Missing Lateral Rectus Force and Absence of Medial Rectus Co-Contraction in Ocular Convergence

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Miller, Joel M., Christopher J. Bockisch, and Dmitri S. Pavlovski. Missing lateral rectus force and absence of medial rectus co-contraction in ocular convergence. J Neurophysiol 87: 2421–2433, 2002; 10.1152/jn.00566.2001. For a given position of the eye in the orbit, mean abducens motoneurons (LRMNs) fire at higher rates in converged gaze than when convergence is relaxed, implying that lateral rectus (LR) muscle force will be higher for a given eye position in convergence. If medial rectus (MR) muscle force balances LR force, it too would be higher in convergence, that is, LRMN recording studies predict horizontal rectus co-contraction in convergence. Three trained rhesus monkeys with binocular eye coils and custom muscle force transducers (MFTs) on LR and MR of one eye alternately fixated near (approximately 7 cm) and far (200 cm) targets with vergence movements of 20–30°. Tonic muscle forces were also measured during conjugate fixation of far targets over a 30 × 30° field. MFT characteristics and effects on oculomotility were assessed. Contrary to predictions, we found small (<1 g) decreases in both LR and MR forces in convergence, for those gaze positions that were used in the brain stem recording studies. This missing LR force paradox (higher LRMN firing rates in convergence but lower LR forces) suggests that motoneurons or muscle fibers contribute differently to oculorotary forces in converged and unconverged states, violating the final common path hypothesis. The absence of MR co-contraction is consistent with, and supports, the missing LR force finding. Resolution of the missing LR force paradox might involve nonlinear interactions among muscle fibers, mechanical specialization of muscle fibers and other articulations of the peripheral oculomotor apparatus, or extraneuronal contributions to muscle innervation.

INTRODUCTION

The part of the oculomotor plant that includes the motoneurons and extraocular muscles has been called the final common path (FCP) (Robinson 1968, 1975a), following Sherrington (Brodal 1981), to emphasize that signals from the various supernuclear control centers lose their identities in a single, homogeneous channel. The oculomotor plant hypothesis further supposes that a simple, machine-like relationship between ensemble motoneuron firing rate and instantaneous eye position (jointly determined by linear relationships between motoneuron discharge rate and conjugate eye position, and the pattern of motoneuron recruitment) holds for all types of eye movement (Keller and Robinson 1971, 1972; Robinson 1981; Skavenski and Robinson 1973), that structures from the motoneurons on out to the eyeball are controlled as opposed to being parts of the controller. Accordingly, the oculomotor plant is described by a simple transfer function (Robinson 1981).

Studies of vergence eye movement have already disproved the oculomotor plant hypothesis by showing that for a given position of the eye in the orbit, mean abducens motoneuron (LRMN) firing rates are higher in converged or near gaze than in unconverged or far gaze. Mays and Porter (1984) recorded in the abducens nuclei of monkeys and found that nearly all abducens neurons (presumably including both LRMNs and abducens internuclear neurons or AINs) decreased firing in ipsilateral adduction, but that the mean decrease in convergent adduction was only 62% of that in conjugate adduction. Because vergence signal strength varied, it was possible that cells with the weakest vergence signals formed a pool of AINs, and the others, a pool of LRMNs, with the latter carrying equal vergence and conjugate signals. Gamlin et al. (1989) disproved the pool hypothesis by comparing identified AINs with indistinguishable abducens neurons. For a given ipsilateral eye position, regardless of whether it was convergent or conjugate, neurons in both classes had similar firing rates. The mean firing rate decrease in convergent adduction was approximately 50% of that in conjugate adduction, similar to the difference found in the Mays and Porter study. Zhou and King (1998) recorded directly from VIth nerve rootlets and found that 66% of LRMNs were modulated with monocular movement of either eye. In particular, many LRMNs increased firing with adduction of the contralateral eye, although the ipsilateral eye was stable. The finding that for a given eye-position LRMNs fire at higher rates in convergence means that the relationship between motoneuron firing rate and eye position depends on which supernuclear eye movement subsystem determines the firing rate, a clear violation of the oculomotor plant hypothesis.

Nevertheless, the studies of Mays and Porter (1984), Gamlin et al. (1989) and Zhou and King (1998) do not refute the FCP hypothesis. Even if there is no fixed relationship between firing rate and eye position, there still might be a fixed relationship between firing rate and muscle force (at a given muscle length). However, in that case, the brain stem recording studies clearly predict that LR forces will be higher in converged than in unconverged gaze for a given eye position. Further, if the higher LR abducting forces were balanced by higher MR adducting forces, overall horizontal rectus co-contraction would result. Some electromyograph (EMG) studies suggest that there is co-contraction in convergence (Tamler and Jampolsky 1967; Tamler et al. 1958), whereas others do not
(Breinin 1957), presumably because of variability of motor unit sampling, small sample sizes, and instability of EMG electrode placement. An alternative to MR co-contraction is for cyclovertical eye muscles to provide adducting forces to balance the excess LR force predicted in convergence. In any case, the prediction of higher LR forces in convergence is an inescapable consequence of the results of the brain stem recording studies in conjunction with the FCP hypothesis.

The studies of Mays and Porter (1984) and Gamlin et al. (1989) sought to clarify a seeming inelegance of oculomotor force comparisons as equivalent conjugate eye rotations, which scales the excess LR force predicted in convergence. In any case, the prediction of higher LR forces in convergence is an inescapable consequence of the results of the brain stem recording studies in conjunction with the FCP hypothesis.

In the present study, we measure LR and MR forces in converged and unconverged gaze and find that there are no convergence-related force increases at gaze positions used in the brain stem recording studies. Our finding of missing LR force, supported by the absence of MR co-contraction, casts the FCP hypothesis into doubt, implying that even the relationship between motoneuron firing rate and muscle force is under supernuclear control.

Parts of this work have been previously presented in abstract form (Miller 1998; Miller et al. 1999a).

**METHODS**

**Muscle force measurement**

LR and MR muscle forces were measured with muscle force transducers (MFTs) of our design, an early version of which is described elsewhere (Miller and Robins 1992). The device measures total oculorotary muscle force at the tendon (see Animal preparation), minimally disturbs extraocular mechanics (see Binocular coordination and saccade dynamics), and is not subject to such sampling errors as are inevitable when recording motoneurons or EMGs. The version of the device used in the current experiments is less subject to failure (and so, more cost-effective) and has even less impact on range of motion and saccade dynamics

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Surgery was performed under aseptic conditions. General Care and Use of Laboratory Animals (National Research Council) approved by the Institutional Animal Care and Use Committee of California Pacific Medical Center. We used pairs of force samples collected within a few seconds of each other as will be discussed.

Animal preparation

Three Macaca mulatta served in these studies. Our protocols were approved by the Institutional Animal Care and Use Committee of California Pacific Medical Center, and followed the Guide for the Care and Use of Laboratory Animals (National Research Council 1996). Surgery was performed under aseptic conditions. General anesthesia was induced with ketamine and maintained with isoflurane gas supplied by a veterinary anesthesiologist. Analgesics and antibiotics were administered postsurgically. In the first of two surgeries, we implanted scleral search coils (Robinson 1963) in both eyes using the method of Judge et al. (1980), except that we sutured coils to the sclera to prevent slip, using 7-0 dacron on a spatula needle. After training monkeys to fixate targets for juice reward, we implanted MFTs on the LR and MR of one eye (Fig. 3). Each rectus muscle was exposed, a traction suture was passed under the muscle just posterior to the insertion, and the transducer, with cross tube removed, was placed face-up on the muscle. While holding the MFT down with forceps designed to engage its branch of the muscle insertion that rotates the eye but not any mechanically important structures. It would be desirable to verify this with careful dissection or imaging of both LR and MR in monkey, but we have not done so. Nevertheless, we can demonstrate that dual MFTs, and the surgery needed to implant them, had little impact on extraocular mechanics (see Binocular coordination and saccade dynamics).

Data collection and analysis

Each experimental session began and ended with eye-position calibration. One eye was occluded with an opaque paddle, suspended just in front of the eye, targets were sequentially lit in random order, and the monkey was manually rewarded. An array of 45 targets in 10° steps over a ±30° vertical and horizontal field with the 4 corner targets omitted was presented three times (see Fig. 5). The occluder was switched to the other eye and the procedure repeated. We also measured muscle force when the instrumented eye was fixating to assess saccade dynamics and for tonic muscle force data. For tonic forces, we calculated the median of seven 250-Hz samples before and after the reward was delivered.

In most of our vergence experiments the monkey alternately fixated near (approximately 7 cm) and far (200 cm) targets, arranged to require asymmetric vergence, by which we mean the case in which near and far targets are aligned with the instrumented eye (Fig. 4). To the degree that asymmetric vergence stimuli bring the aligned eye to the same position in near and far gaze, they allow muscle force changes related to convergence state to be isolated, and eliminate any misalignment of a fraction of a degree assured that the far target was to that of the far LEDs. For “aligned” near and far targets, a vertical misalignment of a fraction of a degree assured that the far target was visible by the aligned eye.

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Other instrumentation

Miller and Robins (1992) describe the calibration of eye coils and measurement of tonic forces using custom software on a Masscomp MC-5500 lab computer, also used here. A LabVIEW program (National Instruments, Austin, TX) on a Macintosh 8100 computer (Apple Computer, Cupertino, CA) controlled vergence experiments, sequencing visual targets, sampling eye position and muscle force at 250 Hz, and delivering juice rewards for accurate binocular fixation. Visual targets were red light-emitting diodes (LEDs), adjusted to have similar brightnesses. The near target was a single miniature red LED suspended by its leads such that it could be precisely positioned in the monkey’s frontal plane and masked to subtend a visual angle similar to that of the far LEDs. For “aligned” near and far targets, a vertical misalignment of a fraction of a degree assured that the far target was visible by the aligned eye.

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predict positive convergence forces. We suppose that converged gaze and unconverged gaze are states with characteristic muscle forces. In contrast, it is possible to imagine that the path taken to a particular gaze position is critical so that a test of the co-contraction prediction would require that we compare forces immediately before and after a pure vergence movement. Path dependence would be unusual in the oculomotor system, as exemplified by Donders’ Law (Donders 1870) and the near-absence of hysteresis in saccades (Goldstein and Robinson 1986). Nevertheless, to check this possibility, with one monkey, ERL, we elicited symmetric vergence movements and compared forces immediately before and after.

In one monkey, ERL, we also elicited asymmetric vergence with the horizontal position of the aligned targets varied over about ±12° (Fig. 4). In each experimental session, blocks of >30 successful far and near fixations were run with each of the aligned and offset near targets.

LR and MR force signals showed small, apparently random, uncorrelated drifts during and between experiments. We suspect these slowly varying forces are physiologic, because of the high stability of MFTs outside the body (see Fig. 2) and because gradual intrusion of body fluids would, in our experience, result in roughly monotonic signal changes, followed by device failure. To eliminate any effects of slow drift in MFT signals on the main asymmetric vergence data, we computed force differences for successive near-far fixations. For the symmetric vergence data, we compared successive fixations separated by a smooth vergence movement. For the asymmetric vergence data in which we varied near and far target positions over a 24° horizontal range, we included a reference fixation target at 200 cm in the mid-sagittal plane (0° far target in Fig. 4), which the monkey fixated several times each minute. In these experiments, forces are expressed relative to those fixating the reference target. The same target was the referent during our measurements of tonic muscle forces in conjugate gaze at different horizontal and vertical target positions.

RESULTS

Binocular coordination and saccade dynamics

In addition to their coils, eyes in which we measured muscle forces were burdened with two MFTs and their lead wires. Impairment of normal extraocular mechanics would be problematic for symmetric vergence studies, in which instrumented eye position is different in converged and unconverged fixations. In contrast, our asymmetric vergence results are insensitive to artifacts related to eye position to the degree that the measured eye was in the same average position during far and near fixation (e.g., Figs. 9A and 10A) or that residual misalignments were removed by calculation (e.g., Figs. 9B and 10B).

Nevertheless, we first show that the MFTs did not significantly disturb the eye’s static mechanics. The effect of MFT implantation on static binocular alignment was assessed by recording binocular eye positions as the monkey fixated monocularly the array of 45 LEDs, before and after implantation. Implantation might cause scarring or otherwise restrict the implanted eye so that the most sensitive test for misalignment would be to measure following eye (covered eye) positions with the implanted eye fixating (in clinical terms, we would hereby measure the “secondary deviation”).

For vertical gaze components, we adopt the convention that positions above straight ahead, supraductions, are positive. For horizontal gaze components, we show positions right of straight ahead as positive where we represent both eyes together (as in Figs. 4, 5, 9A, and 10A). Otherwise, we show abducted (AB) positions as positive, and adducted (AD) positions as negative.
monkey, overshoot of saccades, from before to after implantation. In one
records of saccades before and after implantation.
MFT implants on motility. Figure 6 shows randomly selected
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mals.
implantation. Similar results were obtained in the other ani-
horizontal and vertical, misalignments were no greater than before
° 5
35
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position less than 10% of the horizontal change), with sizes
of predominantly horizontal saccades (vertical change in eye
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FIG. 5. Binocular alignment before and after MFT installation. With his
left, implanted eye viewing, the monkey fixated an array of 45 points, spanning
a field ±30° horizontal by ±30° vertical at 10° increments, with the 4 corner
points omitted. +, mean fixations across several days. ●, corresponding posi-
tions of the right, covered eye.

Figure 5 shows representative alignment data, each point
being an average of samples from at least three fixations on a
given day, averaged over 2 days before MFT implants and over
4 days after. The small misalignments in the left panel are
characteristic of normal phoria, manifest when the two eyes
are visually dissociated, although it is not possible to assert
that eye coil implantation was not contributory. Two effects of
MFT implantation are apparent. First, after implantation,
the monkey had difficulty fixating the upper-right (30°, 20°) point,
as is shown in the figure by the absent data point. Second,
implantation slightly stiffened the left, implanted, orbit in
adduction. This is shown by the column of eye positions near
30° right. That is, before MFT implantation, the covered eye
did not turn quite as far to the right as the fixating eye, whereas
after MFT implantation the covered eye turned farther right,
relative to the fixating eye. This suggests that the fixating eye
had become slightly stiffer in adduction, requiring stronger
innervation to reach 30° right; supplied to the following eye,
this stronger innervation caused it to rotate too far to the right.
We interpret such misalignments as changes in stiffness rather
than innervational adaptations because most of the monkeys’
time was spent in normal, binocularly viewed visual surround-
ings, so that adaptation would tend to reduce misalignments or
restore the preimplant pattern. As Fig. 5 makes clear, implan-
tation-related misalignments were only seen in extreme right
gaze. In the region of our vergence measurements, ±20° hor-
izontal and vertical, misalignments were no greater than before
implantation. Similar results were obtained in the other ani-
mals.

The conclusions of the present study concern only tonic gaze
positions and forces. Nevertheless, measurements of saccadic
eye movements and associated dynamic forces are of general
interest and provide additional indications of the effects of
MFT implants on motility. Figure 6 shows randomly selected
records of saccades before and after implantation.
In no monkey did we find clear differences in sharpness or
overshoot of saccades, from before to after implantation. In one
monkey, MLS, we calculated the main sequence characteristics
of predominantly horizontal saccades (vertical change in eye
position less than 10% of the horizontal change), with sizes
5–35°. We found that MFT implantation had a modest effect
on dynamics; overall, peak velocity declined 10% (8% for
abducting and 12% for adducting saccades), and saccade du-
ration increased 17% (18% for abducting and 17% for adduct-
ing saccades).

In summary, MFT implantation resulted in small binocular
misalignments and restriction but only in extreme gaze, prob-
ably due to increased stiffness of the implanted eye, and
modest damping of saccades, presumably due to increased
viscosity. But no monkey had binocular misalignments in the
range of eye positions used in our vergence studies, and tonic
muscle forces measured over the field of gaze varied as ex-
pected (see Tonic muscle forces). There was no evidence in any
animal that MFT implantation resulted in any eye movement
abnormality in the oculomotor range relevant to our experi-
ments.

It is worth noting that monkeys in the present study were
able to fixate over a ±30° × ±30° field, compared with ±20° ×
±20° for monkeys with the earlier version of the device (Miller
and Robins 1992). This may be a direct result of the smaller
size of the current implant, which is less likely to interfere with
extraocular mechanics, or a result of decreased scarring, sec-
ondary to the smaller implant. The new devices were also more
reliable, routinely performing well for ≥4–5 mo after implan-
tation.

Tonic muscle forces

We first measured tonic muscle forces in conjugate gaze for
eye positions ranging ±30° horizontally and vertically in 10°

FIG. 6. Saccades before and after MFT installation. Saccades with left eye
fixing and right eye covered, to successively lit light-emitting diodes (LEDs)
in the calibration array. Both before and after MFT installation, saccades
appeared normal, with little evidence of slowing or overshooting. For eye
positions, solid lines are horizontal (abduction +) and interrupted lines are
vertical (supraduction +) components. For muscle forces, solid lines are LR
and interrupted lines are MR forces.
steps. Tonic forces in monkeys MRL and MLS were similar. In monkey ERL, however, LR forces began to rise in extreme adduction, which may have been related to scarring, secondary to repair of the tendon inadvertently cut and repaired during device implantation. Figure 7A shows average LR forces for three monkeys, with ERL’s LR data at −30° horizontal omitted from the average. LR forces ranged over 10.5 g. Figure 7B shows that MR forces varied over 16.5 g, and tended to decrease as the eye turned upward. Force increased at a higher rate in abduction for LR and adduction for MR, presumably reflecting recruitment of motor units.

Asymmetric vergence

Figure 9A shows eye position and muscle force as monkey MRL, with MFTs on the right eye made asymmetric vergence movements. The top traces show left and right eye positions. Apart from the so-called counter-productive horizontal saccades early in the refixation movement (Enright 1992), the right eye is stable throughout. Muscle forces are shown in the bottom two traces of Fig. 9A. Convergence is associated with a small muscle force decrease, easily seen in the LR trace. Figure 10A shows a similar pattern for monkey MLS with MFTs on the left eye.

Figures 9B and 10B show representative daily summaries for monkeys MRL and MLS, respectively. For each muscle in the instrumented eye, we plot convergence force, the excess force at a given eye position that is due to the eye being in a state of convergence, against horizontal misalignment, the horizontal difference in fixation of the near compared with the far target. For asymmetric vergence, convergence force is equal to the force fixating the near target minus that fixating the far target. Because convergence force is a difference of two forces it should be unaffected by any variations or abnormalities in overall muscle force or its measurement. The three clusters of points for each muscle correspond to the left offset, aligned, and right offset near targets, respectively (see METHODS). Lines fitted to the LR points, and separately to the MR points, cross the y axis (i.e., x = 0) at convergence forces estimating perfect near-far alignment. When misalignment is zero, convergence forces are seen to be slightly negative for both LR and MR.

The closed symbols (●, ▲, ■) in Fig. 11 summarize the asymmetric vergence data for three monkeys, with each point being the mean of 250–300 vergence movements made in one data-collection session. In every session, mean LR and MR convergence forces were negative. Across monkeys and sessions, mean LR convergence force was −0.49 g and MR convergence force −0.13 g.

Convergence force as a function of eye position

Convergence-related muscle force for a given vergence angle could change as a function of eye position, e.g., muscles
might co-contract in some eye positions but not others. To check this possibility, we extended our findings in one monkey, \textit{ERL}, measuring LR and MR forces over an eye-position range of 25°, holding the asymmetric vergence angle at 19.5 \pm 2°.

Medial rectus convergence forces were negative for all eye positions tested (Fig. 12). Lateral rectus convergence forces were negative and similar to MR convergence forces except in abduction where they became positive.

\textbf{Symmetric vergence}

Estimating convergence force for symmetric vergence is less direct than for asymmetric vergence because it is necessary to subtract the forces related to the difference between orbital positions of the instrumented eye at far and near fixations. We estimated these forces using tonic force data for each monkey (similar to the mean tonic force data of Fig. 7).

Forces associated with symmetric convergence can be calculated from the data underlying Fig. 12, although all of the convergence movements in these experimental sessions were asymmetric as we have described. We extracted and analyzed far and near fixation forces in which left and right eyes were in approximately symmetric positions. Referring to Fig. 4, fixation of the 0° far target closely approximated symmetric far gaze, with mean eye positions of 1.0 and 0.4° for instrumented and uninstrumented eyes, respectively. Fixation of the −9 and −12° near targets closely approximated symmetric near gaze, with mean eye positions of −10.6 and −10.8° for instrumented and uninstrumented eyes, respectively (recall that Fig. 4 is not to scale). Mean near forces exceeded mean far forces by −0.68 g for LR and 1.26 g for MR. From the tonic
force data for \( ERL \), the conjugate change in instrumented eye gaze from \( 1.0 \) to \(-10.6^\circ \) was estimated to account for changes of \(-0.24 \) g in LR and \( 1.60 \) g in MR. Subtracting these values, we calculate convergence forces of \(-0.46 \) g for LR and \(-0.34 \) g for MR. These \textit{calculated symmetric} convergence forces are shown as a plus sign (+) in Fig. 11, where they can be seen to be similar to the asymmetric convergence forces.

Finally, we collected six sessions of actual symmetric vergence movements in monkey \( ERL \). The instrumented eye abducted an average of \( 9.7^\circ \) during convergence. Mean near forces exceeded mean far forces by \(-0.90 \) g for LR and \( 0.87 \) g for MR. Conjugate change in instrumented eye gaze of \( 9.7^\circ \) would account for changes of \(-0.20 \) g in LR and \( 1.33 \) g in MR, and subtracting these values, we calculate convergence forces of \(-0.70 \) g for LR and \(-0.46 \) g for MR. These data, similar to our other convergence force data, are shown with a cross (\( \times \)) in Fig. 11.

**DISCUSSION**

**MFT performance**

Our unique MFT chronically measures forces at physiologically varying muscle lengths. The current device is more reliable than the earlier version described by Miller and Robins (1992) and allows a wider range of gaze with only small binocular misalignments at the edges and with saccade dynamics close to normal. Concerning the general utility of MFTs, it is difficult to eliminate the possibility that innervational adaptation (Optican and Robinson 1980) masked other abnormalities caused by implantation. However, for the purposes of the present study, any adaptations tending to restore normal oculomotor function would seem to clarify, rather than obscure, the effects of our experimental manipulations.

If EOMs slide through mid-orbital pulleys as the eye rotates (Miller 1989), how is it possible that an eye encumbered with MFTs on both oculorotary horizontal muscle tendons can rotate almost entirely unimpaired through a \( 60^\circ \) horizontal range (Fig. 5)? The answer is provided by Demer et al. (Demer 2002; Demer et al. 2000), who have demonstrated that horizontal rectus pulleys move anteriorly and posteriorly in precise coordination with eye rotation, thereby maintaining a constant separation between scleral insertion and pulley in which an MFT can comfortably reside.

**Tonic forces**

Over a \( \pm 30 \times \pm 30^\circ \) field of gaze, tonic LR force varied over a range of \( 10.5 \) g, and tonic MR force over \( 16.5 \) g. Within the central \( \pm 20^\circ \), reciprocal changes in MR and LR forces were observed (Miller and Robins 1992). Vertical eye position had only small effects on horizontal rectus forces, confirming our earlier findings.

For horizontal gaze between primary position and \( 30^\circ \) into the muscle’s field of action, we measured tonic LR forces averaging \( 180 \) mg/g, and tonic MR forces averaging \( 323 \) mg/g. Collins et al. (1975) used transducers implanted in series with disinserted human muscles and found mean MR forces averaging \( 467 \) mg/g over this range. Thus fixation forces in monkey EOM appear to be about two-thirds those in humans. However, out of their fields of action, where muscles are stretched by their antagonists, human and monkey EOMs are qualitatively different: human EOM forces drop and then rise, whereas monkey EOM forces decrease approximately linearly, to \( \approx 30^\circ \) (Miller and Robins 1992). This difference is not due to different measurement techniques: we have collected intraoperative human data similar to Collins’, but using MFTs similar to those we use in monkey (unpublished data). It appears that the fibroelastic tissue in monkey EOM does not stiffen rapidly with stretch as does that in human EOM (Miller and Robinson 1984). This is an issue very much in need of further study.

In the present study, we treated drift in LR and MR force signals as noise, controlled by experimental design in most of our data and by analytic methods in the rest. However, as discussed in the preceding text, we have reason to suspect that these slowly varying forces are physiologic. They might reflect oculomotor system instabilities and so require an account of eye-position stability. Force variation could conceivably have a...
function, such as varying intraocular pressure to aid fluid circulation.

Symmetric and asymmetric vergence

The abducens motoneucleus studies of Mays and Porter (1984) and Gamlin et al. (1989) predict higher horizontal rectus forces for a given eye position in symmetric convergence because the reduction in LRMN firing rate for a given convergent gaze change is about half that for an equally abducting conjugate gaze change. From Fig. 7, we expect 11° conjugate abduction to be associated with 2 g decrease in LR force. This predicts that 11° convergent addition would be associated with a force decrease about half this size, which implies positive convergence forces of 1 g for LR, and the same for MR, if the latter provides mechanical equilibrium. However, convergence angles in the present study are more than five times larger than in the preceding cited studies, so that we must expect larger effects of convergence state on LRMN gain. The prediction, then, is that 22° symmetric convergence should be associated with positive convergence forces of ≥ 1 g per muscle, but probably much more. In this region, 1 g per muscle corresponds to 5° of conjugate gaze.

We extracted from our asymmetric vergence data, near and far fixations in which left and right eyes were in approximately symmetric positions and, contrary to the predictions above, calculated negative convergence forces of about −0.5 g for both LR and MR. We ran 22° symmetric vergence trials to test if smooth vergence movement traversing near and far fixations was critical and again found negative convergence forces of about −0.5 g for both LR and MR (Fig. 11). The similarity of the two results supports our assumption that vergence state, rather than vergence movement, is the critical variable.

There is good evidence that convergence-related innervation is delivered equally to both eyes in asymmetric vergence (Allen and Carter, 1967; Rashbass and Westheimer, 1961; Steffen et al., 2000), so because of its methodologic superiority, we collected most of our data in this paradigm. Our asymmetric vergence results can be compared with the results of Zhou and King (1998), who had monkeys perform an asymmetric vergence task of about 20° and found modulated firing in many LRMNs when the ipsilateral eye was stationary. In a sample of 136 LRMNs, the mean ratio of firing rate to eye position was 3.3 spikes per s° for the ipsilateral eye and 1.1 spikes per s° for the contralateral eye. This implies that 22° asymmetric convergence would innervate the LR of the stationary ipsilateral eye at a level appropriate to a rightward movement of about 7.3°. From Fig. 7, this corresponds to an increase in muscle force of 1.5 g. However, the aligned eye in asymmetric vergence is not turned rightward, with consequent shortening of the LR, as was the eye in the conjugate gaze measurements of Fig. 7. We would, therefore measure an additional elastic force in the LR of the stationary eye. Passive LR elasticity in the neighborhood of primary position has been measured to be about 0.2 g/° in both monkey (Fuchs and Luschei, 1971) and human (Robinson et al., 1969). Thus elastic force would add 1.5 g to the increased force we would expect to measure in the monkey LR in asymmetric convergence, for a total predicted asymmetric convergence force of 3.0 g. If we further believed that this abducting force was balanced by the MR, we would predict similar MR convergence force. In contrast to these predictions, and consistent with our symmetric vergence results, our asymmetric vergence data, comprising more than 5,000 pairs of converged and unconverged eye positions in three monkeys, show that convergent positions averaging 22° are associated with negative convergence forces of about −0.5 g for LR and −0.12 g for MR. That is, we find 3.5 g of LR force to be “missing,” and consistent with this find not even a hint of MR co-contraction.

The similarity of the asymmetric and symmetric vergence results, particularly those for LR, for which the motoneucleus studies make direct predictions, supports our assumption that the two paradigms are similar in the effect of vergence state on muscle force. Overall, our measurements consistently fail to confirm even the sign of the convergence force predicted by the motoneucleus studies and the FCP hypothesis and find a force discrepancy equivalent to about 7.3° of conjugate rotation.

In one monkey, we held convergence angle constant and varied eye position (Fig. 12). MR convergence force was always negative, LR convergence force was negative for all adducted eye positions and ±5° in abduction. MR convergence force was near constant, whereas LR convergence force increased in abduction, resulting in an imbalance of 0.6 g in 15° abduction that was presumably balanced by cyclovertical muscles, such as the superior oblique (Mays et al., 1991) or by adjustments in the positions of rectus muscle pulleys (Demer et al., 2000; Miller, 1989). Because these data were collected in only one monkey, they are certainly in need of confirmation. In any case, the finding of positive LR convergence forces in abduction does not mitigate the conflict between the motoneucleus recordings and muscle force measurements because the eyes were never abducted in the motoneucleus studies and convergence forces in straight and adducted gaze positions were always negative.

Missing LR force

Mays and Porter (1984), Gamlin et al. (1989) and Zhou and King (1998) found that LRMNs fire at higher rates in convergence than in distant fixation for a given ipsilateral eye position. Certainly, from the FCP hypothesis, one would then expect to measure positive LR convergence forces. In contrast, mean convergence forces were −1/2 g for LR and −1/10 g for MR (data of Fig. 11). Thus our findings clearly contradict the prediction that LR forces are higher in convergence.

If the motor-nucleus recording studies and the present physiologic muscle-force measurements are both correct, then LRMN firing rates do not predict LR muscle forces. Together, these findings violate the fundamental notion of an oculomotor FCP in which commands from various supernuclear subsystems combine anonymously to produce muscle force. How can such a basic discrepancy be explained? We see several directions in which an explanation might be sought.

Motoneuron sampling bias

Gamlin et al.’s (1989) conclusion that LRMNs have higher firing rates in convergence is an inference based on measurements of identified AINs and sampling of a large population of unidentified abducens cells, presumably including representative numbers of both motor and interneuronal neurons. There are several ways in which LRMNs that strongly decreased their
firing rates in convergence might have been undersampled. Conjugate movements are typically used to position recording electrodes, so vergence-related neurons that were silent during conjugate movements would be missed (Mays et al. 1986). Smaller motoneurons are more likely to be undersampled (Lemon 1984), and motoneuron size might be correlated with muscle properties like contraction velocity and tension production (Barmack 1977). However, abducens neuron size is relatively uniformly distributed (Keller and Robinson 1972), so there is not likely to be a large population of unsampled cells.

Büttner-Ennever et al. (1998) have discovered outer motoneurons that surround the classical inner motoneurons of the abducens, oculomotor, and trochlear nuclei, and receive different premotor inputs. Although their function has not been demonstrated, outer motoneurons appear to multiply-innervate slow EOM fibers, and it is possible that this auxiliary motor system could help reconcile overall LRMN firing with muscle force.

**Recruitment order**

Oculorotary muscle force increases because of increases in motoneuron firing rate and recruitment of additional motor units. The firing rate of each motoneuron is a linear function of conjugate eye position with characteristic threshold and slope (Robinson 1970). However, it appears as though the vergence system drives abducens motoneurons somewhat differently than the conjugate gaze system. King et al. (1994) have shown that as vergence angle increases, abducens motoneurons began firing further in adduction, that is, abducens thresholds decrease. This mechanism could underlie vergence-related increases in LRMN firing rates, but does not account for the missing LR muscle forces.

**Muscle pulleys**

Rectus muscle pulleys deflect EOMs and serve as functional origins with respect to their pulling directions (Miller 1989). Demer builds on this basic notion by proposing at least three distinct active pulley hypotheses (APH), which describe modes in which pulley position might be controlled by smooth and striated muscles to suit extraocular mechanics to different eye-movement regimens (Demer et al. 2000). Pulley movement could affect the relationship of motoneuron activity to oculorotary muscle force in two ways. First, some motoneurons might alter their activities without directly affecting oculorotary forces because they innervate EOM fibers that are connected to pulleys, rather than to the eye. Second, oculorotary forces could change without changes in the activities of oculorotary motoneurons because pulley movements had altered muscle paths and lengths. EOM force is a function of muscle length as well as innervation because muscle length affects both the contractile force component (there is an optimal length for force generation) and the elastic force component (force increases with length) (Miller and Robinson 1984; Robinson 1975b).

Demer’s main APH proposes that orbital EOM fibers with their capsular or pulley insertions control the anterior-posterior location of each horizontal rectus muscle pulley independently of the global fibers with their scleral insertions, which control horizontal eye position. Such differential control of pulley and eye positions by independently moving orbital and global layers of a single EOM could account for the switch from Listing’s Law kinematics, characteristic of saccades and pursuit, to non-Listing kinematics, characteristic of the vestibuloocular reflex. If an orbital-pulley system was independent of a global-scleral system, changes in firing rates of motoneurons serving the orbital layer would lead to little or no change in oculorotary muscle force, and as explained in Animal preparation, MFTs measure only oculorotary force. Thus if the motoneurons showing increased activity in convergence innervated orbital fibers, Demer’s differential control hypothesis would help resolve the missing force paradox. However, differential control has not yet been convincingly demonstrated and, in any case, is supposed to function mainly in connection with the vestibuloocular reflex (Demer et al. 2000) and only as an ancillary mechanism in convergence (see following text).

Misslish and Tweed (2001) have argued that differential control is neither necessary nor sufficient to account for VOR kinematics, and Demer no longer advocates this application of the differential control idea (Demer 2002).

A second APH is that an EOM’s pulley insertion, moving together with its scleral insertion, provides anterior-posterior pulley movements necessary to maintain Listing’s Law in tertiary gaze. Pulley movements that follow eye rotations in this way explain why pulleys do not obstruct extreme eye rotations, particularly when muscles are encumbered with MFTs, as we have discussed. Demer (2002) has shown that horizontal rectus pulleys, located by visualizing with magnetic resonance imaging the muscle path inflections they produce in supraduction and infraduction, were found to translate in accurate coordination with horizontal eye position, thereby supporting the coordinated control hypothesis. Coordinated control might be relevant to the missing force paradox, if orbital-pulley and global-scleral systems were mechanically independent, as in differential control, and coordination was effected by matching innervations to the two EOM layers. However, coordinated control is more parsimoniously explained by dual insertion of an undifferentiated muscle so that demonstration of coordinated control does not demonstrate the mechanism necessary to account for our missing forces.

A third APH hypothesis (Clark et al. 2000; Demer et al. 2000) is that peribulbar smooth muscle, perhaps aided by differential MR orbital fiber activity, moves vertical rectus pulleys nasally to tilt Listing’s plane temporarily in both eyes, as occurs in convergence (Bruno and van den Berg 1997; Mok et al. 1992; Steffen et al. 2000). Such hybrid control might help account for missing MR forces, but only to the degree that independent MR orbital fiber activity is found to increase with convergence, which is currently unknown. It could not account for missing LR forces.

**Motor unit specialization**

Rectus muscle fibers are not homogenous but can be classified into at least six groups (Porter et al. 1995; Spencer and Porter 1988). Motoneuron sensitivity to vergence varies (Gamlin et al. 1989), and if motoneurons with high vergence sensitivities innervated weak muscle fibers, ensemble firing rate could increase in convergence without increasing muscle force. Extraocular motoneurons with high firing rate versus eye-position slopes tend to be associated with weak muscles (Bar-
mack 1977; Goldberg et al. 1998), perhaps supporting the fine control needed for binocular coordination.

**Muscle fiber coupling**

Goldberg et al. (1997) used motor nerve stimulation in cat to show that 25% of lateral rectus motor units contributed only 50% of their twitch force to an aggregate of nerve-activated units. This means that the force exerted by a motor unit at the tendon depends on the activity of other motor units. They also showed that 1/3 width LR myectomy reduced the whole muscle twitch tension by only 5%. This means that there is substantial mechanical cross-coupling among muscle fibers.

Such findings of mechanical, and possibly innervational, interactions among muscle fibers make the notion of parallel, independent muscle fibers untenable and might underlie complex relationships between innervation and force. Serial connections among fibers (e.g., fibers inserting into each other) would make the tendon force produced by shortening one fiber depend on the contractile state of fibers in series with it. Fibrous cross-couplings among fibers could result in force shunting, such that shortening of one fiber would render shortening of another ineffective in generating force at the tendon.

Such mechanisms could underlie cases of high firing rates with low muscle forces. Variation in recruitment order would not only have direct effects on muscle force but also indirect effects on the forces produced by other motor units, including those whose recruitment order is unaltered. We think it is critical that Goldberg et al.’s findings be replicated and extended to primate EOMs.

**Absence of co-contraction and cyclovertical muscles**

If one believes that there is an increase in LR force with no change in eye position, it is natural to predict a corresponding increase in MR force, although it is possible that other muscle forces balance the LR. Our LR force results, of course, remove the need to find large balancing forces in convergence, but showing that no such balancing forces exist provides additional evidence for the correctness of our LR force results.

Mays et al. (1991) found that trochlear motoneuron activity in monkeys decreased during convergence and that the magnitude of this decrease was significantly greater than that seen with conjugate adduction. Steffen et al. (2000) studied asymmetric vergence in normal humans and found that both aligned and unaligned eyes showed convergence-related changes in Listing’s plane similar to those that occur with paralysis of the superior oblique muscle (SO). Mays et al. (1991) went on to hypothesize that SO relaxation in convergence reduces the eye’s total abducting force, helping the MR overcome an insufficiently relaxed LR. Could SO relaxation in convergence help the MR overcome an insufficiently relaxed LR or reduce LR muscle force itself? We constructed a rough model of monkey extraocular static mechanics, based on a model of human extraocular biomechanics (Miller et al. 1999b) and mean values of extraocular geometry measured in 1 M radiata and 3 M mulata eyes (Miller and Robins 1987). This model suggests that, as a consequence of extraocular geometry, only about 20% of SO force abducts the eye, so that a convergence-related reduction in SO abduction could move the eye no more than 1/3 of what would be required to stretch an un-relaxed LR.

The model also estimates the SO depressing force to be four times its abducting force; Mays et al. (1991) report a factor of only 1.5. In either case, significant vertical forces would occur as a side effect of substantial SO relaxation and would need to be balanced by still other muscle forces.

According to our model, 70% of SO force incyclorotates the eye in monkey. Thus relaxing the SO would excyclorotate the eye, giving the superior rectus muscle (SR) an abducting action, and the inferior rectus muscle (IR) an adducting action. Thus in downgaze, where the IR dominates, the vertical recti would provide a net adducting force. However, in upgaze, where the SR dominates, the vertical recti would provide a net abducting force. Thus the indirect mechanical effects of SO relaxation aid adduction only in downgaze. Excyclorotation due to SO relaxation would also influence LR force if it affected LR path length. However, cyclorotation would almost certainly increase LR path length, thereby increasing total LR tension in convergence, an effect opposite to what is needed to account for the forces we have measured.

In summary, cyclovertical muscles do not appear suited to a major role in supplementing adduction. Arguments involving cyclorotation and globe translation suggest that the negative convergence forces we measured are even more discrepant from predictions. Cyclorotation due to SO relaxation in convergence would increase LR path length, thereby increasing LR force. Enright (1980) found in humans that (monocular) near fixation is associated with small temporal globe translations, which also increase horizontal rectus path lengths and forces.

It is popular to speculate that co-contraction accounts for effects of convergence on symptoms of oculomotor pathology, such as its suppression of congenital nystagmus. The logic of these speculations is sometimes unclear; but in any case, our finding that there is no co-contraction in convergence should turn speculation in more promising directions.

**Reconsidering the final common path**

Sherrington’s concept of the FCP originally referred to motoneurons in the ventral horns of the spinal cord and to cranial motor nuclei, which receive impulses from many sources, including sensory fibers, cortical cells, and brain stem nuclei, and provide all innervation to the skeletal musculature (Brodal 1981). Oculomotor physiologists had distinguished several types of eye movement, and anatomists had discovered several types of EOM fibers, so it seemed possible that each oculomotor subsystem drove a specialized subset of muscle fibers. Fast and slow fiber types, for instance, might have been driven by separate populations of motoneurons, controlled by sac-cadic and pursuit subsystems, respectively (Jampel 1967).

Early studies sought, but did not find, motoneurons that respond exclusively to fast or slow movements (Fuchs and Luschei 1970; Keller and Robinson 1972; Robinson 1970; Schiller 1970). The notion of multiple parallel systems was therefore abandoned, and the oculomotor nuclei, their cranial nerves, and extraocular muscles were taken to compose an FCP, in which innervations from the several supernuclear oculomotor subsystems combined anonymously (Robinson 1968). The present findings suggest that the powerful and fruitful simplification afforded by the FCP hypothesis must now be abandoned.
It is not unusual for a new measuring device to yield surprising data. Oculomotor physiologists typically measure neural activity in connection with eye movement but have never had an effective way to measure the muscle forces presumed to result from that neural activity and to cause that movement. Muscle forces contain information about oculomotor control signals that is lost to eye-position measurements. Most importantly, eye rotation loses half of the degrees of freedom in EOM innervations. The present experiments were based on the ability of MFT measurements to distinguish the activity of individual muscles in an “antagonistic pair.” A second advantage of muscle force measurements may become important in future work: because eye position is low-pass filtered by the viscous orbit, muscle force measurements better reflect the high-frequency behavior of motoneurons (Miller and Robins 1992).

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