

Double insertions of extraocular rectus muscles in humans and the pulley theory

Gordon L. Ruskell,^{1†} Inga-Britt Kjellevold Haugen,² Jan Richard Bruenech² and Frans van der Werf³

¹Department of Optometry and Visual Science, City University, London, UK

²Department of Optometry and Visual Science, Buskerud University College, Norway

³Department of Neurosciences, Erasmus MC, Rotterdam, The Netherlands

Abstract

Recent studies have promoted the concept that rectus muscles pass through connective tissue pulleys located near the equator of the eye and act, in effect, as the muscle origins. Orbital muscle fibres (facing bone) terminate in pulleys, permitting adjustment of their position independent of the global fibres responsible for rotating the eye. The structure of pulleys (or muscle sleeves) and the passage taken by their muscle fibre insertions are unclear, and a detailed description is presented here together with a review of the active pulley hypothesis. Segments including the full width of single muscles were removed from the full orbital contents of dissection room cadavers and fresh perfusion-fixed rhesus and cynomolgus monkeys and prepared for light microscopy. Thin longitudinal sections were cut as facets from resin-embedded tissue blocks and montages assembled. Interrupted serial sections of selected regions of both species and ultrathin sections of monkey material were prepared for light and electron microscopy, respectively. Slender tendons leave the orbital surface of rectus muscles at intervals, aggregating and entering sleeves in humans and monkey; less frequently, tendons pass from the global surface to sleeves or insert directly in the posterior fascia bulbi. The orbital sides of sleeve rings are continuous with the fascial canopy of the globe and are 5–6 times as thick as the global sides; sleeve structure differs in the four recti. Medial rectus sleeves are the thickest, and contain smooth muscle, whereas little or none is present in the other rectus sleeves. Superior rectus sleeves are variable in structure and relatively insubstantial. A narrow interval separates muscles from the surrounding connective tissue equatorially in some preparations, consistent with a capacity to slide, but the tissues are contiguous in others, especially in monkey material. The structural organization of sleeves and their tendons, together with other presented factors, is inconsistent with a facility for the separate adjustment of sleeve position. The results favour the theory that sleeve tendons have just one role, to counter the viscoelastic resistance of global fascia – ocular and sleeve muscle fibres acting in unison. Whether the fragile sleeve structure can meet the physical demands of pulleys is questionable; but otherwise the veracity of the pulley hypothesis cannot be assessed from the structural relations of muscles and fascia bulbi reported.

Key words extraocular muscle; eye movement; muscle pulleys; muscle sleeves; orbital fascia.

Introduction

Histological examination of rectus muscles has revealed evidence that not all their fibres insert on the globe.

Correspondence

Professor J. Richard Bruenech, Biomedical Research Unit, Department of Optometry and Visual Science, Buskerud University College, PO Box 251, NO-3601 Kongsberg, Norway. T: +47 32869615; F: +47 32869671; E: jan.richard.bruenech@hibu.no

†Deceased.

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Orbital rim fibres, constituting nearly half the total, insert in the orbital side of the fibroelastic Tenon's capsule ensheathing each muscle at the globe and referred to as the pulley or pulley sleeve (Demer et al., 2000; Oh et al. 2001). The orbital rim fibres were distinguished from the global fibres by infiltrating collagenous connective tissue continuous with surface or capsular collagen and anteriorly with the pulleys. Only the global fibres insert in the globe, effecting ocular rotation, while the orbital fibres manipulate the position of the pulleys. Axial magnetic resonance imaging (MRI) scans appeared to confirm the double insertions of the muscles. A similar

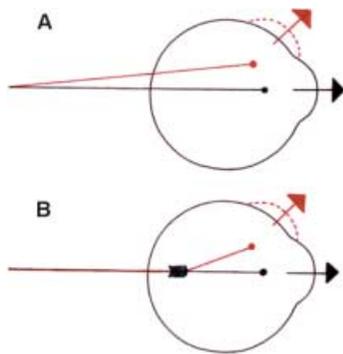


Fig. 1 Schematic representation showing (A) how the extraocular muscles were assumed to slip over the globe during eye rotation as described in the shortest path hypothesis by Boeder (1962) and (B) turning of tendon with no displacement as indicated by Miller (1989) using MRI scans.

arrangement is found in rats (Khanna & Porter, 2001) but otherwise no further reports of double insertions have appeared.

The pulley hypothesis was introduced to explain a revised understanding of muscle disposition during eye rotation. When eyes rotate, extraocular muscles were conventionally assumed to slip over the globe (Fig. 1A), taking the shortest path to their global insertions (Krewson, 1950; Boeder, 1962). This arrangement demands sideways displacement of muscles at the eye, incurring sideslip over the sclera; for example, the lateral rectus would undergo sideslip in vertical gaze and the inferior rectus in horizontal gaze. However, in a detailed theoretical study, Robinson (1975) showed that the shortest path theory would lead to impossibly gross rearrangements of the muscles during gaze changes within the normal range and proposed a model incorporating sideslip restraint and inflection of muscle paths close to the eye. In subsequent studies employing computer tomography (CT) and MRI scans of the orbit in monkey and human subjects, little or no sideways displacement of muscles at the posterior pole was observed when the eye rotated (Simonz et al. 1985; Miller, 1989; Demer et al. 1995), and inflection of the distal ends of muscles was demonstrated (Clark et al. 2000). From these observations it appears that the fascia bulbi forms a harness coupling the anterior muscle sheaths to the globe, limiting sideslip. Miller (1989) argued that muscle sheaths might function as pulleys fixed to the orbital wall, muscle tendons travelling through the pulleys much as the superior oblique travels through the trochlea (Fig. 1B). The notion was adopted by

Demer et al. (1995), who added the role of the dual insertions of muscles permitting movement of pulleys differently from the movement of scleral insertions in formulating the active pulley hypothesis (Demer et al. 2000). In effect, the pulleys act as the muscle origins and, by their adjustment, change the rotational axis of the eye.

The present study was undertaken to seek further evidence of the double insertions and to obtain a high-resolution evaluation of orbital fibre separation from the global fibres and of their insertion into muscle sleeves using thin resin sections longitudinally orientated. The same material is used to describe the structure of pulleys and their connections to supplement existing data based largely on thick coronal section preparations (Demer et al. 1995, 1997; Kono et al. 2002). Some of the results have been published previously in abstract form (Ruskell, 2003).

Materials and methods

All human specimens were obtained from cadavers in conformity with legal requirements. Soft tissues were removed from the orbit and pterygopalatine fossa in one piece from 16 sides of 12 dissection room cadavers taking care to keep the periosteum intact. The cadavers had been fixed from 1 to 3 days after death by perfusion in a mixture containing formalin and methanol. Initial trials indicated that conventional preparation for histological examination using paraffin embedding provided inadequate resolution for the purposes of the study. Consequently, thin sectioning of resin-embedded material was attempted and found to be satisfactory. Whole orbits were cut into anteroposterior quadrants to include a single rectus muscle, the eye quadrant and all connected orbital tissue with the minimum disruption. The apical ends of the quadrants were trimmed to remove the posterior third of the muscles. Quadrants were then cut into two or three longitudinal strips and washed overnight in running tap water, rinsed in distilled water and immersed in 0.5% osmium tetroxide: osmication was used only to facilitate orientating the subsequently embedded blocks of tissue. Thirty muscles were prepared (ten medial rectus, eight lateral rectus, six inferior rectus and six superior rectus). Dehydration in 70%, 90% and absolute ethanol (twice) for a period of 1 day in each solution was followed by immersion in HistoClear for 2 days with one change. Embedding was begun by rotating the slices in Araldite

at room temperature overnight followed by baking in moulds at 60 °C for 2 days. Sections were cut longitudinally at 1- μ m thickness with glass knives of 10-mm width. As the tissues were up to 4 mm or more in width it was necessary to cut facets from the blocks with adjacent facets angled slightly to achieve montages of full sections. Two serial montages were obtained from each slice and a third cut external to muscles to examine intermuscular tissue. In areas of special interest serial sections of single facets were prepared. Sections were stained in a 1% solution of toluidine blue in 2.5% sodium carbonate.

Two sets of transversely sectioned human recti, one medial the other lateral, cut and retained as an interrupted series, were available from stock and found to be satisfactory for the present study. They were obtained following orbital exenteration for a maxillary tumour and immersion fixed in a solution similar to that used for monkeys.

Three young cynomolgus (*Macaca fascicularis*) and two rhesus (*Macaca rhesus*) monkeys were used in the study, four of which had undergone surgery for severance of the ophthalmic nerve intracranially in preparation for another study as described earlier (Ruskell & van der Werf, 1997). The mandibular nerve had been sectioned intracranially in a fifth animal. The surgical procedures were considered not to disqualify animals for the present work. Animals were sedated parenterally with 2–3 mg kg⁻¹ ketamine and anaesthetized with 15–25 mg kg⁻¹ Sagatal (pentobarbital sodium) given intraperitoneally and injected with the anticoagulant heparin sodium (1500 IU). External jugular veins and inferior vena cavae were cut and a 2% glutaraldehyde, 3% paraformaldehyde cacodylate-buffered solution (pH 7.4) was perfused through the left ventricle of the heart. Heads were stored in fixative at 4 °C and dissected while immersed in a buffered sucrose solution. Medial and lateral rectus muscles and associated tissues were prepared in the same manner as the human tissues except that muscles were processed in one piece. The tissues were post-fixed in 1% unbuffered osmium tetroxide, processed for light microscopy in the same manner as the human material. For electron microscopy, 50–80-nm-thick sections were cut with a diamond knife and mounted on unfilmed copper grids. These were immersed in a saturated solution of uranyl acetate in 30–70% ethanol for 20 min, washed and immersed in 0.4% lead citrate in 0.1 N sodium hydroxide for 10 min.

Results

Double insertions

In human preparations, slender groups of fibres extended from the orbital surface of muscles and passed forward towards the fascia bulbi. The first fibres branched from muscles 12–19 mm from their scleral insertions or 0–3 mm from the posterior pole of the globe or more in the case of the superior rectus (5–6 mm). Further fibres passed from the muscles at intervals, accumulating in stacks before merging into a compact collagenous mass of the muscle sleeve, continuous with the fascia bulbi. Occasionally clear evidence that the fibres were indeed muscle tendons became apparent and they will be referred to as sleeve tendons to distinguish them from the scleral tendons of the globe. Sleeve tendons were often followed through interrupted serial sections over a thickness of at least 500 μ m, indicating that some arose as laminae rather than as discrete fibres. Single muscle fibres, or sometimes two or three, continued for a short distance into tendons as they left the surface of the muscle, confirming their identity, and significantly, putative tendons observed without a muscle fibre in a section were seen to contain one in the same tendon in another, indicating a common identity. Less frequently, thicker tendons carried bundles of muscle fibres. Where this occurred the muscle fibres persisted in the tendon for up to 1 mm and the generating muscle fibres sometimes could be traced back an equal distance into the fabric of the muscle itself. Tendons containing muscle fibres were found in all preparations sectioned serially. Sleeve tendons were regularly more frequent and thicker in the horizontal recti in humans.

A few delicate fibres, rather than advancing to the sleeves, are angled acutely, away from the muscle axis, into the surrounding fat. They make sparse junctions with neighbouring fibres and with the periosteum and were regarded as contributors to the system of septa enclosing orbital fat.

Sleeve tendons also issued from the global aspect of muscles, sharing the same characteristics of the orbital tendons but were variable in thickness and regularly less substantial. They again showed single, sometimes two or three, muscle fibres within tendons and one example of fibre bundle entry was found in an inferior rectus muscle; in some preparations muscle infiltration of the tendons was not found but otherwise they shared common characteristics of sleeve tendons. The

staggered tendons often aggregated to form a single thin lamina before inserting in the fascia bulbi lining the back of the globe but, not infrequently, they joined the fascia separately. The fibres represent the global sleeves, and dense collagen, typical of orbital sleeves, was rarely present in medial recti and absent from the others.

In horizontal recti of both monkey species the pattern of sleeve tendons issuing from the orbital surface was similar to that observed in human muscles. Tendons separated from the muscle surface less frequently, tending to aggregate in apposition to muscles, and interposed fat laminae were less common or absent. Single muscle fibres or fibre bundles entered the tendons where they shortly terminated. Orbital sleeve tendons of the medial rectus were thicker than those of the lateral rectus. Again, tendons were found issuing from the global side of muscles with the occasional entry of single but not groups of muscle fibres.

Monkey material, being better preserved, permitted a more detailed examination of the sleeve tendons and at the muscle surface each tendon fibre was of regular width, its boundary typically delineated by fibroblast processes and stacked in parallel arrays aligned with the muscle fibres. Closer to the globe as they were displaced from the muscle surface by the input of further tendons, regularity was lost and the less frequent fibroblasts took a sinuous course. However, the light microscopic appearance was, in part, misleading as rather than the expected regular parallel arrays of collagen fibrils their ultrastructure revealed a variety of orientations, some parallel and others oblique to the muscle surface, suggesting that tendon fibres may not take the shortest course to the sleeve.

Muscle sleeves (pulleys)

Medial rectus

The composition of the muscle sleeves was different in the four recti and will be described separately. In humans, on receipt of tendons the part of the sleeve on the orbital side, i.e. the orbital sleeve, is initially slender, dense, composed of collagen, and sometimes split by one or two interposed laminae of fat. Sleeves thicken gradually to a maximum of 2.9–4.5 mm (mean 3.3 mm, $n = 10$) opposite the equator of the globe, becoming fibroelastic in composition and complex in form. Numerous islands of smooth muscle were present,

interrupted by numerous small lacunae filled with fat. The size and shape of the lacunae differed between specimens and the amount of smooth muscle differed approximately three-fold. The smooth muscle consisted of well-spaced bundles of 10–50 fibres predominantly arranged longitudinally in some specimens, transversely in others, but in most the bundle orientation was mixed. Distally, the sleeve diminished sharply, a thin loose fibrous extension continuing towards the conjunctiva. The plica terminated in a sharp free edge, but in some preparations it was a blunt fold and in others the plica was not seen, the sections being cut above the level of its root. Externally, lacunae widened and were broken, the diminished matrix continuing to the periosteum as slender ligaments – the suspensory or check ligaments. The strongest ligaments swept forward behind the orbicularis muscle and turned back to reach the periosteum. The sleeve was 9–15 mm in length and in every specimen it had become separated from the globe (Fig. 2A,B).

The sleeve on the global side, the global sleeve, was a fraction of the thickness of the orbital sleeve, reaching a maximum thickness of 0.2–0.9 mm (mean 0.4 mm, $n = 10$) at its reflection onto the fascia bulbi. Opposite the reflection, in comparison, the orbital sleeve reached a thickness of 1.4–3.7 mm (mean 2.2 mm, $n = 10$). The sleeve was composed of a lamina of packed fibres often enclosing a strip of fat cells. Transition from tendon to the dense matrix characteristic of the orbital sleeve was found in only two sleeves: lacunae and smooth muscle were not present.

In monkeys, as in humans, the dense orbital sleeve increased in thickness after receipt of its tendons, reaching a maximum opposite the equator where its uniform structure was interrupted externally by small fat-filled lacunae, centrally by a plate of cartilage and internally, adjacent to the scleral tendon, by two or three slender laminae. Thin ligaments extended beyond the lacunae, passing forward then sweeping back adjacent or close to the orbicularis muscle to attach to the periosteum, similar to the human ligaments. The laminae were contiguous with the sclera-inserting tendon but in some preparations a narrow space was interposed between the two structures. The cartilage plate, buried anteriorly in the dense connective tissue of the sleeve, was about 100 μm thick, of half moon shape, its straight anterior border opposite the root of the prominent plica and its posterior border convex. Thin longitudinally orientated bundles of smooth muscle were

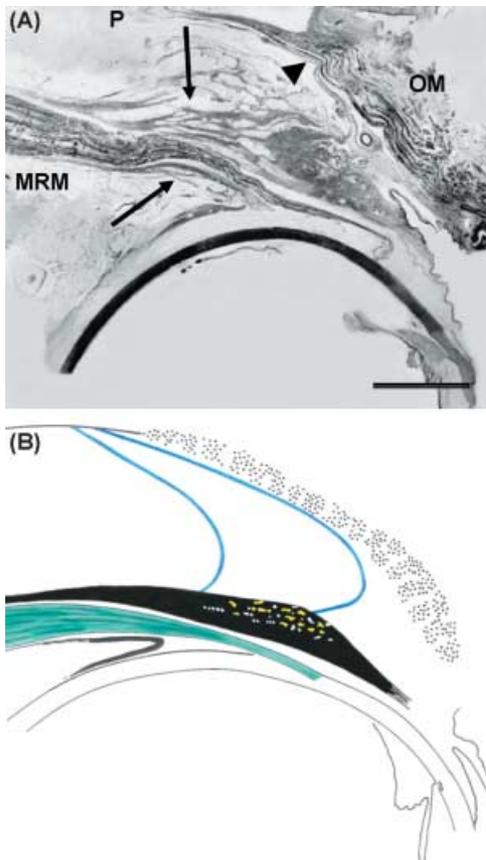


Fig. 2 (A) Photomontage of human medial rectus muscle (MRM). Fibres branch off from the orbital surface of the muscle (superior arrow) before merging into a compact collagenous mass of the muscle sleeve. The matrix diminishes and continues to the periosteum (P) as slender ligaments – the suspensory or check ligaments (arrowhead). Less substantial sleeve tendons issue from the global aspect of the muscle (inferior arrow) and reflect before inserting in the fascia bulbi. OM, orbicularis muscle. Scale bar = 5 mm. (B) Schematic representation of the medial rectus muscle as seen in A. Opposite the posterior pole the global and orbital sleeve thickness ratio is 1 : 6. Equatorially, the orbital sleeve thickens further to form a dense plate containing smooth muscle (yellow) and small lacunae filled with fat (white). The plate is attached to the orbital wall by fine ligaments (blue) looping behind the orbicularis muscle (stippled) to reach the periosteum.

regularly embedded in the sleeve adjacent to and aligned with the plate and also proximal to its convex border, but muscle fibres were few compared with those of human sleeves. A small nictitans gland was interposed between the plate and the plica and beneath the plate inferiorly. At its widest part the plate measured 1.6–1.9 mm, occupying at least one-third of the length of the sleeve. The global sleeve was much thinner and lacked the complexity of the orbital sleeve.

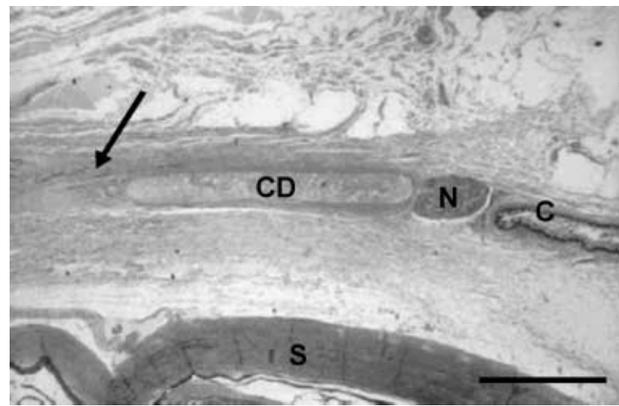


Fig. 3 Micrograph of the medial rectus muscle in monkey showing thin longitudinally orientated bundles of smooth muscle (arrow) embedded in the sleeve adjacent to the cartilage plate (CD). A small nictitans gland (N) is interposed between the plate and the conjunctiva (C). S, sclera. Scale bar = 400 μ m.

As in humans, it was composed of packed tendons and reflected at the globe posteriorly, continuous with the fascia bulbi (Fig. 3).

Adherence of orbital tendons to the surface of muscles, noted above, continued at the level of the sleeve. Similarly, the sleeve tendons on the global aspect remained adherent until they reflected onto the fascia lining at the back of the globe. The reflection occurred several millimetres behind the position of the insertion of the scleral tendon, and the narrow space between tendon and globe was either free of tissue or contained scattered short fibres. In some preparations a space was present between sleeve tendons and muscle either at intervals or throughout. In adjacent sections on the same microscope slide, some displayed full adherence, others a narrow fissure, the apposed layers linked by fine fibrous filaments bridging the space, suggesting that the fissure was attributable to manipulation of the sections.

Lateral rectus

At its junction with tendons, the orbital sleeve in humans was similar to the medial rectus sleeve, increasing in thickness, but without the formation of fat-filled lacunae and rarely with embedded smooth muscle. Only two of eight sleeves contained smooth muscle consisting of one or two small bundles, but other smooth muscle was found in five preparations in the form of the superior palpebral muscle (of Müller) lying almost in contact with the sleeves. External to the palpebral

muscle, encapsulated lobules of the lacrimal gland separated by the aponeurosis of the levator palpebrae superioris muscle were regularly present. The sleeve gradually thinned and became less dense, a slender extension terminating opposite the fornix. Ligaments, thicker than those of the medial rectus, either passed back obliquely or took an arcuate course behind the orbicularis muscle to attach the sleeve to the periosteum. In contrast, the global sleeve had relatively little substance, consisting of a few slender tendons joining the fascia bulbi separately without forming a dense matrix. It measured 0.2–0.4 mm (mean 0.26 mm, $n = 8$) in thickness at the globe where, at the same level, the orbital sleeve measured 0.9–1.6 mm (mean 1.3 mm), increasing to a maximum of 2.2 mm opposite the equator. Shortly after their formation the tendons were separated from the muscle by a narrow space that was maintained throughout the sleeve on both sides (Fig. 4A,B).

In monkeys the sleeve tendons were fewer and the sleeves thinner than in the medial rectus. A thin lamina of fat, no more than one cell in thickness, separated the tendons in some preparations but neither smooth muscle nor the auxiliary structures characteristic of the medial rectus sleeve were present. The orbital sleeves remained adherent to the muscle and the lengthy scleral tendon in most preparations but a space appeared at intervals in others. The global tendons, typically slender, followed a similar pattern. Fine suspensory ligaments bridged the narrow space between the sleeve and the periosteum. The space between globe and periosteum was very narrow compared with that seen in humans and the suspensory ligaments were commensurately short.

Superior rectus

The fine and widely dispersed orbital tendons advanced between the rectus and the levator muscle above and were received by a sleeve differing in structure between specimens. In some, it consisted of a relatively insubstantial flat oval body of dense, transversely orientated fibroelastic tissue measuring about 0.5 mm anteroposteriorly and containing one or more small bundles of smooth muscle fibres. The junction between tendons and sleeve was abrupt, unlike the gradual transition typical of the horizontal recti. The dense sleeve is known as the intermuscular transverse ligament or the inferior ligament of Whitnall (Lukas

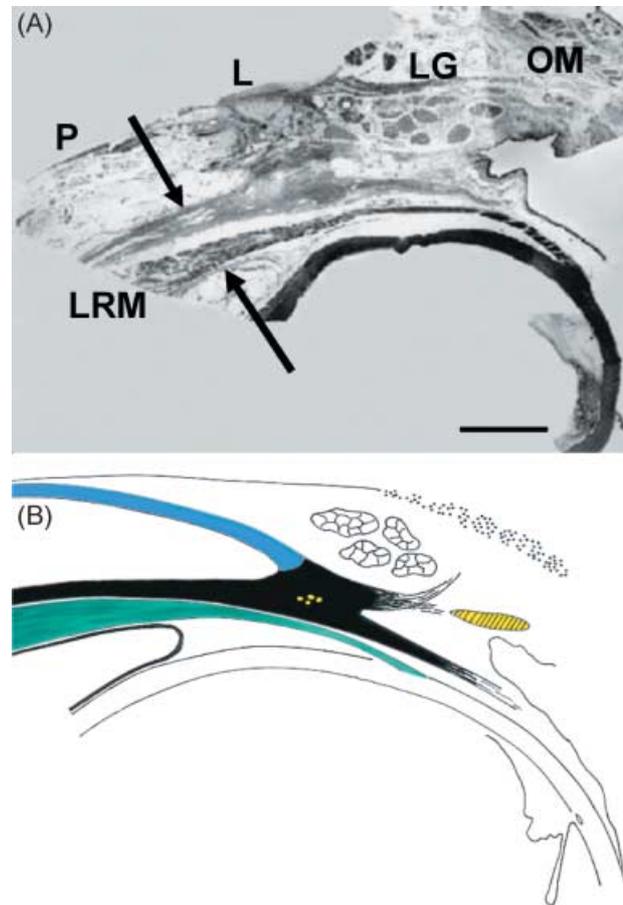


Fig. 4 (A) Photomontage of human lateral rectus muscle (LRM) showing fibres orbital and global fibres merging into the muscle sleeve (superior and inferior arrow, respectively). The distal portion of the orbital sleeve becomes thinner and slender extensions terminate opposite the fornix. Ligaments (L) attach the sleeve to the periosteum (P). Encapsulated lobules of lacrimal gland (LG) are interposed between the orbital sleeve and the orbicularis muscle (OM). Scale bar = 5 mm. (B) Schematic representation of the lateral muscle as seen in A. Opposite the posterior pole the orbital/global sheath thickness ratio is 5 : 1. The orbital sheath doubles in thickness at the equator. The sleeve is attached to periorbital by one or more strong ligaments (blue). There is little or no smooth muscle other than tarsal muscle (yellow).

et al. 1996). In three of six specimens the structure of the sleeve was singular in being composed of an open mesh of fibres only slightly thicker than the attached tendons and possessing no smooth muscle. It bore little resemblance to the other sleeves. Being overlapped by the levator muscle, its position precludes the possibility of ligament attachment to the periosteum; only a few fragile fibrous connections were noted between the two muscles. Thin fibrous laminae extended from the sleeve anteriorly, directed towards the fornix of the

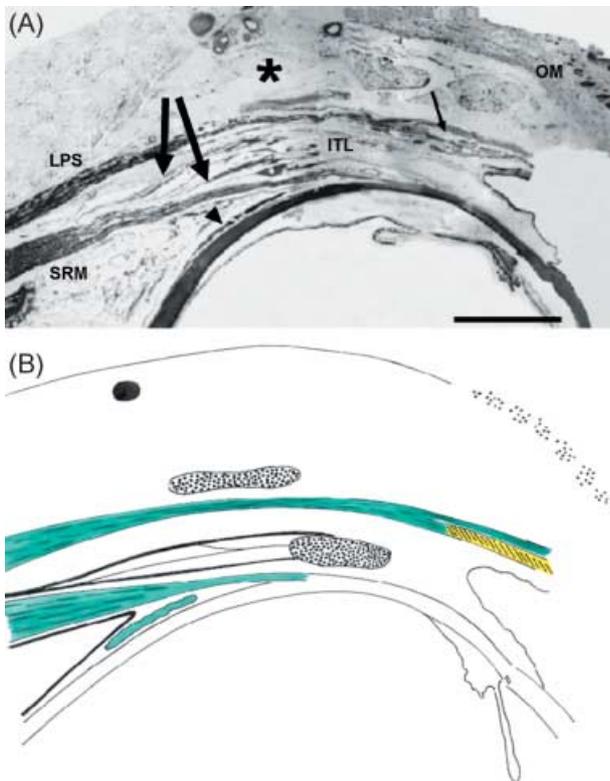


Fig. 5 (A) Photomontage of human superior rectus muscle showing strands of orbital tendons (thick arrows) advancing between the superior rectus muscle (SRM) and levator palpebrae superior muscle (LPS) before blending with the dense intermuscular transverse ligament (ITL). Small arrow indicates the position of the superior tarsal muscle. Asterisk, Whitnall's ligament; OM, orbicularis muscle; arrowhead, superior oblique. Scale bar = 5 mm. (B) Schematic representation of the superior rectus muscle as seen in A. Global sheath is delicate and the orbital sheath divides into several discrete bands that insert into the intermuscular transverse ligament. There are no direct attachments to the orbital wall. No smooth muscle is present other than superior tarsal muscle (yellow).

conjunctiva. The global arm of the sleeve was very thin (< 0.2 mm), consisting of the grouped tendons that joined the fascia bulbi without modification (Fig. 5A,B). A space was present between both sides of the sleeve and the muscle in all specimens.

Inferior rectus

The sleeve differs again from those of the horizontal muscles, sharing some of the characteristics of the superior rectus sheath. Whereas orbital tendons of the horizontal muscles become compacted well before they reached the sheath opposite the myotendon, those of the inferior rectus remain separate almost to

the equator, one or two of them becoming well separated from the muscle to pass beneath the inferior oblique. The majority passed between the inferior rectus and the inferior oblique terminating in the dense sleeve varying from 7 to 11 mm in length and containing a few fat-filled lacunae or laminae. Its lower surface was smooth and no ligaments passed from it to the periosteum. A thin layer of smooth muscle, the inferior palpebral muscle of Müller, lined its upper surface anteriorly close to the fornix. Fibrous extensions passed forward to the bulbar conjunctiva and the fornix but most entered the palpebral conjunctiva, joined by the fibres passing beneath the inferior oblique, as the so-called capsulopalpebral ligament. Its fibres terminated at the margin of the inferior tarsal plate. The orbital tendon sleeve thus represents the posterior margin of the suspensory ligament of Lockwood. The global tendon sleeve was thin and fibrous, composed of the aggregated tendons, measuring up to 0.3 mm in thickness and therefore slightly thicker than that of the superior rectus (Fig. 6A,B). A space was present between the tendon and sleeve inferiorly but the global tendon sleeve displayed fibrous continuity with the muscle – quite the reverse of the superior rectus data.

Discussion

Double insertions

The present results confirm and extend the observation of Demer et al. (2000) that orbital fibres of rectus muscles separate from the global fibres and insert in the muscle sheath and that they are unlikely to contribute significantly to ocular rotation. The continuity of tendons to sleeve from their separation from the main muscle mass to the insertion into the sleeve is shown for the first time. Identifying muscle tissue in the fibres leaving the muscle surface is unequivocal evidence that they are tendons and, by tracing forward, that they insert into muscle sleeves. Examples were noted in every muscle examined and putative tendons could often be traced back within the substance of muscles and related to specific groups of muscle fibres. It is unlikely that all the fibrous structures leaving muscles anteriorly represented tendon, such as those that turned away from the muscle towards the periosteum remote from the globe. Both cynomolgus and rhesus monkeys possess a similar split insertion of the recti to that of humans and coupled with the positive results in

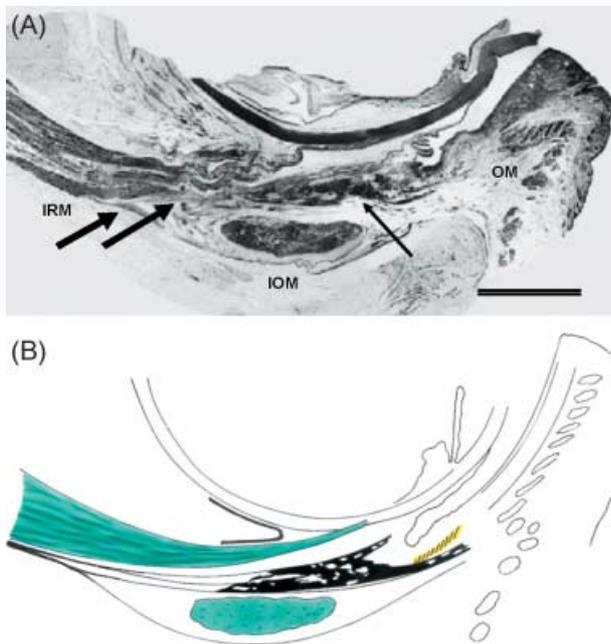


Fig. 6 (A) Photomontage of human inferior rectus muscle (IRM) showing orbital tendons advancing between the inferior rectus and the inferior oblique muscle (IOM) while a minority of them pass under the inferior oblique (superior and inferior black arrows, respectively). The global tendon is thin and fibrous. Thin arrow indicates Lockwood's ligament. OM, orbicularis muscle. Scale bar = 5 mm. (B) Schematic representation of the inferior rectus muscle as seen in A. The global sheath is delicate and the thicker orbital sheath forms several discrete strands that insert into the suspensory ligament of Lockwood (triangular-shaped black structure). There are no direct attachments to the orbital wall. Smooth muscle is not present other than inferior tarsal muscle (yellow).

rats (Khanna & Porter, 2001) it appears that the feature may be common among mammalia.

The observation of sleeve tendon issuing from global fibres in both humans and monkey was unexpected and contrary to a recent report in which they were claimed to be absent (Oh et al. 2001). This negative finding was based on quantitative studies of the total fibre population of human and monkey recti viewed in transverse section. The orientation used, less helpful than longitudinal sections, and their lower frequency could account for their being missed. Given that sleeves receive insertions from both global and orbital fibres, the variety of fibre classes involved is potentially greater than stated in earlier studies. Most of the orbital fibres are of the singly innervated twitch variety and approximately 20% are multiply innervated non-twitch fibres (Porter et al. 1996). The fatigue-resistant twitch variety is favoured for the role of maintaining

tension against the elastic pulley suspensions (Demer et al. 2000; Oh et al. 2001). As there are four further recognized fibre types in the global part of rectus muscles (Porter et al. 1996) the variety of fibres inserting on the sleeves will be enhanced and the possibility that specific fibre classes are utilized in sleeve manipulation distinct from those mediating ocular rotation is discounted.

Orbital fibres comprise about 40% of the total population in each of the rectus muscles and all of them are considered to insert on sleeves (Demer et al. 2000; Kono et al. 2002). The present results permit agreement that large numbers of fibres are involved but a precise figure could not be determined from the longitudinally orientated sections. The added contribution of global fibres inserting on sleeves suggests that the figure may be higher but, on the other hand, although orbital fibres may be absent from the anterior part of muscles (Oh et al. 2001) whether all their tendons leave the muscle for the sleeve is uncertain.

Structure of sleeves and their suspension

The longitudinal sections provide another view of the muscle sleeves to add to the coronal sections widely used hitherto, and a feature of particular interest and largely neglected in earlier studies is revealed, i.e. the orbital and global halves of the sleeves are significantly different in thickness. The global side of the sleeve of the horizontal recti is only one-fifth or one-sixth the thickness of the orbital side measured in the same frontal plane. Kono et al. (2002) reported a difference in the thickness of the orbital and global parts of the sleeves while analysing their tissue content but, except for the superior rectus, the differences noted were very small compared with the present results. Global sleeves of the four recti, measured from three cadavers, were 0.5–1.75 mm thick (mean 1.2) for the medial rectus compared with 0.2–0.9 mm (mean 0.4) in the present study and a mean of 1.65 mm for the lateral rectus compared with 0.2–0.4 mm (mean 0.26). A similar disparity of the two aspects of the sleeve was present in monkeys. Neither chance variation nor the greater age of the present group are likely to account for the marked difference in the results but the connective tissue structures constituting the sleeves may have been interpreted differently or sampled at different positions. The examples shown in the figures, clearly revealing the disparity, are representative. If they act as pulleys,

the global aspect of the sleeves appears surprisingly frail to withstand the mechanical stress of obliquely angled muscle passage. This comment applies to all the recti but the structure of the superior rectus sleeve demands further comment because of its questionable overall stability. In those instances where an intermuscular transverse ligament was present it could be argued that an adequate physical presence is available to meet the requirements of a pulley, although the ligament has a fraction of the bulk of the other sleeves. A similar argument could not be made in those instances where a wide mesh of fibres was present rather than the ligament.

The longitudinal sections permitted a clear representation of the structure and contours of the ligament attaching muscle sleeves to the periosteum of the orbital wall. They were delicate, as Koornneef (1977) observed to his surprise, having understood them to be thick stout bands according to earlier published descriptions of check ligaments. The strongest of the ligaments take an arcuate course, passing forward then looping back behind the orbicularis muscle to attach to the periosteum. Their shape suggests a capacity to change position, straightening to facilitate backward displacement of a contracting muscle or forward displacement with contraction of an antagonist. Passive displacement of the ligaments was considered to be an integral part of the concept of their role to constrain muscles preventing over-contraction, as indicated by the increased range of excursion of the globe after severance of a check ligament (Whitnall, 1932; Scobee, 1948; Dimitrova et al. 2003). However, the sleeves or pulleys to which the ligaments are attached receive the insertion of nearly half of each of the rectus muscle fibres (Demer et al. 2000), consistent with the present report and, presumably, may be displaced by muscle force.

Pulley hypothesis

Given that rectus muscles are not displaced at the globe during rotation but that tendons are inflected, the active pulley hypothesis states that the distal ends of muscles slide through sleeves, the pulley in effect acting as the muscle origin, and that their position may be separately adjusted through the action of the orbital fibres, changing the axis of rotation. The attraction of the theory is that theoretically, pulley positions could be manipulated in such a way to comply with Listing's

law, i.e. any eye orientation can be reached by rotation about a single axis lying in a single plane, Listing's plane. In support of this contention, ocular kinematics were modelled mathematically to demonstrate that the neural control of saccades and the implementation of Listing's law may be greatly simplified provided that the pulleys are correctly placed (Quaia & Optican, 1998). A graphical representation based on anatomical findings and MRI data was presented with a plausible arrangement of pulleys for compliance with Listing's law for principal and possibly oblique rotations (Demer et al. 2000). Other graphics were used to account for torsion associated with convergence and for the particular kinematics of VOR (Vestibulo-ocular reflexes) (Demer et al. 2000; Thurtell et al. 2000), but subsequently the latter was argued not to require pulley adjustment (Misslisch & Tweed, 2001).

Clearly, the validity of the active pulley hypothesis rests on the evidence for muscle slide and appropriate adjustment of the position of pulleys. These two items will be discussed in the context of the present observations. First, what is the evidence for sliding?

Separation of the distal ends of muscles from their sleeves seen in most of the human preparations is helpful to the notion that they are free to slide. But equally, their separation may be attributed to artefacts imposed by the rigors of preparation coupled with different densities of tissues. The freshly perfusion-fixed monkey material offered an improved chance of preserving the normal relationship between structures, but separation again sometimes occurred. However, more commonly, the connective tissue housing the tendon vessels merged imperceptibly with that of the orbital sleeves offering no indication that sliding could occur. This relationship was observed commonly in the medial and lateral recti of both rhesus and cynomolgus monkeys. Similarly, when the human orbit and its contents were sectioned whole and suitably embedded the separation was not observed (Koornneef, 1977), and mechanical manipulation of tissue freshly exenterated and untreated from the orbit of patients suggests firm attachment of encircling white connective tissue to the outside of rectus muscles (Simonz et al. 2003). Notwithstanding, separation between muscle and sleeve in much of the present material indicates that, at least, the relationship is weak. The present results must be considered equivocal with regard to the possibility of movement between muscle and sleeve and they illustrate the inadequacy of the anatomical methods used, and

perhaps of any anatomical method, for providing a definitive answer to the question.

Secondly, what is the evidence for the separate movement of the sleeves or pulleys? Muscle sleeves and intermuscular membranes form the largest part of global fascial bulk and they are continuous. Any manipulation of the sleeves will necessarily invoke shifting of the full fascial canopy as the longitudinal sections indicate. Elasticity of a particular orbital sleeve might create a differential pull but the sleeve will not be separately shifted from the canopy as proposed in the pulley hypothesis. The concept of separate movement is more obviously jeopardized by the probable result of traction on the global arm of the sleeve, where the tendons of muscle fibres commonly insert directly on the thin posterior fascia of the globe. As retraction of fascia from the globe is unlikely, the more reasonable result is retraction of the globe itself together with its sleeve. This argument applies to all the recti.

Sleeve tendons of the inferior rectus passed forward to insert into the suspensory ligament of Lockwood, which may be regarded as the muscle sleeve, and the ligament continues forward to the lower eyelid as the capsulopalpebral ligament (Hawes & Dortzbach, 1982; Koornneef, 1988). This represents the mechanism for lowering the eyelid in downgaze, eye and lid movement being tightly linked (Goldberg et al. 1994; Lasudry et al. 1998), and must be considered in conjunction with the oculorotatory duties of the inferior rectus. A facility for separate positioning of the sleeve is unlikely, considering the continuity of dense fibrous tissue, and impractical if both functions are to be adequately served. A similar argument pertains to the superior rectus because, although it does not have responsibility for elevating the upper eyelid, it functions in synchrony with the levator palpebrae in directing gaze (Goldberg et al. 1994; Lasudry et al. 1998). Again, separate manipulation of the sleeve, would potentially prejudice this activity. It should be added that neither the superior nor the inferior rectus sleeve is stabilized by attachment to bone.

If sleeves are to be manipulated by muscles independent of oculorotation then the two functions must be served by differential innervation (Demer et al. 2000). However, the availability of such a mechanism has been questioned as there is no supporting electrophysiological evidence indicating selective recruitment of neurons (Fuchs et al. 1988; Scudder et al. 2002) – presumably pulley adjustment should

precede muscle contraction for a desired rotation. All motoneurons are reported to participate in all types of movements (Scudder et al. 2002) and electromyographic recordings indicate a differential recruitment according to fibre size but not to position within muscles (Collins, 1975). The potentially greater variety of muscle fibre types serving sleeve tendons, implied by the presence of a global fibre contribution, reduces further the potential for selective control of the sleeves.

Role of smooth muscle

The presence of smooth muscle in rectus muscle sleeves suggested to Demer et al. (1995) that it might form part of the mechanism regulating the position of pulleys, although its slow contracting characteristics would appear to render a direct role in saccadic movement regulation unlikely. The largest concentration of smooth muscle is present in the orbital part of the medial rectus muscle sleeve in both human and monkey and the presence of nerves in the region of the sleeves suggested that it may be functional (Demer et al. 1997), but terminals within the muscle were not observed (Porter et al. 1996) nor were they seen in the monkey preparations of the present study. An alternative view is that the smooth muscle is part of a redundant third eyelid either lacking a capacity to contract or contracting ineffectively. This would appear to apply to monkeys because the sleeve, its sequestered cartilage, smooth muscle and nictitans gland represent the full apparatus of the third eyelid. It has a limited function in some mammals such as the cat and none in others such as primates, including all three species studied here. In cats the third eyelid extends across the cornea with contraction of the retractor bulbi muscle and is retracted by the contraction of smooth muscle, although details of control are debated (Acheson, 1938; Thompson, 1961).

Can the connective tissues associated with the medial rectus be regarded as representing a vestigial third eyelid as in monkeys? Generally, only the sleeve and smooth muscle is found in humans but there is good evidence that the cartilage plate (Adachi, 1906) and even the full complement of structures are sometimes present (Giacomini, 1883; Bartels, 1911). Although these data encourage the answer that the plica semilunaris is the exposed part of a third eyelid remnant in humans, the more substantial smooth muscle in

humans compared with monkeys is possibly inconsistent. However, it was noted that the amount of smooth muscle is variable in the human sleeve. As a rough measurement of the differences, the number of smooth muscle bundles was counted in single sections and found to differ three-fold. Similarly, the amount also varied in monkeys. Consequently, the variation may not detract from the tentative conclusion that the muscle is part of a vestigial structure and without function.

There is no question that other smooth muscles in the orbit such as the superior and inferior palpebral muscles are functional, but, on the other hand, the orbital smooth muscle bridging the inferior orbital fissure is arguably another without function. Returning to muscle sleeves, a case can be made for further smooth muscle redundancy.

Smooth muscle in the sleeves of the lateral, superior and inferior recti was regarded as further evidence of sleeve manipulation (Demer et al. 1995). Examples were found in the present study but irregularly. For example, smooth muscle was present in the sleeves of only two of eight lateral rectus preparations but the superior palpebral muscle (of Müller) was also commonly present close by and easily confused with sleeve muscle. Smooth muscle is regularly reported in the inferior rectus muscle sleeve, but as shown, the sleeve is one with the suspensory ligament of Lockwood – the forward extension of which contains the inferior palpebral smooth muscle that is another source of possible confusion. Finally, the superior rectus muscle sleeve is without smooth muscle or it runs transversely in the intermuscular transverse ligament representing the sleeve, an orientation unlikely to influence the antero-posterior position of the ligament (pulley). It is proposed that these instances of irregularly occurring sleeve smooth muscles are also examples of redundancy and may play no part in adjusting sleeve or pulley position.

Finally, each of these comments and observations questioning the existence of a facility for repositioning sleeves in secondary positions of gaze independent of ocular control becomes redundant if direct positive evidence was available. However, sleeve movement has not been satisfactorily demonstrated, although it has been attempted using MRI (Demer et al. 2000). The resolution required is very demanding and even with the clearest images problems remain – for example, distinguishing the diverging orbital sleeve fibres from the sleeves themselves.

If one takes the view that the purpose of the sleeve insertions is to assist in ocular rotation by overcoming resistance of the connective tissue elements surrounding the globe and that to fulfill this purpose both orbital and global fibres act together, then none of the criticisms outlined above applies. If independent adjustment of sleeves does not occur then the determination of ocular kinematics in terms of the active pulley theory appears invalid. The logic of pulley theory as first stated is compelling, proposing a rational application of the peculiar arrangement of muscle inflections but, again, the present findings raise some questions regarding its validity and further examination of the hypothesis is indicated.

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