Published in final edited form as:

Prog Brain Res. 2008 ; 171: 21–28. doi:10.1016/S0079-6123(08)00604-3.

Functional Anatomy of the Extraocular Muscles During Vergence

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Abstract

Magnetic resonance imaging (MRI) now enables precise visualization of the mechanical state of the living human orbit, enabling inferences about the effects of mechanical factors on ocular kinematics. We used 3-dimensional magnetic search coil recordings and MRI to investigate the mechanical state of the orbit during vergence in humans. Horizontal convergence of 23° from a remote to a near target aligned on one eye was geometrically ideal, and was associated with lens thickening and extorsion of the rectus pulley array of the aligned eye with superior oblique muscle relaxation and inferior oblique muscle contraction. There was no rectus muscle cocontraction. Subjective fusion through a 1° vertical prism caused a clockwise (CW) torsion in both eyes, as well as variable vertical and horizontal vergences that seldom corresponded to prism amount or direction. MRI under these conditions did not show consistent torsion of the rectus pulley array, but a complex pattern of changes in rectus extraocular muscle (EOM) crosssections, consistent with co-contraction. Binocular fusion during vergence is accomplished by complex, 3D eye rotations seldom achieving binocular retinal correspondence. Vergence eye movements are sometimes associated with changes in rectus EOM pulling directions, and may sometimes be associated with co-contraction. Thus, extraretinal information about eye position would appear necessary to interpret binocular correspondence, and to avoid diplopia.

Keywords

active pulley hypothesis; extraocular muscles; magnetic resonance imaging; pulleys; vergence

INTRODUCTION

Some important aspects of ocular kinematics are not specified by explicit neural commands, but are instead determined by mechanical properties of extraocular muscles (EOMs) and orbital

connective tissues (Demer, 2004; 2006). With the head stationary, Listing's Law (LL) constrains ocular torsion to that specified by rotation from a primary position about a single axis lying in Listing's plane (Tweed and Vilis, 1987). This torsion is not encoded in the discharges of motor neurons innervating cyclovertical EOMs (Ghasia and Angelaki, 2005), yet even for abduction evoked by artificial abducens nerve stimulation, torsion conforms to LL (Klier et al., 2006). The ability of EOMs and orbital connective tissues to implement LL is explained by the active pulley hypothesis, which states that pulling directions of rectus EOMs are constrained by connective tissue pulleys that constitute their functional origins (Demer et al., 2000). Insertions of rectus EOM orbital layers on the rectus pulleys actively control their anteroposterior locations to make rectus EOM pulling directions depend on eye position as required to implement LL (Kono et al., 2002a). However, the transverse locations of rectus pulleys are separately under active control, due to insertion upon them of the orbital layers of the inferior (IO) (Demer et al., 2003b) and superior oblique (SO) (Kono et al., 2005) EOMs. Smooth muscle in Tenon's fascia is also positioned for transversely shifting rectus EOM pulleys (Demer et al., 1995; Demer et al., 1997; Kono et al., 2002b; Miller et al., 2003). MRI demonstrates that the human rectus pulley array counter-rotates during head tilting associated with ocular counter-rolling, a vestibulo-ocular reflex (Demer and Clark, 2005).

METHODS

We used MRI to study the functional anatomy of the orbit during vergence, disconjugate ocular rotations bringing images into binocular sensory correspondence. Subjects were young adults confirmed by detailed ophthalmologic examination to have normal binocular alignment and stereo thresholds 40 arcsec or better. All subjects gave informed consent according to a protocol approved by an institutional review board. Eye movements were recorded using binocular, dual-winding scleral magnetic search coils applied using topical anesthesia. Although subjects' heads were firmly restrained, residual head movement was measured and compensated using dual magnetic search coils affixed to a mold of the upper teeth.

Proximal convergence was studied in response to shifting a small lighted target, aligned to one eye, from 500 cm to 15 cm, so that all of the required adduction was in the fellow eye; this was accomplished in an MRI scanner using fiber optics and a half mirror, as elsewhere described (Demer et al., 2003a). Vertical vergence was induced during viewing of a target cross at 20 or 400 cm by placing a 1° base up prism over one eye; ideally, this also requires movement of only the eye viewing through the prism. Orbital MRI was performed in a separate session using a surface coil array in a 1.5 T scanner as previously described (Demer et al., 2003a). Data were analyzed only when subjects reported single binocular vision of the target.

Eye positions were represented as quaternions, and converted into Fick angles for display of time sequences and vergence (Crane et al., 2005). Rectus EOM cross sections and pulley locations were determined quantitatively after correction for head positioning and normalization (Demer et al., 2003a).

RESULTS

Horizontal Proximal Vergence

As described elsewhere for 8 subjects (Demer et al., 2003a), fusion of a target at 15 cm aligned to one eye was associated with 22.4° convergence of the fellow eye, geometrically ideal for bifoveal correspondence. During convergence, there was also thickening of the crystalline lens indicating accommodation. However, there was an extorsional shift in rectus pulley locations, apparently in both the aligned and converging orbits (Fig. 1). This effect was quantified in the aligned orbit for the medial rectus (MR), inferior rectus (IR), and superior rectus (SR) pulleys,

all of which shifted significantly in extorsion by $1.5 - 2.0^\circ$ ($P < 0.05$). Due to interference from the lacrimal gland, it was not possible to quantify shift of the lateral rectus (LR) pulley.

Vertical Fusional Vergence

Preliminary data are illustrated in Figure 2 for Subject P fusing a 1° base up prism placed over either eye for 10 s intervals alternating with equal periods of normal vision. Seated upright, this subject reported achieving single binocular vision through the prism within 1 – 3 s of each transition. Typical of all 8 subjects studied, Subject P exhibited a stereotypic pattern of binocular, 3D eye movements, regardless of which eye viewed through the prism: $1 - 2^\circ$ right eye infraduction, $2 - 3^\circ$ right eye abduction, and $4 - 6^\circ$ CW cyclovergence as illustrated in Fig. 2 for prism placed before the left eye. Since a prism deviates gaze towards its base, optically appropriate vertical vergence for left eye base up prism would have required left, but not right, infraduction. Actual vertical vergence paradoxically increased vertical retinal disparity from 1° to $\sim 2.5^\circ$, despite subjective binocular fusion. In most trials with base up prism over the left eye in every subject, vertical vergence increased, rather than decreased, objective retinal image disparity, and torsion was similarly directed in both eyes. Findings were similar at 20 and 400 cm viewing distances, and in $\pm 20^\circ$ horizontal and vertical secondary gaze positions. Subjective tilt was not reported.

Subjects were supine for MRI, and viewed a black cross surrounded by concentric squares 20 cm away inside the scanner. Using T2 fast spin echo, quasi-coronal MRI was performed perpendicular to the long axis of each orbit, and quasi-sagittal MRI transverse to this at 312 μm resolution. Representative images in Subject P showed no consistent torsion of the rectus pulleys associated with subjective fusion through a 1° prism base up over either eye, although the left SO cross section increased with prism over either eye consistent with CW torsion (Fig. 3).

Changes in maximal EOM cross sections represent contractility, and were computed for each EOM under prism viewing and control conditions (Fig. 4). It was sometimes impossible to distinguish the SR from the levator throughout the orbit, but it was treated in the same manner within subjects for all viewing conditions. Consistent with its abduction during prism viewing, right eye MR cross section declined with prism before either eye, with smaller change for the left eye. Correspondingly, LR cross-section generally increased with prism viewing. This suggests that the horizontal vergence response conformed to Sherrington's law of reciprocal innervation. Remaining changes in EOM cross section were frequently paradoxical. Despite the observation that the right eye infraducted during prism viewing, SR cross section generally increased or was unchanged, while IR cross section uniformly increased, with base up prism viewing by either eye. Despite observed CW cyclovergence during prism viewing, corresponding to right eye extorsion and left eye intorsion, changes in IO cross section were similar in the two eyes. With left eye base up prism, both the right IO and SO cross sections increased. These paradoxical contractile changes suggest cyclovertical EOM co-contraction during vertical vergence, with all of the cyclovertical EOMs participating in the eye movements.

DISCUSSION

Torsion is considered intrinsic to convergence. Excyclotorsion in convergence has been repeatedly confirmed in humans (Allen and Carter, 1967; Bruno and van den Berg, 1997; Mikhael et al., 1995; Minken and Van Gisbergen, 1994; Mok et al., 1992; Somani et al., 1998) and monkeys (Misslisch et al., 2001). During asymmetrical convergence, temporal rotation of Listing's plane occurs in both the aligned and converging eyes, independent of eye position (Steffen et al., 2000), corresponding to excyclotorsion in depression and incyclotorsion in elevation (Kapoula et al., 1999; Somani et al., 1998; van Rijn and van den

Berg, 1993). A form of Herring's Law of equal innervation has been proposed for the vergence system, such that both eyes receive symmetric version commands for remote targets, and mirror symmetric vergence commands for near targets (van Rijn and van den Berg, 1993). MRI suggests that convergence is associated with extorsion of the array of rectus EOM pulleys (Demer et al., 2003a), altering pulling directions of the rectus EOMs. This extorsion is apparently mediated by the coordinated actions of the oblique EOMs.

Vertical vergence has received less attention. Enright reported conjugate cyclovergence during vertical vergence, and proposed that vertical vergence may be mediated exclusively by the SO muscles (Enright, 1992). Van Rijn and Collewijn also observed conjugate cyclovergence whose direction was reversed by reversal of the vertical disparity, but discounted the exclusive role of the SO because the cyclovergence was independent of horizontal eye position (Van Rijn and Collewijn, 1994). The present data are also incompatible with Enright's proposition, since we also consistently observed right eye infraduction with extorsion (Fig. 2). The SO alone produces infraduction with intorsion. However, in the current study, reversal of the vertical disparity by placing the prism before the opposite eye did not reverse the associated cyclovergence, which was consistently CW. Enright also reported mediolateral globe translation (Enright, 1992), which may be compatible with the present MRI evidence of co-contraction of multiple EOMs.

Hara *et al.* studied adaptation to gradually increasing vertical disparity presented using a virtual reality display (Hara et al., 1998). Most of the subjects studied by Hara *et al.* exhibited vertical movements of both eyes, even though the target was shifted for only one eye, but vertical vergence compensated for about 90% of the visual disparity. Hara *et al.* did not observe consistent ocular torsion during vertical vergence (Hara et al., 1998). The current study imposed transient vertical disparity using prisms, with strikingly different findings. Although all subjects reported binocular fusion within a few seconds, vertical vergence with base up prism before the left eye was typically misdirected, increasing, rather than decreasing the vertical image disparity. This effect often doubled the prism-induced vertical disparity. While vertical vergence responses exceeding stimulus demand have been reported (Perlmutter and Kertesz, 1982), the present finding of misdirected vertical vergence appears novel. Nevertheless, it is consistent with the recent finding in monkeys with superior oblique palsy that binocular vision increases, rather than decreases, a small vertical phoria (Shan et al., 2007).

Unlike the torsion of the rectus pulley evident by MRI during horizontal proximal convergence to a target aligned on one eye (Demer et al., 2003a), the large cyclovergence induced by prism-induced vertical vergence in the present study was not associated with consistent torsion of the rectus pulley array, and was not associated with a subjective sensation of tilt. MRI also demonstrated lack of consistent reciprocal contractile pattern in the rectus and oblique EOMs, and rules out implementation of vertical vergence by any one EOM. Unless the mechanical effect is simply too small to be detected by MRI, absence of a simple mechanical basis for cyclovergence during prism-induced vertical vergence suggests novel mechanisms may be playing a role, potentially including co-contraction with globe translation, or differential contraction of subsets of fibers within rectus or oblique EOMs. This possibility deserves further investigation, as does the possibility that the EOM mechanisms of vergence might depend strongly on visual conditions.

Stereopsis presumes internal information of where each eye is pointing in order to interpret retinal image disparity as a veridical sense of depth. In theory, efference copy could serve this purpose if it were accurate. Alternatively, proprioception may permit the interpretation of retinal disparities. Jean Büttner-Ennever has suggested that multiply innervated fibers in the EOMs form part of a proprioceptive system (Büttner-Ennever, 2007). A strong proprioceptive horizontal and vertical eye position signal exists in primary somatosensory cortex (Wang et

al., 2007). The observed changes in torsional configuration of rectus pulleys during horizontal vergence, as well as the lack of pulley changes but paradoxical changes in binocular alignment during vertical vergence, argue that the brain probably monitors eye positions and mechanical states of EOMs. Merely knowing the foveal directions of the two eyes apparently does not uniquely determine binocular sensory correspondence, or determine the effect on eye position resulting from change in activity of any single EOM. Conversely, even afferent signals reflecting tension in individual EOMs would require interpretation in context of the tensions and pulling directions of all other EOMs. Given the complex mechanical interactions among EOMs in the orbit, proprioception would seem one essential input both to ocular motor control, and to sensory interpretation of binocular correspondence. In particular, torsional proprioception would seem to be a valuable sensory input to the ocular motor system, yet one unexplored at present.

Acknowledgments

Grant Support: Supported by National Institutes of Health EY08313. JLD is Leonard Apt Professor of Ophthalmology.

Abbreviations

3D	three-dimensional
CW	clockwise
EOM	extraocular muscle
IO	inferior oblique muscle
IR	inferior rectus muscle
LL	Listing's law
LR	lateral rectus muscle
MR	medial rectus muscle
MRI	magnetic resonance imaging
SO	superior oblique muscle
SR	superior rectus muscle

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Fig. 1. MRI of orbits showing effects of proximal convergence on transverse pulley location. Target, aligned to left eye, moved from 500 cm (left column) to 15 cm (right column), evoking a 23° convergence movement in right eye only, seen in axial view in upper row. Anterior quasi coronal images in the middle row at level of pulleys demonstrate transverse, extorsional shift highlighted by white lines through muscle centroids. Posterior quasi-coronal images in lower row suggest reduction in SO cross section in convergence associated with extorsion.

Fig. 2.

Eye rotations during vertical fusional vergence in representative subject. A 1° (2 Δ) base up prism was placed before left eye for 10 s intervals marked by black bars. Note paradoxical abduction and infraduction of right eye, with CW cyclovergence of both eyes, while horizontal and vertical positions of left eye remained paradoxically unchanged despite viewing through prism.

Fig. 3.

Quasi-coronal MRI of left orbit of subject during vertical fusional vergence with a 1° prism. Images at the level of the pulleys (top row) suggest no transverse shifts in rectus muscle paths, although the superior oblique cross section (arrows) is increased during prism viewing by either eye (far left and far right columns) as compared with control (middle column).

Fig. 4.

Effect of fusion of a 1° base up vertical prism on maximal EOM cross sectional areas in Subject P. Note consistent reduction of MR and increase in LR cross section, consistent with reciprocal activity in observed divergence. However, SR and IR, and IO and SO, both frequently increased in cross section, suggesting co-contraction of cyclovertical EOMs.