

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

JOEL M. MILLER, CHRISTOPHER J. BOCKISCH, AND DMITRI S. PAVLOVSKI
The Smith-Kettlewell Eye Research Institute, San Francisco, California 94115-1813

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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, most 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 extranuclear 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).

Address for reprint requests: J. M. Miller, Smith-Kettlewell Institute, 2318 Fillmore St., San Francisco, CA 94115-1813 (E-mail: jmm@eidactics.com).

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 undistinguished 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

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(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 system design: that vergence innervation to the MRs might need to cancel inappropriate innervation from AINs via the medial longitudinal fasciculus. A finding that abducens neurons behaved the same in version and vergence would have confirmed the "wasteful" design but been otherwise unproblematic. Instead, the results of these studies, and also those of Zhou and King (1998), lead to problems accounting for LR as well as MR forces, and in combination with the results of the present experiments lead to a serious paradox.

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 gaze (see *Binocular coordination and saccade dynamics*). There is no exposed wiring near the lead exit, a region susceptible to intrusion of body fluids, and protective coatings of low-viscosity epoxy resin are applied beneath a Parylene-C envelope. Reliability of the new devices has been very good. The new device is smaller (approximately 1/3 the area) and interferes less with eye rotation. Its 6-mm width approximates the width of a Macaque rectus muscle (Miller and Robins 1987), although consequently its central aperture narrows the enclosed tendon by about 33%. Narrowing the tendon decreases its resistance to sideways bending, but this is probably helpful because it tends to offset the effects of connective tissue that grows to bind the tendon to the MFT, increasing resistance to sideways bending. In any case, the convergence data of the present study were collected near level gaze and would not be affected by abnormal horizontal rectus sideways bending. It might be thought that insinuation of connective tissue during healing would unload the MFT, preventing it from bending under changes in muscle tension. However, the steel MFT frame is far stiffer than surrounding connective tissue, which tends to make the later mechanically invisible. Nevertheless we also express critical force comparisons as equivalent conjugate eye rotations, which scales them to compensate for possible changes in transducer sensitivity with

implantation. In any case, all that is essential in the present study is that MFT sensitivity be sufficient to show force differences across experimental conditions. Except as noted, we always compare forces in converged and unconverged positions taken within a few seconds of each other.

MFT frames (Fig. 1) were photochemically etched from 0.25-mm-thick, half-hard, type 304L stainless steel sheet and electropolished (Elcon, San Jose, CA). Frame tabs were bent upward to form bearings for a 27-gauge hypodermic tubing cross-rod. U-shaped silicon strain gauges, solder pads, Formvar-coated wiring, and lead wires were mounted (Modern Machine and Tool, Newport News, VA). Lead wires were Teflon insulated 40 gauge, 10 strand stainless steel (Bioflex AS-631, from Cooner Wire, Chatsworth, CA), fitted with silicone rubber sleeves and tied down to the frame with soft 34-gauge stainless steel wire (not shown). Completed frames were coated and heat-cured with AE-15 epoxy (Measurements Group, Raleigh, NC). Parylene-C was then vapor-deposited to a thickness of 0.015 mm (Specialty Coating Systems, Ontario, CA). Detailed fabrication instructions are available at www.eidactics.com/Projects/EOMF_proj/MFT_Fabrication.

Each MFT was calibrated before implantation and after excision. The MFT was connected to a strain gauge amplifier (Model 2120A, Measurements Group), and excitation of 2.0 v applied. A length of Mylar tape was threaded through the MFT, as a muscle would be, and static loads applied to measure sensitivity and hysteresis. Typical sensitivity functions are shown in Fig. 2. All devices had very similar sensitivities and negligible hysteresis. Sensitivity changed less than 5% from before implantation to after excision. Sensitivity creep was negligible, averaging approximately 1% for a 50-g load over 20 min. For reasons that are not clear (see RESULTS and DISCUSSION), force signals show more drift *in vivo* than on the bench. Accordingly, our experiments were designed to compare

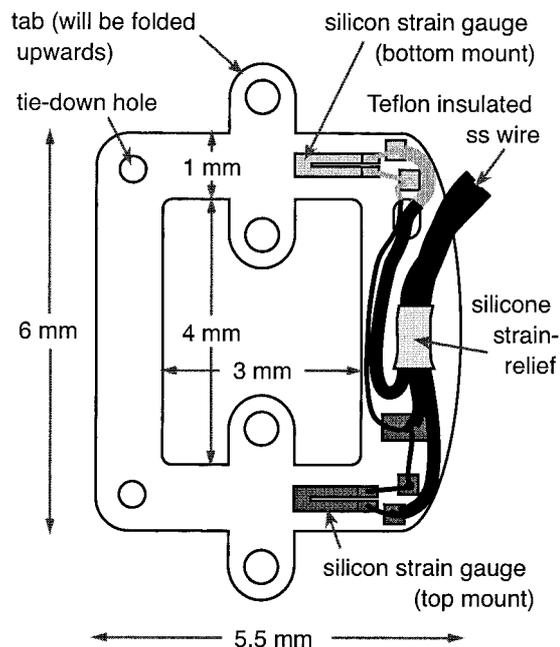


FIG. 1. Muscle force transducer (MFT) for chronic installation in monkey. Schematic shows the stainless steel frame (0.25-mm thick) with tabs, which are bent upward slightly more than 90° to serve as bearings for a cross-rod that passes under the muscle (see Fig. 3). During installation, nonabsorbable sutures are passed through the tie-down holes and muscle margins to secure the MFT's orientation. Silicon strain gauges are bonded to the surface and wired in push-pull arrangement to form a half Wheatstone Bridge, providing temperature compensation and summing forces across the width of the measured muscle. The device is coated with low-viscosity epoxy resin, followed by Parylene-C (0.015-mm thick).

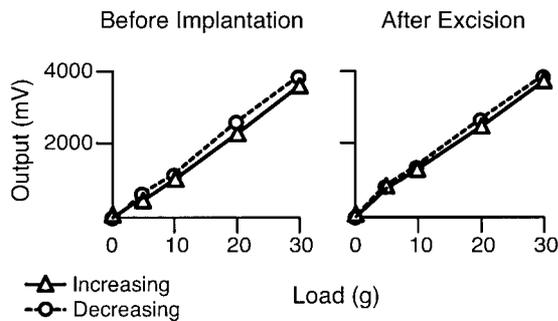


FIG. 2. Typical MFT load sensitivity, before implantation and after excision. Devices have linear response to load, have negligible hysteresis, and are not significantly degraded by several months of implantation. The difference between increasing and decreasing loads can be shown to be related to the Mylar tape used in bench testing and not the MFT. The sensitivity of this device (implanted in LMR of monkey *MLS*), as a typical example, was 127 mV/g before implantation and 124 mV/g after excision.

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 supervised 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 “tie-down” holes, the muscle was tented-up through the aperture of the frame by pulling the traction suture, and the cross tube was pushed through the bearing holes in the four tabs and under the muscle. Thus the MFT was installed so as to engage the branch of the muscle insertion that rotates the eye but not the *capsular insertion* (Bonnet 1841), or *pulley insertion*, which is involved in anterior-posterior pulley movement (Demer 2002; Demer et al. 2000). Nonabsorbable sutures were placed through the tie-down holes and the muscle margins to stabilize the MFT squarely on the muscle, 2 or 3 mm posterior to the insertion.

Demer et al. (2000) have shown in humans that about 12 mm separate the scleral and pulley insertions of the MR, suggesting that there is sufficient space for our 5.5 mm wide MFT to be placed 2–3 mm posterior to the MR insertion in monkey, without interfering with 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*). Lead wires were positioned in a pocket blunt dissected into the fascia, as shown in Fig. 3 and were brought out of the orbit under the skin of the brow and scalp to an acrylic head plate. In one monkey, *ERL*, we inadvertently disinserted the LR while exposing it. Fortunately, we were able to locate the muscle, slip the MFT with cross-tube onto it, and suture the tendon to its original insertion. The eye with MFTs will be referred to herein as the *instrumented eye*.

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.

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 $\pm 30^\circ$ 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

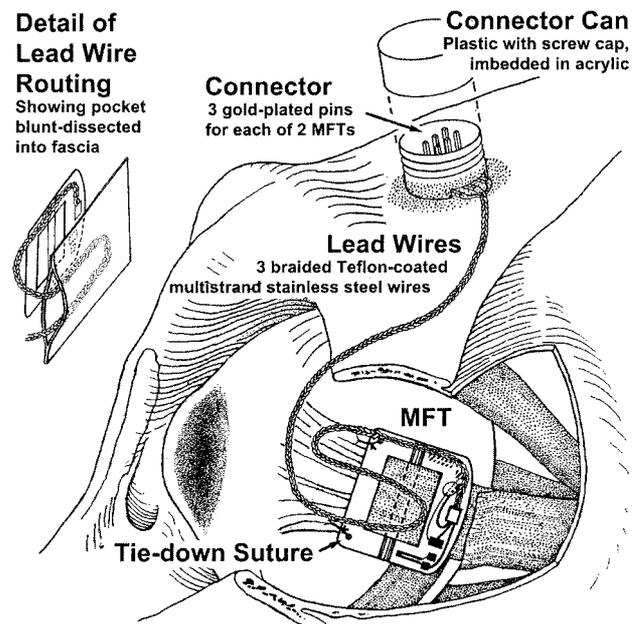


FIG. 3. MFT installation in monkey. The MFT frame is placed on the oculorotary muscle-tendon, which is tented-up through the frame’s central aperture. A stainless steel cross-rod is then pushed through the bearing holes and under the muscle. The braided Teflon-coated leads exit the orbit in the same way as eye coil leads (Judge et al. 1980). The capsular or pulley insertion is shown to branch off posterior to the MFT. The figure is not to scale.

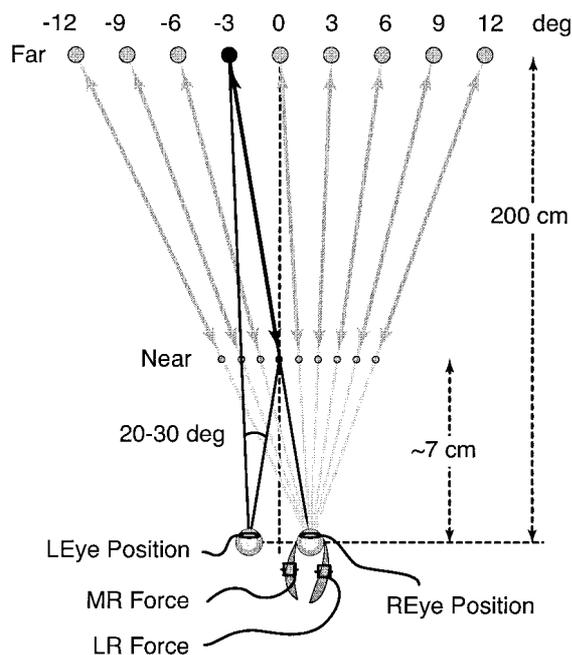


FIG. 4. Target positions. Near and far target positions are aligned with the instrumented right eye in this figure. For most experiments, only one pair of near and far targets was used: the “-3” far target shown in black, and the near target shown in black, connected by the black double-headed arrow suggesting the nominal path of binocular refixations. To estimate far and near fixation forces at exactly equal mean instrumented eye positions, the near target was also presented at left and right offset positions, each about 4° from the aligned near target. For simplicity, offset positions are not shown in the figure. In additional experiments in one monkey, the near and far target positions varied across blocks over a 24° horizontal range in 3° steps, maintaining far-near alignment with the instrumented eye, as shown by the double-headed gray arrows. In these experiments, a distant reference target (“0”) was also presented, as discussed in the text. For symmetric vergence experiments, we presented the 0° far target and centered the near target array on the dotted midline. Targets are labeled with their angular eccentricities at the instrumented eye (the right eye in the figure), with 0 straight ahead. Figure not drawn to scale.

MFT artifacts that might depend on the position of the instrumented globe in the orbit. Physically aligning near and far targets with the instrumented eye does not, of course, guarantee that the monkey's eye will be in the same average positions during voluntary fixations of the two targets. Therefore in asymmetric vergence sessions we presented the near target, not only at the position in which it was aligned with the far target and the instrumented eye (the *aligned* near target, as shown in Fig. 4), but also at horizontal positions about 4° to the left and 4° to the right of the aligned near target (left and right *offset* near targets, not shown in Fig. 4). With the aligned near target, many individual trials had the eye in the same position in converged and unconverged states (e.g., Figs. 9A and 10A). From full, unselected data sets collected with aligned as well as offset near targets, it was possible to estimate by interpolation muscle forces for an eye that was precisely aligned in far and near fixation (Figs. 9B and 10B). In most sessions, the far target was fixated at about 3° adduction for the instrumented eye. Vergence movements were $20\text{--}30^\circ$, depending on near target position and interocular distance. The monkey received a reward for fixating each target and, to encourage steady gaze, another for maintaining fixation for a random time of 1.5–3.0 s. We averaged eye position and force during the final 600 ms of the fixation period to allow fixation to stabilize and to avoid the pulse and slide components of saccade-related muscle forces (Miller and Robins 1992).

We define *convergence force* as an increment in muscle force related to convergence in excess of the force that maintains a given eye position with convergence relaxed. Thus the motoneuron studies

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's 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 $\pm 12^\circ$ (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 thereby 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.

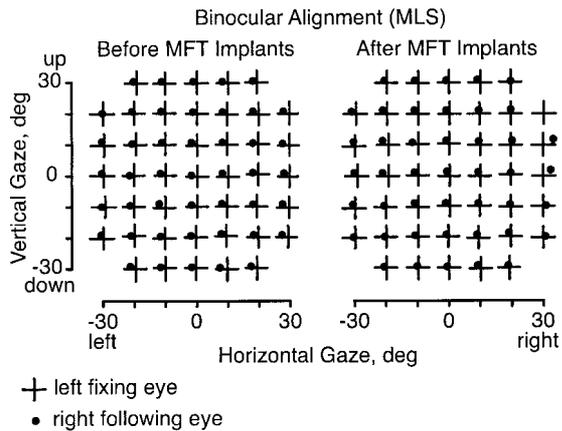


FIG. 5. Binocular alignment before and after MFT installation. With his left, implanted eye viewing, the monkey fixated an array of 45 points, spanning a field $\pm 30^\circ$ horizontal by $\pm 30^\circ$ vertical at 10° increments, with the 4 corner points omitted. +, mean fixations across several days. •, corresponding positions 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 disassociated, 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 ($30^\circ, 20^\circ$) 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 surroundings, so that adaptation would tend to reduce misalignments or restore the preimplant pattern. As Fig. 5 makes clear, implantation-related misalignments were only seen in extreme right gaze. In the region of our vergence measurements, $\pm 20^\circ$ horizontal and vertical, misalignments were no greater than before implantation. Similar results were obtained in the other animals.

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 $5\text{--}35^\circ$. 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 duration increased 17% (18% for abducting and 17% for adducting saccades).

In summary, MFT implantation resulted in small binocular misalignments and restriction but only in extreme gaze, probably 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 expected (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 experiments.

It is worth noting that monkeys in the present study were able to fixate over a $\pm 30^\circ \times \pm 30^\circ$ field, compared with $\pm 20^\circ \times \pm 20^\circ$ 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, secondary to the smaller implant. The new devices were also more reliable, routinely performing well for $\geq 4\text{--}5$ mo after implantation.

Tonic muscle forces

We first measured tonic muscle forces in conjugate gaze for eye positions ranging $\pm 30^\circ$ horizontally and vertically in 10°

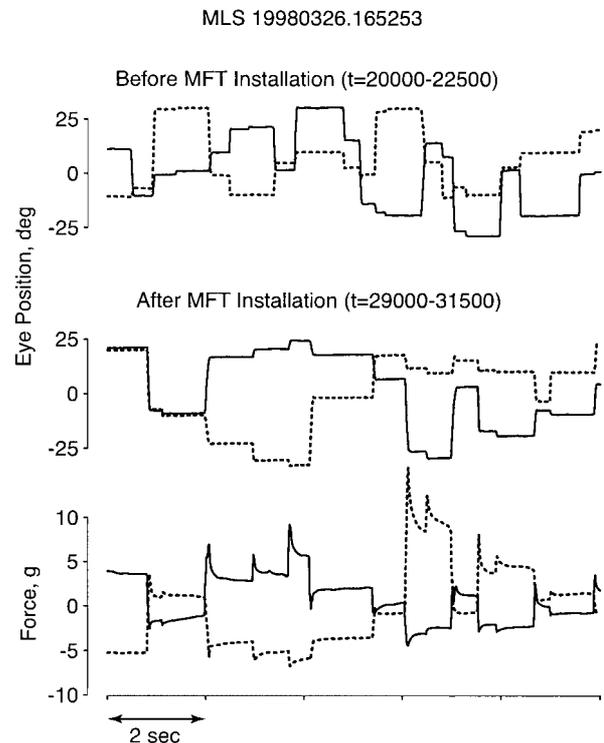


FIG. 6. Saccades before and after MFT installation. Saccades with left eye fixing and right eye covered, to successively lit light-emitting diodes (LEDs) in the calibration array. Both before and after MFT installation, saccades appeared normal, with little evidence of slowing or overshooting. For eye 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.

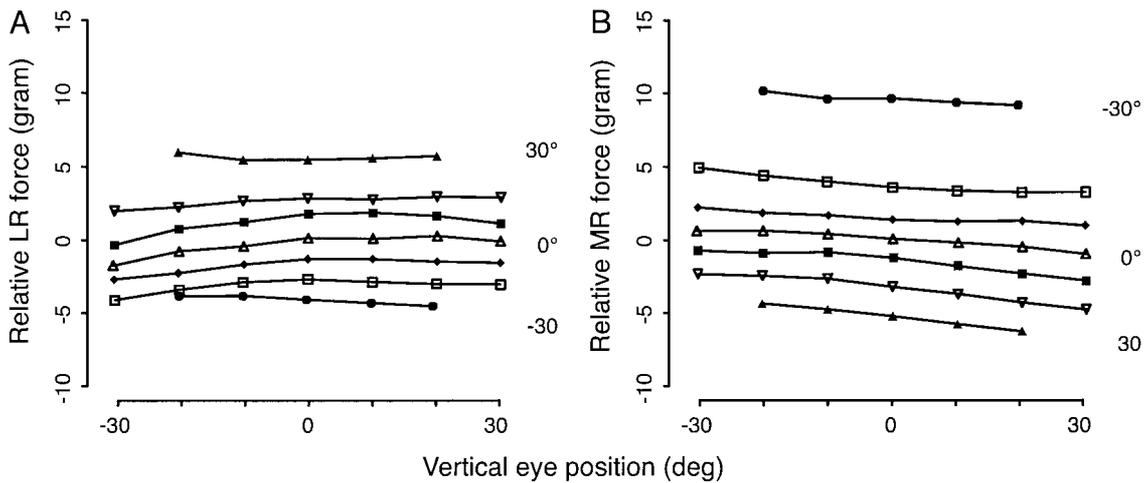


FIG. 7. Average fixation forces for 3 monkeys. Each line shows forces for a horizontal position -30° (adduction) to 30° (abduction) in 10° increments. Muscle forces are relative to the mean force at $(0^\circ, 0^\circ)$, computed within each experimental session. The monkey fixated each of the 45 targets about 100 times over several days. *A*: lateral rectus forces. *B*: medial rectus 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 7*A* 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 7*B* 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.

Figure 8 re-plots the average tonic data to show the antagonistic relationship of MR and LR forces. There is no clear dependence on vertical eye position, particularly in the central 20° . Except for large MR forces (30° adduction), relative MR and LR forces fall close to the line with slope -1 .

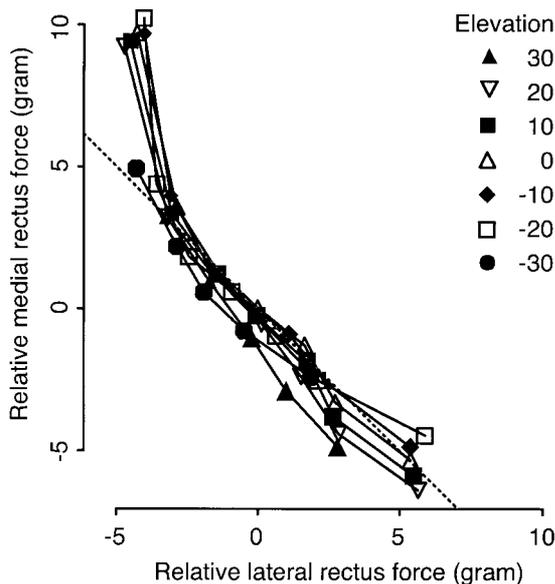


FIG. 8. Antagonistic relationship of medial and lateral rectus (MR and LR) force is shown by plotting MR vs. LR force. Each line with symbols represents a different vertical position component; the interrupted line has slope $= -1$. Forces are expressed relative to those when the animal fixated a target at straight ahead.

Asymmetric vergence

Figure 9*A* 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. 9*A*. Convergence is associated with a small muscle force *decrease*, easily seen in the LR trace. Figure 10*A* shows a similar pattern for *monkey MLS* with MFTs on the left eye.

Figures 9*B* and 10*B* 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 (\bullet , \blacktriangle , \blacksquare) 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, *ERL*, measuring LR and MR forces over an eye-position range of 25° , holding the asymmetric vergence angle at $19.5 \pm 2^\circ$.

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.

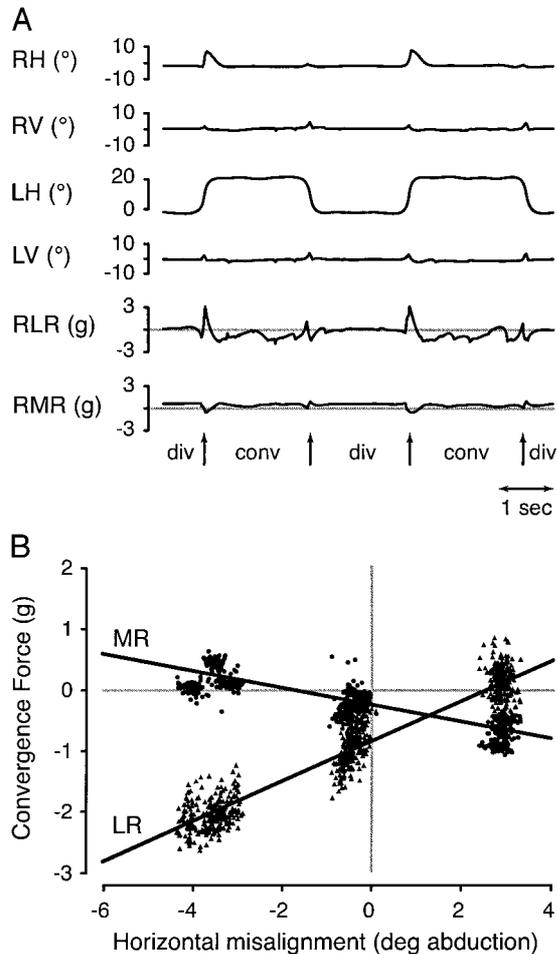


FIG. 9. Asymmetric vergence data for *monkey MRL*. MFTs were on the lateral and medial recti of the aligned right eye. *A*: representative signals. RH, horizontal component of right eye position (rightward +); RV, right eye vertical component (upward +); LH, left eye horizontal; LV, left eye vertical; RLR, right eye lateral rectus muscle force; RMR, right eye medial rectus muscle force. Forces are relative to those at steady fixation of the distant target. Beginnings of convergent ("conv") and divergent ("div") phases are marked with arrows. *B*: representative daily summary. Convergence force, the increase in muscle force when fixating near compared with far targets is plotted as a function of near minus far misalignment of the instrumented eye. Each data point is convergence force of lateral rectus (\blacktriangle) or medial rectus (\bullet), calculated from a pair of consecutive near-far fixations. The central clouds of points, which correspond to fixations of the horizontally aligned near and far targets, have mean horizontal misalignment of about -0.4° . This means that the monkey fixated the near target with his eye 0.4° more adducted than when he fixated the aligned far target, on average. The left and right clouds of points correspond to fixations of left and right offset near targets, respectively, alternating with fixations of the same far target. Straight lines were fit to estimate forces at 0° misalignment (vertical dashed line) for lateral rectus ("LR") and medial rectus ("MR"). It can be seen that, without this calculation, we would have slightly overestimated MR convergence force and underestimated LR convergence force because the monkey did not fixate near and far targets with the same accuracy.

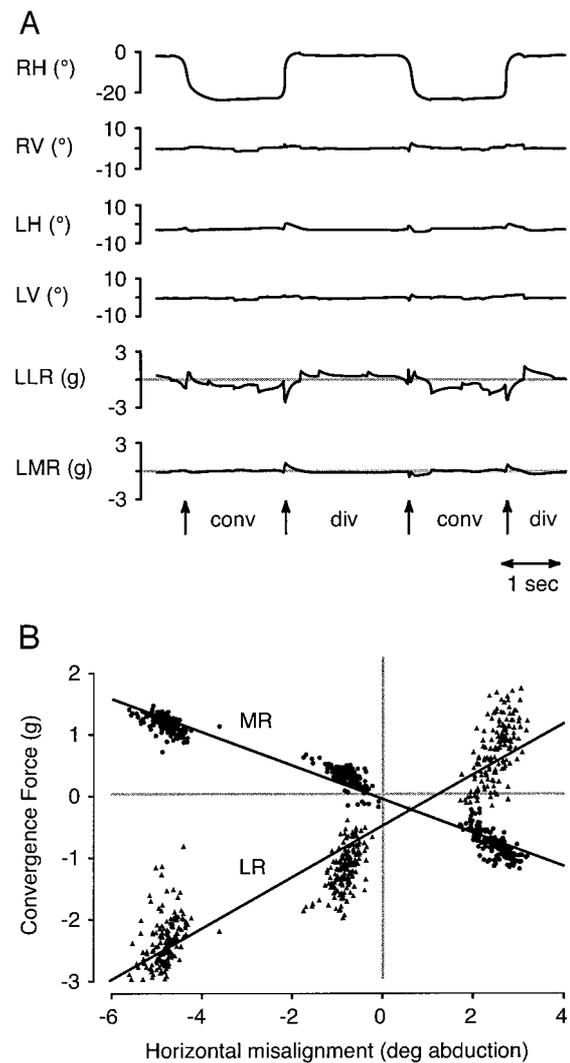


FIG. 10. Asymmetric vergence data for *monkey MLS*. MFTs were implanted on the lateral and medial recti of the left eye. *A*: representative signals. *B*: representative daily summary. Labels are as in Fig. 9.

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

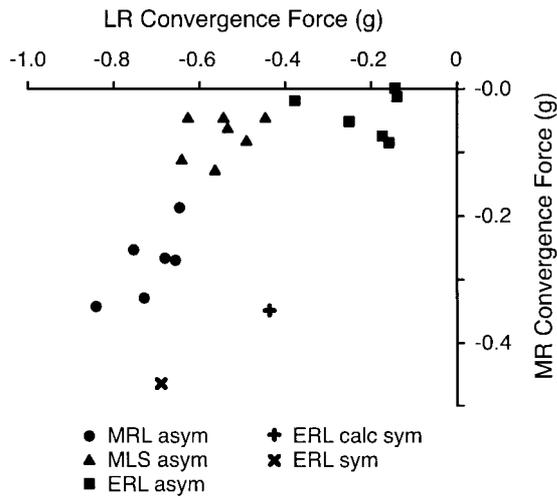


FIG. 11. Convergence force summary. MR convergence force is plotted against LR convergence force (note different scales on the 2 axes). Each point gives LR and MR convergence forces, the force differences for an instrumented eye in the same position fixating near compared with far targets, interpolated as described in connection with Figs. 9B and 10B. Vergence movements were between 20 and 30°, averaging 22°. Asym, data from asymmetric vergence movements; calc sym, symmetric fixation data extracted from asymmetric vergence sessions; sym, data from symmetric vergence movements.

force data for *ERL*, the conjugate change in instrumented eye gaze from 1.0 to -10.6° 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 *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 adducted an average of 9.7° 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° 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 (x) 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

tate almost entirely unimpaired through a 60° 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° into the muscle's field of action, we measured tonic LR forces averaging 180 mg° , and tonic MR forces averaging 323 mg° . Collins et al. (1975) used transducers implanted in series with disinserted human muscles and found mean MR forces averaging 467 mg° 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 $\geq 30^\circ$ (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

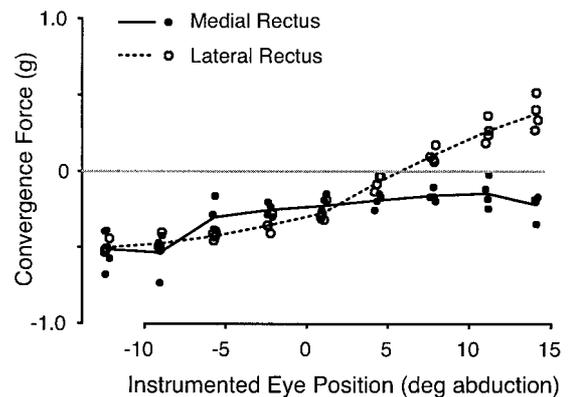


FIG. 12. Convergence forces in asymmetric vergence at different gaze positions. *Monkey ERL* fixated paired target at near (7 cm) and far (200 cm) positions, respectively. Pairs at different horizontal positions were presented (see Fig. 4) to elicit different eye positions while maintaining a convergence angle of about 19.5° . Each point represents mean force difference from far to near fixations within a single experimental session.

function, such as varying intraocular pressure to aid fluid circulation.

Symmetric and asymmetric vergence

The abducens motonucleus 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 adducting conjugate gaze change. From Fig. 7, we expect 11° conjugate adduction to be associated with 2 g decrease in LR force. This predicts that 11° convergent adduction 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 motonucleus 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 motonucleus 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 $\leq 5^\circ$ 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 motonucleus recordings and muscle force measurements because the eyes were never abducted in the motonucleus 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 internuclear 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). Misslisch 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 temporally 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 saccadic 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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REFERENCES

- ALLEN MJ AND CARTER JH. The torsional component of the near reflex. *Am J Optom* 44: 343–349, 1967.
- BARMACK NH. Recruitment and suprathreshold frequency modulation of single extraocular muscle fibers in the rabbit. *J Neurophysiol* 40: 779–790, 1977.
- BONNET A. Sur l'anatomie des aponévroses et des muscles de l'oeil. *Gaz Méd* 9: 108–109, 1841.
- BREININ GM. The nature of vergence revealed by electromyography. II. Accommodative and fusional vergence. *AMA Archs Ophthalmol* 58: 535–549, 1957.
- BRODAL A. *Neurological Anatomy: In Relation to Clinical Medicine*. New York: Oxford, 1981.
- BRUNO P AND VAN DEN BERG AV. Relative orientation of primary positions of the two eyes. *Vision Res* 37: 935–947, 1997.
- BÜTTNER-ENNEVER JA, HORN AKE, SCHERBERGER H-J, AND HENN V. The location of motoneurons innervating slow extraocular eye muscle fibers in monkey. *Soc Neurosci Abstr* 24: 145, 1998.
- CLARK RA, MILLER JM, AND DEMER JL. Three-dimensional location of human rectus pulleys by path inflections in secondary gaze positions. *Invest Ophthalmol Vis Sci* 41: 3787–3797, 2000.
- COLLINS CC, O'MEARA D, AND SCOTT AB. Muscle tension during unrestrained human eye movements. *J Physiol (Lond)* 245: 351–369, 1975.
- DEMER JL. The orbital pulley system—a revolution in concepts of orbital anatomy. In: *Neurobiology of Eye Movements*, edited by Leigh RJ and Kaminsky HJ. New York: New York Academy of Sciences, 2002.
- DEMER JL, OH SY, AND POUKENS V. Evidence for active control of rectus extraocular muscle pulleys. *Invest Ophthalmol Vis Sci* 41: 1280–1290, 2000.
- DONDERS FC. Die Bewegung des Auges, veranschaulicht durch das Phaenophthalmotrop. *Arch Ophthalmol* 16: 154–175, 1870.
- ENRIGHT JT. Ocular translation and cyclotorsion due to changes in fixation distance. *Vision Res* 20: 595–601, 1980.
- ENRIGHT JT. The remarkable saccades of asymmetrical vergence. *Vision Res* 32: 2261–2276, 1992.
- FUCHS AF AND LUSCHEI ES. Firing patterns of abducens neurons of alert monkeys in relationship to horizontal eye movement. *J Neurophysiol* 33: 382–392, 1970.
- FUCHS AF AND LUSCHEI ES. Development of isometric tension in simian extraocular muscle. *J Physiol (Lond)* 219: 155–166, 1971.
- GAMLIN PD, GNADT JW, AND MAYS LE. Abducens internuclear neurons carry an inappropriate signal for ocular convergence. *J Neurophysiol* 62: 70–81, 1989.
- GOLDBERG SJ, MEREDITH MA, AND SHALL MS. Extraocular motor unit and whole-muscle responses in the lateral rectus muscle of the squirrel monkey. *J Neurosci* 18: 10629–10639, 1998.
- GOLDBERG SJ, WILSON KE, AND SHALL MS. Summation of extraocular motor unit tensions in the lateral rectus muscle of the cat. *Muscle Nerve* 20: 1229–1235, 1997.
- GOLDSTEIN HP AND ROBINSON DA. Hysteresis and slow drift in abducens unit activity. *J Neurophysiol* 55: 1044–1056, 1986.
- JAMPEL RS. Multiple motor systems in the extraocular muscles of man. *Invest Ophthalmol* 6: 288–293, 1967.
- JUDGE SJ, RICHMOND BJ, AND CHU FC. Implantation of magnetic search coils for measurement of eye position: an improved method. *Vision Res* 20: 535–538, 1980.
- KELLER EL AND ROBINSON DA. Absence of a stretch reflex in extraocular muscles of the monkey. *J Neurophysiol* 34: 908–919, 1971.
- KELLER EL AND ROBINSON DA. Abducens unit behavior in the monkey during vergence movements. *Vision Res* 12: 369–382, 1972.
- KING WM, ZHOU W, TOMLINSON RD, McCONVILLE KM, PAGE WK, PAIGE GD, AND MAXWELL JS. Eye position signals in the abducens and oculomotor nuclei of monkeys during ocular convergence. *J Vestibul Res* 4: 401–408, 1994.
- LEMON R. Theoretical background to recording and stimulation in conscious animals. In: *Methods for Neuronal Recording in Conscious Animals*, edited by Lemon R. Chichester, UK: Wiley, 1984, p. 35–36.
- MAYS LE AND PORTER JD. Neural control of vergence eye movements: activity of abducens and oculomotor neurons. *J Neurophysiol* 52: 743–761, 1984.
- MAYS LE, PORTER JD, GAMLIN PD, AND TELLO CA. Neural control of vergence eye movements: neurons encoding vergence velocity. *J Neurophysiol* 56: 1007–1021, 1986.
- MAYS LE, ZHANG Y, THORSTAD MH, AND GAMLIN PD. Trochlear unit activity during ocular convergence. *J Neurophysiol* 65: 1484–1491, 1991.
- MILLER JM. Functional anatomy of normal human rectus muscles. *Vision Res* 29: 223–240, 1989.
- MILLER JM. No co-contraction during convergence. *Soc Neurosci Abstr* 24: 1499, 1998.
- MILLER JM, BOCKISCH CJ, PAVLOVSKI DS, AND SCHMIDT EK. No co-contraction during convergence (Abstract). *Invest Ophthalmol Vis Sci* 40: S772, 1999a.
- MILLER JM, PAVLOVSKI DS, AND SHAMAEVA I. *Orbit 1.8 Gaze Mechanics Simulation*. San Francisco, CA: Eidactics, 1999.
- MILLER JM AND ROBINS D. Extraocular muscle sideslip and orbital geometry in monkeys. *Vision Res* 27: 381–392, 1987.
- MILLER JM AND ROBINS D. Extraocular muscle forces in alert monkey. *Vision Res* 32: 1099–1113, 1992.
- MILLER JM AND ROBINSON DA. A model of the mechanics of binocular alignment. *Comput Biomed Res* 17: 436–470, 1984.
- MISSLISCH H AND TWEED D. Neural and mechanical factors in eye control. *J Neurophysiol* 86: 1877–1883, 2001.
- MOK D, RO A, CADERA W, CRAWFORD JD, AND VILIS T. Rotation of Listing's plane during vergence. *Vision Res* 32: 2055–2064, 1992.
- NATIONAL RESEARCH COUNCIL. *Guide for the Care and Use of Laboratory Animals*. Washington, DC: National Academy Press, 1996.
- OPTICAN LM AND ROBINSON DA. Cerebellar-dependent adaptive control of primate saccadic system. *J Neurophysiol* 44: 1058–1076, 1980.
- PORTER JD, BAKER RS, RAGUSA RJ, AND BRUECKNER JK. Extraocular muscles: basic and clinical aspects of structure and function. *Surv Ophthalmol* 39: 451–484, 1995.
- RASHBASS C AND WESTHEIMER G. Independence of conjunctive and disjunctive eye movements. *J Physiol (Lond)* 159: 361–364, 1961.
- ROBINSON DA. A method of measuring eye movement using a scleral search coil in a magnetic field. *IEEE Trans Biomed Electron* 10: 137–145, 1963.
- ROBINSON DA. Eye movement control in primates. The oculomotor system contains specialized subsystems for acquiring and tracking visual targets. *Science* 161: 1219–1224, 1968.
- ROBINSON DA. Oculomotor unit behavior in the monkey. *J Neurophysiol* 33: 393–403, 1970.
- ROBINSON DA. Oculomotor control signals. In: *Basic Mechanisms of Ocular Motility and Their Clinical Implications*, edited by Lennerstrand G and Bach-y-Rita P. Oxford: Pergamon, 1975a, p. 337–392.
- ROBINSON DA. A quantitative analysis of extraocular muscle cooperation and squint. *Invest Ophthalmol* 14: 801–825, 1975b.
- ROBINSON DA. Control of eye movements. In: *Handbook of Physiology. The Nervous System. Motor Control*. Bethesda, MD: Williams and Wilkins, 1981, p. 1275–1320.

- ROBINSON DA, O'MEARA DM, SCOTT AB, AND COLLINS CC. Mechanical components of human eye movements. *J Appl Physiol* 26: 548–553, 1969.
- SCHILLER PH. The discharge characteristics of single units in the oculomotor and abducens nuclei of the unanesthetized monkey. *Exp Brain Res* 10: 347–362, 1970.
- SKAVENSKI AA AND ROBINSON DA. Role of abducens neurons in vestibuloocular reflex. *J Neurophysiol* 36: 724–738, 1973.
- SPENCER RF AND PORTER JD. Structural organization of the extraocular muscles. *Rev Oculomot Res* 2: 33–79, 1988.
- STEFFEN H, WALKER MF, AND ZEE D. Rotation of listing's plane with convergence: independence from eye position. *Invest Ophthalmol Vis Sci* 41: 715–721, 2000.
- TAMLER E AND JAMPOLSKY A. Is divergence active? An electromyographic study. *Am J Ophthalmol* 63: 452–459, 1967.
- TAMLER E, JAMPOLSKY A, AND MARGE E. An electromyographic study of asymmetric convergence. *Am J Ophthalmol* 46: 174–182, 1958.
- ZHOU W AND KING WM. Premotor commands encode monocular eye movements. *Nature* 393: 692–695, 1998.