Objectives
At the conclusion of this program, participants will be able to:
1. Describe the anatomy of the extraocular muscle pulleys.
2. Explain the kinematic function of the extraocular muscle pulleys.
3. Describe the functional specializations of the orbital and global layers of the extraocular muscles.

CME Questions
1. True or false: The rectus extraocular muscles pull from their origins in the annulus of Zinn, directly toward their insertions on the sclera.
   a. True
   b. False
2. Which statement concerning the rectus extraocular muscle pulleys is correct?
   a. The rectus pulleys are composed of rings of cartilage.
   b. The rectus pulleys are rigidly attached to the walls of the orbit.
   c. Each rectus pulley receives an insertion from the global layer fibers of its rectus extraocular muscle.
   d. The global layer fibers of the extraocular muscles do not insert on the pulleys.
   e. The rectus pulleys shift to allow the rectus muscles to follow the shortest paths over the globe during gaze shifts.
3. Which statement concerning the orbital layers of the extraocular muscles is correct?
   a. The primary function of the orbital layers is to control the direction of force application by extraocular muscles.
   b. The orbital layers exhibit primarily phasic activity during saccades.
   c. The primary function of the orbital layers is visual fixation.
   d. The orbital layers have low vascularity, barely greater than the connective tissue pulleys.
   e. The primary function of the orbital layers is in convergence.

History. The stereotypic structure and location of the orbital connective tissues have long been known. The idea that these tissues might control extraocular muscle (EOM) paths was proposed in the late nineteenth century, when Sappey applied the French word *poulie* to their function of bowing EOM paths. The concept was promptly forgotten, displaced by the idea that EOM actions were fully determined by the geometry of their origins and insertions. In the 1970s, attempts by biomedical engineers to calculate predicted results of strabismus surgery based on known geometry of the globe and EOM insertion failed without constraints on the EOM paths, about which nothing was then known. In a groundbreaking paper in 1989, Miller used magnetic resonance imaging (MRI) to assess EOM paths, cross sections, and contractile changes with gaze. Based on the surprising finding that posterior EOM paths remain stable even during large gaze shifts, Miller made the first proposal of the modern notion of *pulleys*, muscle sheaths at and posterior to the globe equator and coupled to the orbital wall so to constrain rectus EOM paths. The further demonstration by Miller et al. that posterior EOM paths remain stable even after surgical transposition of the scleral insertions provided compelling evidence for existence of pulleys. Pulleys have since proven fundamental to ocular motility.

Structure of Pulleys. Rectus pulleys probably escaped earlier recognition because their mechanical necessity was unappreciated, and because of technical problems in the study of orbital anatomy. Removal of soft tissues from the orbit, particularly piecemeal at dissection, severely distorts connective tissue relationships normally maintained by a mutual distribution of elastic and muscular tension against dense adhesions to the bony orbit. Pulleys are easily missed at dissection and microscopy unless the entire orbit is maintained intact, or unless noninvasive imaging is employed. Motivated by the compelling MRI evidence of the existence of pulleys, we undertook the process of serially sectioning intact human and animal orbits for histological processing and ultimate digital reconstruction at microscopic resolution. This effort has demonstrated consistent anatomy of the pulleys and orbital connective tissues across species as diverse as rat, rabbit, dog, horse, monkey, and human.

The following general properties of pulleys have emerged. Each rectus pulley consists of a sleeve and ring of collagen in Tenon’s fascia, linked to the orbital wall, adjacent EOMs, and equatorial Tenon’s fascia by sling-like bands containing collagen, elastin, and richly-innervated smooth muscle. Ultrastructure of pulley collagen reveals specialization for high internal rigidity. Pulleys inflect rectus and inferior oblique (IO) EOM paths in a similar manner to the inflection of the superior oblique (SO) tendon path by the trochlea, although the rectus pulleys are less rigid. As might have been expected from the classically understood uniformity of orbital connective tissue structure, the coronal plane location of each rectus...
pulley as determined by MRI is highly uniform in normal subjects. Pulleys are arrayed in the coronal plane roughly as the ends of the arms of a cross. It was classically noticed that the EOMs insert not only on the globe via their tendons, but on the enveloping connective tissues of Tenon’s capsule. Later histological examinations revealed that the fibers of the orbital layer (OL) of each rectus EOM terminate on the connective tissue. The global layer (GL) of each rectus EOM, containing about half of the EOM fibers, passes through the pulley and becomes contiguous with tendon to insert on the globe; the OL, containing the remaining roughly half of the EOM fibers, inserts on the pulley. In simple terms, GL fibers rotate the globe, while OL fibers translate their respective pulleys to control the direction of globe rotation.

**Kinematics.** In 1989 Miller first suggested that orbitally-fixed pulleys would make the eye’s rotational axis dependent on eye position. This insight that pulleys constrain ocular torsion has proved pivotal. Rectus pulleys are important to ocular kinematics, the rotational properties of the eye. Successive rotations of an object are not mathematically commutative in that final eye orientation depends on the order of rotations. Furthermore, angular velocity differs from the rate of change of orientation; angular velocity is a function of both the time derivative of and instantaneous value of orientation. Each combination of horizontal and vertical orientations of a general sphere could be associated with infinitely varied torsional positions. The eye, however, is constrained (with the head upright and immobile) by a relationship known as Donder’s Law, stating that there is unique torsion for each combination of horizontal and vertical eye positions. Listing’s Law, a specific case of Donder’s Law, states that ocular torsion in any orientation is the torsion the eye would have if it had reached the orientation from primary position by a single rotation about an axis lying in a plane, Listing’s plane. Tweed and Villis showed that Listing’s Law is always satisfied if the ocular rotational axis shifts by half of the shift in ocular orientation. For example, if the eye elevates by 20°, then the vertical axis about which it rotates for subsequent horizontal rotation should tip back by 10°. This is called the “half-angle rule.” It can be shown mathematically that conformity to the half angle rule renders successive ocular rotations effectively commutative to motor control centers in the brain. This property of commutativity is the important feature of the pulley system for neural control of ocular movement.

A direct test of the role of rectus pulleys in half angle kinematics provided by MRI of EOM paths in some cases can directly demonstrate that the EOM path anterior to the pulley inflects by half the angle of eye position. The muscle’s pulling direction, defined by the direction of the segment anterior to the inflection at its pulley, changes by half the gaze change. The rotational axis, which is perpendicular to the path of the terminal segment, also changes by half the gaze change. It is seen from small angle trigonometry that to achieve this each rectus pulley must be located as far posterior to globe center as the scleral insertion is anterior to globe center. This arrangement compels the EOM to exhibit half angle kinematics consistent with Listing’s Law. All four rectus EOMs behave identically. Since the rotational axis of each muscular force acting on the globe observes half angle kinematics, ocular rotation conforms to Listing’s Law.

Inflections in rectus EOM paths due to pulleys are not dependent on presence of the globe at all. In fact, after surgical enucleation of the globe for choroidal melanoma, the MR path inflection at its pulley continues to shift anteroposteriorly with horizontal gaze, but the angle of inflection sharpens to as much as 90° at the pulley.

Appropriate pulley location can implement half angle kinematics during shift between primary and secondary gaze positions that are trigonometrically small angles typical of the oculomotor range. The distance from pulley to globe center need only be equal to distance from globe center to scleral insertion for each rectus EOM. If primary and secondary gaze positions were the only ones ever required, the rectus pulleys could be rigidly fixed to the orbit in the proper position. However, tertiary gaze positions such as adducted supraduction require the rectus pulleys to shift anteroposteriorly in the orbit along the EOM’s length, so that the relationship of pulley to globe center to insertion is maintained in an oculocentric reference.

**Active Pulley Hypothesis.** Evidence of posterior shifts of pulley tissues during rectus EOM contraction obtained in humans by MRI motivated proposal of the active pulley hypothesis (APH) that these shifts are generated by the contractile activity of the OLs of each EOM acting against the elasticity of the pulley suspensions. Specific action of the IR OL to shift the IO pulley can be demonstrated in vivo using MRI in a quasisagittal plane parallel to the IR’s path. In the IR, the OL and GL are often demarcated by a bright fatty septum. The GL is in continuity with the scleral insertion, exhibiting modest contractile thickening in infoduction. The OL terminates in the region of the coupled IR and IO pulleys, exhibiting marked contractile thickening in infoduction associated with straightening of associated connective tissue bands as the IO muscle shifts posteriorly. The coordinated control postulate of the APH is a conjecture for kinematics conforming to L1. Under coordinated control, the rectus pulleys shift anteroposteriorly in the orbit by the same distance as the scleral insertion, while remaining stable in the transverse direction. Quantitative confirmation of this behavior has been obtained for each of the four rectus EOMs in living humans by using MRI to locate the path inflections corresponding to the pulleys.
Even during coordinated movements, however, ocular rotations by the GL and pulley translation by the OL require fundamentally different EOM actions and neural commands. The mechanical load on the GL is predominantly the viscosity of the relaxing antagonist EOM, a load proportional to the speed of eye rotation, and thus slight during sustained eccentric gaze. The mechanical load on the OL, however, is mainly the elasticity of the pulley suspension. This elastic load is independent of rotational speed, but proportional to the angle of eccentric gaze. Selective electromyography (EMG) in humans shows pulse activity in the GL during rapid saccadic eye movements, with only small step change in activity in sustained eccentric gaze. In the OL, EMG shows high step activity in eccentric gaze, but no pulse during saccades.

**Muscle Compartmentalization.** Differing mechanical loads on the OL and GL are associated with corresponding structural, vascular, genomic, and metabolic specializations. Within individual people, GLs of each of the rectus EOMs contain similar numbers of fibers, ranging from 8,000 to 16,000. This similarity is appropriate, since all four rectus OLs rotate the globe, and the globe has considerable symmetry. Within individuals, the number of OL fibers varies more widely from 7,000 to 14,000, numerically in proportion to the amount of connective tissue suspending each pulley. Most OL fibers are fast, twitch-generating, singly-innervated fibers (SIFs), while 10% are slow, non-twitch MIFs having a broad range of fatigue resistance. Orbital SIFs are specialized for intense oxidative metabolism and fatigue resistance. Vascularity in the OL is so much higher than in the GL that intravenous MRI contrast can be seen to perfuse the OL first. The high metabolism, fatigue-resistance, and luxurious blood supply of the numerous OL SIFs are tailored to their continuous elastic loading by the pulley suspensions. About 90% of GL fibers are fast, twitch-generating SIFs, while 10% are slow, non-twitch MIFs having a broad range of fatigue resistance. The motor nerve arborization for the OL is distinct from that of the GL for all four human rectus EOMs. Motor unit size is exceedingly fine in the GL, averaging about one axon per muscle fiber for each of the four human rectus EOMs. This probably reflects the precision required of ocular rotation. Motor unit size is coarser in the OL, averaging five fibers per axon in horizontal rectus and 2.5 in vertical rectus EOMs. Coarser OL motor unit size probably reflects less required precision for pulley control.

**Oblique Muscles.** The rectus EOMs by themselves seem capable of implementing this rich spectrum of ocular kinematics, even leading some to suppose that the oblique EOMs might be unnecessary to Listing’s Law behavior. However, the vestibulo-ocular reflex (VOR) and convergence do not conform to Listing’s Law. The oblique EOMs are Listing’s Law violators.

The IO muscle also observes half angle kinematics. Histological examination of human and monkey orbits indicates the IO inserts on the conjoined IO-IR pulleys, as well as the LR pulley. In primary position these two OL insertions constrain the distal segment of the IO to lie in the plane of the IR and LR pulleys, so that IO rotational axis is perpendicular to the primary gaze line, and perpendicular to the rotational axes of the rectus EOMs. In the Listing’s coordinate system of the pulleys, the IO then has a purely torsional action, capable of nothing other than violating Listing’s Law. (In other coordinate systems such as the clinical one, the IO would also have supraducting and abducting actions.) With oblique gaze shift from supraducted adduction to infraducted abduction, the IO pulley moves anteroposteriorly by half the amount of the equal movements of the IR pulley and scleral insertion. The half coupling of IO pulley to IR pulley motion in turn causes half angle shift of the IO rotational axis. Following similar reasoning, during horizontal gaze shift this anteroposterior IO pulley shift is also half the amount of the equal movements of the LR pulley and scleral insertion. Anteroposterior shift of the IO pulley during vertical and horizontal ductions fulfills the kinematic requirements of commutativity, albeit without direct contribution to Listing’s Law.

The SO, with its immobile trochlea, is special. The remote location of the SO insertion from the trochlea implies that this pulley cannot, as do the other five soft pulleys, stabilize SO tendon path by preventing sideslip over the globe. Instead, the broad shape of the SO insertion on the sclera resists sideslip as it courses from the narrow trochlea. The SO nevertheless approximates half angle kinematics because its path spans the diameter of the globe. Since the distance from trochlea to globe center is approximately equal to the distance from globe center to insertion, the SO rotational axis shifts by half the gaze angle during horizontal duction. An analogous geometry provides a similar effect for vertical duction.

**Kinematics of Convergence.** In addition to horizontal convergence, stereopsis requires torsional adjustments to maintain alignment of corresponding retinal meridia. Observed excyclotorsion in convergence violates Listing’s Law. During asymmetrical convergence to a target aligned to one eye, both the aligned and converging eyes extort, independent of eye position. A concise description of this behavior is that Listing’s plane for each eye tilts temporally with convergence, and the binocular extension of Listing’s Law. A form of Herring’s Law of equal innervation probably exists for the vergence system, such that both eyes receive symmetric vergence commands for remote targets, and mirror symmetric vergence commands for near targets.
Convergence to a target aligned to one eye has been performed in an MRI scanner using a mirror arrangement. The experiment confirmed and extended to humans the finding in monkeys that the horizontal rectus EOMs do not co-contract in convergence. In the orbit aligned to the target, analysis of IR, MR, and SR muscle paths demonstrated extorsional shift of their pulleys in the coronal plane during 22° convergence. Although the lacrimal gland prevented determination of LR pulley location, it is likely that all four rectus pulleys shifted extorsionally about 1.9°. This amount is similar to estimates of globe extorsion under these conditions. These findings suggest that during convergence, the rectus pulley array rotates in the coronal plane in coordination with ocular torsion. One consequence of this binocular pulley array extorsion is vertical misalignment of the horizontal pulling directions of the horizontal rectus EOM pairs. Unless the brain adjusted cyclovertical EOM innervation to compensate for this misalignment, this finding predicts that other eye movements superimposed on convergence will become vertically misaligned in the two eyes. This prediction has been confirmed for the horizontal angular VOR, evoked by transient, whole body yaw rotation in darkness. While the vertical positions of the two eyes remain matched during the VOR for distant viewing, during 22° convergence in central gaze the adducting eye elevates slightly above the adducting eye. Simple, fixed pulley shifts during convergence do not account for the temporal tilting of each eye’s Listing’s plane specified in the binocular extension of Listing’s Law. Temporal tilting during convergence seems most consistent with variable torsional reconfiguration of the rectus pulley array with vertical gaze: extorsion in downward gaze and intorsion in upward gaze, that should concomitantly further misalign the pulling directions of the rectus EOM pairs. This prediction has also been confirmed for the horizontal angular VOR, evoked by transient, whole body yaw rotation in darkness. Vertical skewing of the horizontal angular VOR during convergence increases significantly when the target is moved downward 20° from the center, but reverses significantly when the target is moved upward 20°.

Examination of orbital microanatomy suggests how the rectus pulleys shift in convergence. The OL of the IO muscle inserts on the IR pulley and, at least in younger specimens, also on the LR pulley. Contraction of the IO OL would directly produce an extorsional shift of the LR pulley and IR pulleys, and MRI has directly demonstrated corresponding IO contraction during convergence. Inferior LR pulley shift could be coupled to lateral SR pulley shift via the dense connective tissue band between them. The OL of the SO muscle inserts on the SO sheath posterior to the trochlea, with both the tendon and sheath reflected at that rigid pulley. Anterior to the trochlea, the SO sheath inserts on the SR pulley’s nasal border. Although not directly demonstrated by MRI, relaxation of the SO OL during convergence is consistent with single unit recordings in the monkey trochlear nucleus, and could contribute to extorsional shift of the pulley array. The inframedial peribulbar smooth muscle might also contribute to rectus pulley extorsion in convergence.

Histological evidence for mechanical intercouplings among rectus pulleys is supported by in vivo MRI showing small but stereotypic shifts in the coronal plane positions of some rectus pulleys even during non-converged, visually guided eye movements. The IR pulley shifts nasally in supraduction, and temporally in infraduction, consistent with mechanical coupling to the IO. Also consistent with action of the IO, the LR pulley shifts inferiorly in supraduction, and superiorly in infraduction. These shifts do not have any known visual function, but allow experimental testing of the role of pulleys in binocular alignment. The pattern of vertical LR pulley shift in supraducted gaze to a distant target produces extorsion of the pulley arrays of the two orbits qualitatively identical to the effects of convergence in central gaze, leading to a similar prediction concerning vertical skewing of the horizontal angular VOR. When looking up during the VOR, the adducting eye is predicted to elevate significantly above the adducting eye, with the reverse true when looking down. This is the opposite of vertical gaze shift on the pattern of skewing of the horizontal angular VOR during convergence. Magnetic search coil recording in humans undergoing transient, whole body yaw rotation in darkness confirms this prediction of significant vertical skewing of the horizontal angular VOR during distance viewing, and that the pattern is opposite the pattern observed during convergence. The evidence supports the notion that neural control of the VOR does not compensate for deviations of rectus pulleys from the Listing’s Law kinematic positions.

**Kinematics of the Vestibulo-ocular Reflex.** Altering head orientation relative to gravity evokes the ocular tilt reaction, the static torsional VOR. Gravitational stimulation of the otoliths by sustained 90° head tilt induces counterrolling of the eyes around the visual axis of 3 – 7°. MRI scanning in right and left lateral decubitus positions shows a mean 3.4° difference in conjugate torsional position of the rectus pulley array consistent in direction with the ocular counter-rolling. This reconfiguration is associated with appropriate contractile changes in the cross sections of the IO and SO muscles. Recordings of the preferred ocular directions of burst neurons in monkeys are compatible with torsional shift of rectus pulleys during ocular counterroll induced by static head tilt. In monkeys the displacement plane for 3-D eye positions during pursuit and saccades also shifts.
opposite to changes in head orientation.\textsuperscript{58} Taken together, these observations strongly suggest that brainstem motor and pre-motor neurons that control rectus EOMs do not explicitly compute or compensate for changes in pulling directions produced by rectus pulley shifts. Neural commands to the rectus EOMs are effective only in the context of instantaneous pulley geometry, and so pulley position probably modulates the neural control of all types of eye movements.

Listing’s Law could theoretically be achieved without a contribution from the oblique EOMs.\textsuperscript{35} In patients with chronic SO paralysis, for example, Listing’s Law is observed, but with a temporal tilting of Listing’s plane.\textsuperscript{59, 60} It has been pointed out that even if the oblique EOMs did not actively participate in generation of visually-guided eye movements conforming to Listing’s Law, the passive elastic tensions arising from stretching and relaxation of the obliques would lead to violations of Listing’s Law unless oblique innervations were adjusted to compensate.\textsuperscript{61} Consequently, single unit neural recordings of changes in oblique EOM innervations during eye movements conforming to Listing’s Law (such as pursuit tracking\textsuperscript{62}) would not negate the contribution of pulleys, nor would observed dynamic violations of Listing’s Law during saccades in SO\textsuperscript{49} or IO palsy. Additional mechanical contributions from the oblique EOMs are essential to the VOR, which ideally produces compensatory ocular rotations along axes identical to those of externally imposed head rotations, independent of eye orientation. An ideal VOR should therefore violate the half angle requirement of Listing’s Law and instead follow a “zero angle” rule. Depending upon species, the VOR is observed to follow something between a zero and quarter angle rule, closely correlated with the strength of the torsional VOR.\textsuperscript{63} While the horizontal and vertical angular VORs are nearly perfectly compensatory for head rotations, the torsional VOR has a much lower gain.\textsuperscript{63} Pulley repositioning due to the VOR explains why heal tilt alters the Listing’s plane for both saccades and pursuit,\textsuperscript{64} keeping the sensory coordinate system of the torsionally rotated retina in register with the pulling directions of the EOMs.

**Overview of Kinematics and Neural Control.** The following general concepts are useful if oversimplified. All EOMs have pulleys implementing half angle behavior to achieve commutative kinematics. For visually guided eye movements with the head upright and stationary, this results in Listing’s Law. In special situations non-Listing’s Law ocular torsion is advantageous: in convergence, torsion facilitates stereopsis, and for the VOR, torsion facilitates retinal image stability during head motion. Rectus pulley reconfiguration coordinated with ocular torsion maintains commutative ocular kinematics even during violations of Listing’s Law. The binocular misalignments resulting from disconjugate pulley array torsion are typically small enough to be compensated by fusional vergence during normal vision.

The retina, and consequently much lower level central visual processing, provide a two dimensional (2-D, horizontal and vertical) representation of the world. The ability to perform central ocular motor control in 2-D rather than 3-D is highly simplifying but consistent with single unit neural recordings. In the superior colliculus, saccade targets are encoded in 2-D, implying that any computation of a third dimension, such as torsion, is accomplished downstream.\textsuperscript{32, 65, 66} Even in the oculomotor nucleus and rostral interstitial nucleus of the medial longitudinal fasiculus, saccade targets are encoded in 2-D, implying that any computation of a third dimension, such as torsion, is accomplished downstream.\textsuperscript{32, 65, 66} The foregoing analysis indicates that during visually-guided eye movements, the pulley system renders horizontal and vertical eye position commands essentially commutative,\textsuperscript{32} at the same time achieving ocular torsion conforming to Listing’s Law. The angular VOR consists of relatively simple brainstem circuits receiving input from 3-D sensory organs in the inner ear. Non-commutativity of the angular VOR\textsuperscript{68} is appropriate to the non-commutativity of the physiological stimulus, head rotation. During self-rotation, rectus pulley re-configuration, coordinated with ocular torsion, violates Listing’s Law as required to stabilize images on the retina. Rectus pulley reconfiguration might also occur during ocular torsion associated with voluntary gaze shifts involving both eye and head movements, also achieving stability of images on the retina at the end of the gaze shift,\textsuperscript{66} and in a more complex way during simultaneous activation of the angular and linear VORs.\textsuperscript{69}

Rectus pulley reconfiguration during convergence appears to be a binocularly symmetrical function of both the convergence and vertical gaze angles,\textsuperscript{50} and indirect evidence suggests it also depends on visual features.\textsuperscript{49} Central processing of vergence commands must include explicit specification of torsion and therefore the ocular motor commands during vergence must include all three degrees of freedom. Perhaps the greater complexity of 3-D vergence processing as compared to 2-D processing of monocular visually-guided eye movements underlies the susceptibility of the binocular system to misalignment. This clinically relevant topic is addressed in the second lecture.

**Answers to CME Questions**

1. b
2. d
3. a
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References

45. Minken AWH, Van Gisbergen JAM. A three-dimensional analysis of vergence movements at various levels of elevation. Exp Brain Res. 1994;101:331-345.


56. Demer JL. Magnetic Resonance Imaging (MRI) of human extraocular muscles (EOMs) during the static torsional vestibulo-ocular reflex (VOR). *ARVO Abstr.* 2003;#2736.


