy includes the trochleus, that unique pulley-like loop of cartilage through which the unusually long tendon passes, redirecting the muscle's torques by some 130 deg (Fig. 3A and B); and an innervation that arises on the opposite side of the brain, in its own clearly distinct nucleus, while four of the other five extra-ocular muscles of each eye are innervated ipsilaterally, and four out of those other five have their motoneurons in a single common nucleus (the third: Carpenter, 1988). Nevertheless, the contribution of the superior obliques to visual function has seemed to be of secondary importance – so much so that oculomotor surgeons commonly simply disconnect one or another of them from the globe (Helveston, 1985, 1990). The two pairs of rectus muscles of each eye are, in principle, sufficient to produce all ordinary changes in direction of gaze, as well as to achieve binocular retinal congruency, at least in the centre of fovea; and most recent models of oculomotor dynamics, whether they deal with saccades, pursuit or vergence movements, consider only the rectus muscles, relegating the oblique muscles to 'the plant'. The only role for which the oblique muscles seem to be uniquely suited is the control of rotation *around* the line of sight, recognizing, of course, that they could in principle serve an 'accessory' role by assisting in vertical and horizontal shifts of gaze (Alpern, 1962; Carpenter, 1988); but for generating torsional rotation, the obliques seem to be poorly positioned, with an alignment more than 40 deg from the optimal orientation. There is, furthermore, no convincing evidence that regulating torsion matters very much for human visual perception; torsional re-orientation does not appreciably compensate for head rotation (Miller, 1962; Collewijn, van der Steen, Ferman & Jansen, 1985) – as it does in lower animals (Baarsma & Collewijn, 1974) – nor does temporal variability in torsion appreciably affect our ability to evaluate the subjective vertical (Enright, 1990).

The results presented here suggest a very different perspective: it now appears that the superior oblique muscles are the primary effectors for reflex fusional movements in the vertical direction; and torsional rotation, which is then resisted by the inferior oblique muscles, would be a tolerable but incidental result of forces produced by the superior oblique muscles, when they perform their fusional task. This revised view of the vertical fusional reflex has significant implications for both neurophysiology and for oculomotor surgery. (1) Binocularly driven visual neurons that encode vertical target disparity – which are often encountered in recordings from the visual cortex of the monkey (Poggio & Fischer, 1977) – can be expected to provide systematic input, either directly or indirectly, to the trochlear nuclei, but none to those portions of the third-nerve nuclei that innervate the vertical rectus muscles. Because the trochlear nuclei innervate only the superior oblique muscles, the vertical fusional reflex may provide a particularly tractable system in which to investigate the mechanisms by which binocular image disparity is translated into compensatory motor output. (2) If the oblique muscles are the only effectors of the

vertical fusional reflex (with each eye contributing about equally; Table 1A), then it may be ill-advised to treat paralysis of one of the superior oblique muscles by simply disconnecting the intact, contralateral superior oblique, as is common practice today (Helveston, 1985, 1990). That sort of intervention would seemingly deprive the patient of the only residual effector of the fusional reflex that might still be useful for vertically divergent eye movements.

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