

**PARTIAL FASCIOTOMY HAS MAJOR EFFECTS ON MUSCULAR
MECHANICS DUE TO ALTERED EPIMUSCULAR MYOFASCIAL
FORCE TRANSMISSION**

by

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ABSTRACT

PARTIAL FASCIOTOMY HAS MAJOR EFFECTS ON MUSCULAR MECHANICS DUE TO ALTERED EPIMUSCULAR MYOFASCIAL FORCE TRANSMISSION

In remedial orthopedic surgery (e.g., aponeurotomy), partial fasciotomy is widely applied; however, is seen as a preliminary step to the main operation only. It is aimed at studying the effects of partial fasciotomy on muscular mechanics on the basis of epimuscular myofascial force transmission. Before (intact condition) and after proximal partial fasciotomy, isometric muscle forces of the rat were measured at proximal and distal tendons of extensor digitorum longus (EDL) muscle as well as at the tied distal tendons of tibialis anterior (TA) and extensor hallucis longus (EHL) muscles in two different conditions: after distal lengthening of (1) EDL exclusively and (2) EDL and TA+EHL muscles simultaneously. Secondary goal was to test the role of increased recovery time on history effects. For EDL lengthening exclusively (1) at lower muscle lengths, partial fasciotomy removed distally directed net epimuscular loads acting on EDL (2) at intermediate and higher lengths, proximally directed epimuscular loads measured in intact condition decreased; however, remained after partial fasciotomy. Moreover, partial fasciotomy caused major changes in EDL length-force characteristics: EDL active forces decreased substantially and muscle optimum length shifted to a higher muscle length distally. Simultaneous muscle lengthening changed intact EDL forces substantially: net epimuscular loads as well as most active and passive forces decreased, optimum length shifted to a lower length and optimal force changed. Added partial fasciotomy caused further force decreases and additional shift of optimum force to a lower length. Increase in recovery time increased the differences between control and actual forces i.e., history effects. Yet, history effects themselves were affected by epimuscular myofascial force transmission: partial fasciotomy reduced the force difference between control and actual forces. We conclude that partial fasciotomy alone has major effects on muscular mechanics which may be highly important for a full control over the outcome of the actual operation.

Keywords: Myofascial force transmission, Partial fasciotomy, Epimuscular load, EDL lengthening exclusively, EDL and TA+EHL lengthening simultaneously

ÖZET

PARSİYEL FASYATOMİNİN KAS MEKANİĞİNE MİYOMAĞDOKUSAL KUVVET İLETİMİNDEKİ DEĞİŞİM SONUCU ETKİLERİ

Eklem hareketini düzeltme hedefli ortopedi cerrahisinde (örneğin aponörotomi) parsiyel fasyatomi sıklıkla kullanılmasına rağmen sadece ana girişim için bir ön işlem olarak görülmektedir. Bu çalışmada parsiyel fasyatominin kas mekaniği üzerine etkilerinin epimüsküler miyomağdoksal kuvvet iletimi temelinde incelenmesi amaçlandı. Sıçan izometrik kas kuvveti, parsiyel fasyatomi öncesi ve sonrası, ekstansör digitorum longus (EDL) kasının distal ve proksimal tendonlarında ve tendonları birbirine bağlanmış olan tibialis anterior (TA) ve ekstansör hallusis longus (EHL) kaslarının distal tendonunda iki ayrı koşulda ölçüldü: (1) sadece EDL kasının ve (2) EDL ve TA+EHL kaslarının birlikte distal uzatılması. Çalışmadaki ikincil amacımız deneysel dinlenme süresinin kas mekaniği geçmişine etkisini test etmektir. Sadece EDL uzatıldığına parsiyel fasyatomi (1) düşük uzunluklarda, EDL üzerine distal yönde etki eden net epimüsküler yükleri ortadan kaldırdı (2) parsiyel fasyatomi sonrası orta ve yüksek uzunluklarda intact durumda ölçülen proximal yöndeki epimüsküler kuvvetler azaldı ancak yok olmadı. EDL aktif kuvvetleri büyük ölçüde azalırken kas optimum uzunluğu distale doğru yüksek uzunluklara kaydı. EDL ve TA+EHL kaslarının birlikte uzatılması intact EDL kuvvetlerini büyük ölçüde değiştirdi: net epimüsküler kuvvetler ile aktif ve pasif kuvvetler pek çok kas boyu için azaldı, optimum uzunluk daha düşük uzunluklara kaydı ve optimal kuvvet değişti. Parsiyel fasyatomi kas kuvvetlerinin daha da düşmesine ve optimum kuvvetlerin düşük uzunluklara kaymasına sebep oldu. Dinlenme süresi artışı kontrol ve gerçel (deney verisi) kuvvetler arasındaki farkı arttırdı. Buna karşın, kas mekaniği geçmişi etkilerinin kendisi de epimüsküler miyomağdoksal kuvvet iletiminden etkilendi: parsiyel fasyatomi kontrol ve gerçel kuvvetler arasındaki farkı azalttı. Tek başına parsiyel fasyatominin kas mekaniği üzerinde büyük ölçüde etkin olduğu ve bu etkileri hesaba katmanın istenen ameliyat sonuçları üzerinde tam bir kontrol sağlamak için önemli olabileceği sonucuna vardık.

Anahtar Kelimeler: Miyomağdoksal kuvvet iletimi, Parsiyel fasyatomi, Epimüsküler yük, Sadece EDL uzatma, EDL ve TA+EHL birlikte uzatma

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LIST OF SYMBOLS

α	Angle
$^{\circ}\text{C}$	Degree Celsius
$F_m(\text{N})$	Muscle Force (Newton)
Δl_{m+t}	Deviation from Optimum Length
$(F_{\text{distal}} - F_{\text{proximal}})$	Proximo-distal Total Force Difference

LIST OF ABBREVIATIONS

n	Number
g	Gram
SD	Standard Deviation
ml	Milliliter
FT	Force Transducer
TA	Tibialis Anterior
EDL	Extensor Digitorum Longus
EHL	Extensor Hallucis Longus
SIA	Anterior Intermuscular Septum
STMISOC	Biopac System Stimulator
ms	Millisecond
Hz	Hertz
mA	Milliamper
mm	Millimeter
SE	Standard Error
ANOVA	Analysis of Variance
μm	Micrometer

1. INTRODUCTION

1.1 Muscle

Muscle is the contractile tissue of the body which produces force (see Fig. 1.1 for hierarchical organization). It is mainly composed of muscle cells (muscle fibers) that contain myofibrils. The myofibrils are suspended inside the muscle fiber in a matrix called sarcoplasm. The sarcolemma is the cell membrane of the muscle fiber. The surface layer of the sarcolemma fuses with a tendon fiber, and the tendon fibers in turn collect into bundles to form the muscle tendons and insert into bone. Individual muscle fibers are surrounded by endomysium. Muscle fibers are bound together by perimysium into bundles called fascicles: the bundles are then grouped together to form muscle, which is enclosed in a sheath of epimysium [1].

Figure 1.1 Diagrammatic breakdown of typical muscle. The figure is modified from Human Kinetics, (2000) [2].

1.2 Fascia

Fascia is a form of connective tissue which provides a supportive environment for muscles, to suspend organs in their proper place, to transmit movement from muscle to the bones they are attached to, and to provide a reinforcing wrapping for nerves and blood vessels as they pass through and between muscles. It varies in thickness, density, composition and mechanical properties.

Three different layers of fascia can be distinguished:

1) *Superficial fascia* is the layer that primarily determines the shape of a body which is composed mainly of loose connective tissue and adipose. It surrounds organs and glands, neurovascular bundles.

2) *Deep fascia* (Fig. 1.1) is the dense fibrous connective tissue that interpenetrates and surrounds the muscles, bones, nerves and blood vessels of the body. It provides connection and interaction in the form of aponeuroses, ligaments, tendons, retinacula, joint capsules, and septa. The deep fasciae envelop all bones and blood vessels and become specialized in muscles (epimysium, perimysium, and endomysium).

3) *Visceral fascia* suspends the organs within their cavities and wraps them in layers of connective tissue membranes [3].

1.3 Structure of Muscle Fibers

Myofibril (Fig. 1.2) contains myosin (thick) filaments and actin (thin) filaments, lying side-by-side, which are protein molecules that are responsible for muscle contraction. The light bands that contain only active filaments are called I bands. The dark bands contain the myosin filaments as well as the ends of actin filaments where they overlap the myosin and are called A bands. Small projections from the sides of the myosin filaments are called cross-bridges which interact with the actin filaments and cause contraction. The Z disc which attaches to the ends of the actin filaments passes from myofibril to myofibril, attaching the myofibrils to each other all the way across the muscle fiber. The portion of a myofibril that lies between two successive Z discs is called a sarcomere, basic contractile unit of the muscle [1].

Figure 1.2 Organization of skeletal muscle from gross to molecular level. The figure is modified from Benjamin Cummings (2001) [4].

1.4 Myofascial Force Transmission

Classical experiments on determining muscle isometric length-force characteristics depend on two principles: 1) muscle force exerted at the tendon from which measurements are taken was considered to be equal to the force exerted at the other tendon 2) length-force characteristics determined were considered as unique properties of the target muscle studied [5].

These principles arose from the widely accepted mechanism of force transmission referred to as *myotendinous force transmission* (Fig. 1.3), in which the force generated within sarcomere is transmitted to the tendon and from there onto the bony skeleton via the ends of myofibers. This mechanism involves a morphological specialization of the ends of the myofibers: the diameter of myofibers decreases substantially at the tendinous origin and insertion and the sarcolemma folds extensively in the myofiber's longitudinal direction. In these folds referred to as invaginations, collagen fibers are located. A

combination of many collagen fibers forms a sheet-like intramuscular aponeurosis, which is reshaped into a tendon outside of the muscle belly [6].

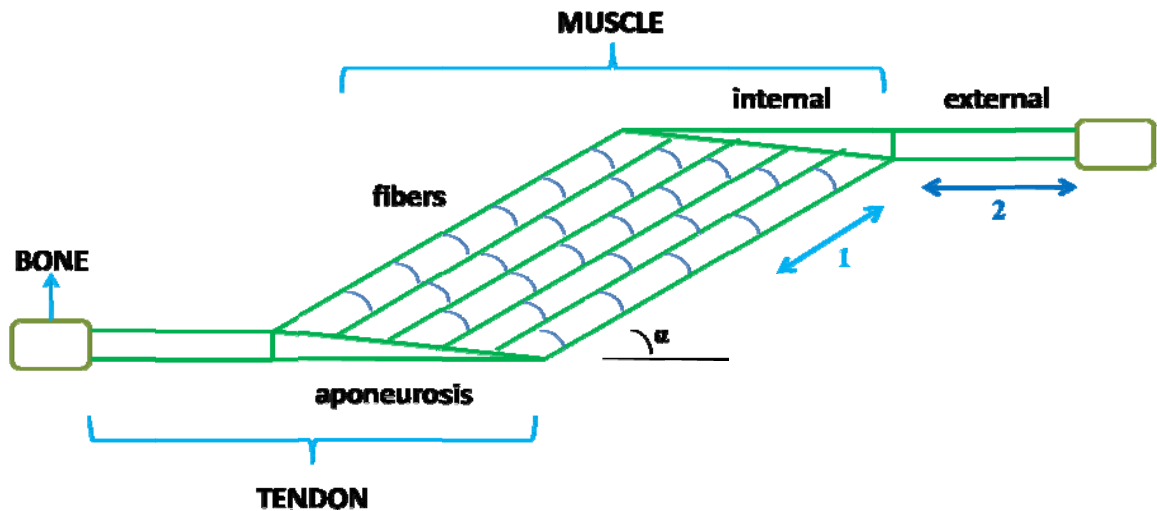


Figure 1.3 Relation among muscle fibers and tendon in a pennated muscle. Muscle fibers lie in parallel and are oriented at some angle α to the tendon axis of pull. Functionally tendon can be considered to consist of an internal portion (i.e., aponeurosis of muscle origin and insertion). As muscle fibers shorten, muscle is assumed to maintain isovolume, tendon to move only along its axis, and fibers to become more pennated (i.e., α increases). Note that the fiber and tendon shortening are not collinear (compare the arrows 1, 2).

However, recent studies have shown that also other structures (fig.1.4) such as cytoskeletal lattice, trans-sarcolemmal molecules and basal lamina within muscle play a role in force transmission, laterally from the intracellular milieu of the muscle fiber to the extramuscular environment [7]. Accordingly, functional independence of muscle fibers as assumed in the classical approach is not representative [5].

Therefore, within a muscle, the pathways via which force generated by sarcomeres is transmitted are 1) via sarcomeres arranged in series within a muscle fiber and the myotendinous junction (i.e., myotendinous force transmission); and 2) via complexes of structural proteins connecting parallel sarcomeres onto the subsarcolemmal cytoskeleton and endomysium. Note that from the endomysium, force may be transmitted onto the neighboring muscle fibers. Such additional mechanism is referred to as *intramuscular myofascial force transmission*.

Moreover, in vivo, skeletal muscles are far from being isolated: they are surrounded by synergistic muscles and are embedded within the connective tissues of a compartment. Such structures comprise 1) intermuscular connections (i.e., collagenous connections at the immediate interface between muscle bellies), as well as 2) extramuscular connections. Examples to the latter type are connective tissues that support the nerves and blood vessels (neurovascular tracts) and fascia representing the compartmental borders (e.g., septa, interosseous membranes and even periosteum).

Figure 1.4 Schematic representation of general connections from within the myofiber to extracellular space. The figure is modified from Roberts (2001) [8].

Recent experiments on rat EDL muscle have shown that inter- and extramuscular connective tissues are important pathways for transmission of a substantial fraction (up to 37%) of muscle force. Such force transmission is referred to as inter- and extramuscular myofascial force transmission [9].

1.4.1 Intramuscular Myofascial Force Transmission

In intramuscular myofascial force transmission muscle force is transmitted onto the endomysium (fig.1.5) and from there further onto the whole intramuscular connective

tissue stroma, consisting of the network of endomysial, perimysial and epimysial tubes or tunnels [10].

Force transmission pathways are formed by the connections between the trans-sarcolemmal molecules of the muscle fiber via the laminin molecules of the basal lamina to the collagen network of the same structure and from there on to the endomysium. The walls of endomysial tunnels themselves form a pathway to the perimysial tunnels. The shared walls of the perimysial tunnels of adjacent fascicles form connections to the epimysium. As a consequence, the whole intramuscular stroma acts an integral unit [10].

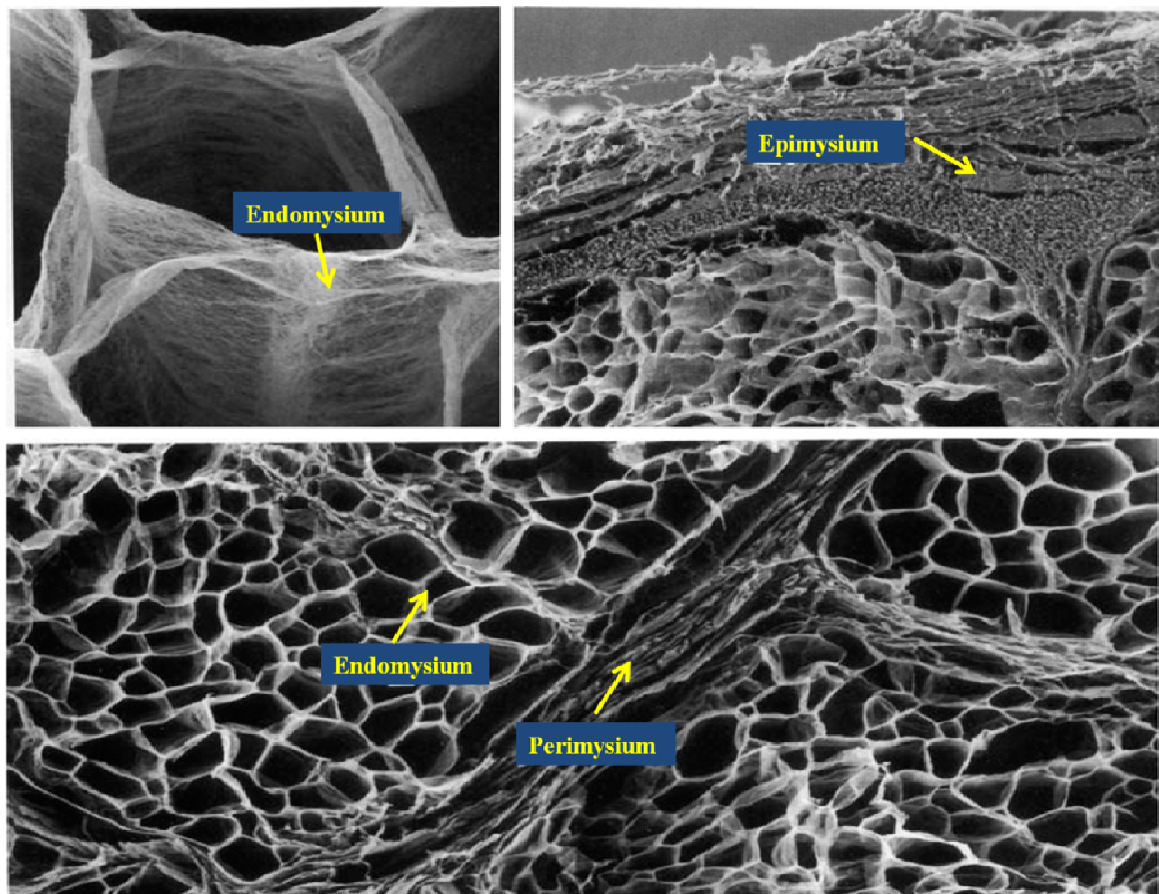


Figure 1.5 Scanning electron micrographs of epimysium (top right), perimysium (bottom) and endomysium (top left and bottom) of bovine semitendinosus muscle. The figure is modified from Nishimura (1994) [11].

Intramuscular myofascial force transmission has been shown to play an important role in muscular mechanics [6, 12, 13] as well as in maintenance of the physiological state of muscle [14].

1.4.2 Epimuscular Myofascial Force Transmission

In epimuscular myofascial force transmission, muscle force has to be transmitted beyond the epimysium laterally. There are two potential paths: (1) intermuscular path, in which there is direct transmission between the two adjacent muscles through intramuscular stromata; and (2) extramuscular path, in which the force is transmitted from a muscle onto nonmuscular neighboring tissues such as neurovascular tracts and compartment delimiting connective tissues. The only structures that are not connected directly to this extramuscular system are the aponeuroses or tendon plate within the muscle tendon-complex, which is covered by epimysium but not attached to it [10].

Epimuscular myofascial force transmission has been shown to affect muscular mechanics substantially leading to (1) major proximo-distal force differences [e.g. 15], (2) condition dependency of muscle length-force characteristics [e.g. 5] and (3) sarcomere length distributions [e.g. 15].

1.5 Control Measurements to Test History Effects in Muscle Experiments

A muscle cannot be regarded as a single contractile element uniform throughout its length [16]. There are some factors such as architecture, fiber type distribution, tendon length, fiber diameter, fiber length, contraction type, frequency of stimulation, amplitude of stimulation and recovery time which may cause differences in muscle properties after lengthening or shortening of muscle during experiments. This is the adaptation of muscle to a new state and the effects of previous activity to new state are referred to as history effects.

In order to minimize these changes constant conditions must be provided so that the history effects do not interfere substantially with the purpose of the experiment [10]. For such confirmation, control measurements are performed: at selected muscle lengths force measurement is repeated after collection of the actual data. In experiments reported by our research groups, for both actual muscle length-force data measurements and for testing history effects a recovery time of two minutes has been utilized in order to avoid e.g., potentiation [e.g. 17]. However, due to viscoelastic properties of muscular tissue, such

history effects are conceivable to be affected also by the recovery time. Yet, longer recovery time has not been applied and tested.

1.6 Fasciotomy as a Corrective Surgical Intervention

Fascia is specialized in muscles as epimysium, perimysium and endomysium. These structures are routes for intramuscular myofascial force transmission. Diseases of fascia or surgical interventions that comprise it, effect force transmission but the consequences of this effect have not been taken into consideration much in post operation outcome analysis. It is not taken into consideration as a treatment by itself.

Fasciotomy is a surgical procedure in which the target fascial structures (e.g. compartmental fasciae), are dissected to reach the target tissue, or to relieve tension or pressure in muscle compartments.

In most orthopedic surgeries related to muscle diseases fasciotomy is widely applied. It is a preliminary step in surgeries such as tendon transfers, tendon lengthening and fractional myotendinous lengthening which are especially used in treatment of spasticity caused by cerebral palsy.

Cerebral palsy is the term for a range of non-progressive syndromes of posture and motor impairment that results from an insult to the developing central nervous system (CNS). The characteristic signs are spasticity, movement disorders, muscle weakness, ataxia, and rigidity. Therefore, cerebral palsy is the most common cause of severe physical disability in childhood [18].

Long-established orthopaedic surgical procedures are designed to lengthen contracted myotendinous units, balance joint forces, transfer motor power, fuse unstable joints by arthrodesis, correct bony deformity to improve biomechanical alignment, reduce joint subluxation and dislocation to improve joint congruency, diminish painful spasticity, and maintain, restore, or stabilise spinal deformity. Orthopedic surgical techniques include neurectomy, tenotomy, arthrodesis, osteotomy, ostectomy, tendon transfer, tendon lengthening, fractional myotendinous lengthening or a combination of these procedures [18].

Tendon transplantation represents a possibility for replacement of active muscular action to carry out a particular motion when it would otherwise be permanently lost by paralysis or some other cause. The usual indication for transplantation is paralysis of a muscle or muscles that have a major functional responsibility in a region where strong muscles are available for transfer. The indication may also be that of a deforming imbalance that interferes with stability and produces deformity [19].

In tendon transplantation surgery passage of the tendon through good gliding structures with adequate space is important. The passage of tendons beneath the deep fascia in gliding compartments or tendon sheaths is preferred. When a muscle must be passed through intramuscular septums or deep fascia, a large tunnel must be developed through such septums, with such excision of them as seems appropriate so that the muscle and will have adequate room [19]. While interpreting results of such surgeries generally not much attention is paid on change in integrity of fascia.

For correction of hip deformity in cerebral palsy i.e., in selective lengthening of the psoas muscle surgery, the fascia over the sartorius was incised and then fascia over the iliacus muscle is defined and incised longitudinally so that the iliacus is exposed. Under this fascia by retracting the iliacus muscle laterally, the psoas muscle is exposed and a dissection along the psoas tendon is made [20]. Note that such surgery causes integrity of fascia to be lost.

The most common condition for which fasciotomy is performed is plantar fasciitis, an inflammation of the fascia beneath the arch of the foot. Fasciotomy removes a small portion of the fascia to relieve tension and pain. Connective tissue grows back into the space left by the incision, effectively lengthening the fascia. Successful outcome was reported however, the effect of such partial fasciotomy on muscular mechanics has not been taken into consideration.

Another goal of fasciotomy is to relieve pressure from a compression injury to a limb. This type of injury often occurs during contact sports or after a snake bite. Blood vessels of the limb are damaged and swell and leak, causing inflammation. Fluid accumulates in the area contained by the fascia. A fasciotomy is performed to relieve this pressure and prevent tissue death. Similar injury occurs in high-voltage electrical burns that cause deep tissue damage.

Compartment syndrome is a condition in which either exertion or trauma causes increased pressure within a musculofascial compartment, causing pain that may be associated with neurologic deficits and muscle dysfunction. It can be acute or chronic. Chronic exertional compartment syndrome of the lower leg is a common exercise-related injury in young active people, particularly those involved in running sports and in military training. It is treated by total fasciotomy with or without partial fasciotomy [21]. Although decreasing pressure is central aim of surgery, a potential change in muscle force may occur because of altered epimuscular myofascial force transmission and it must not be underestimated.

In an experiment done by Garfin et al [22] the effect of complete fasciotomy was studied on muscle tension in the anterolateral compartments of dog hindlimb. Fasciotomy was made longitudinally for the entire length of the compartment. The surgery includes a skin incision over the fascia of the compartment, a complete fasciotomy, and a secure skin closure with suture that did not include fascia. Results show that skin incisions and closures had no statistically significant effect on muscle forces, whereas force decreases associated with fasciotomy were significant: the fascial release causes approximately 15% reduction in the forces produced. This study suggests that fasciotomy may not be an entirely benign procedure clinically. In many cases, as in acute compartment syndromes, the benefits clearly outweigh the deficits but the cost to the individual of this procedure, may not be negligible, at least during the early recovery phase.

Recently, Smeulders et al [23] studied the effect of progressive surgical dissection for tendon transposition on length-force characteristics of rat flexor carpi ulnaris muscle. Fasciotomy had to be made before any clinical dissection: the distal part of the antebrachial compartmental fascia was incised longitudinally, dorsally over the muscle belly over two-thirds of the muscle length and without damaging the underlying muscle fibers. These authors showed that active force decreased approximately by 40% at low lengths compared to the intact situation providing strong evidence on the role of fascia in muscular force transmission.

Most of the experiments done by our research groups showed that any intervention on myofascial connections affects muscular mechanics substantially [10, 24, 25]. All connective structures in this chain are expected to play important roles. Therefore, fascia

may not only be an obstacle that needs to be removed before reaching the actual target but may also be seen as a functionally important pathway for force transmission in such surgeries. Note that, the effects of total fasciotomy on muscle mechanics have been studied recently [6, 26, 28], however, the effects of partial fasciotomy which intervention is routinely used in aponeurotomy surgeries in spasticity treatments have not been investigated. Based on earlier findings on the major role of epimuscular myofascial force transmission, we hypothesized that partial fasciotomy by itself may have sizable effects on muscle force.

1.7 Goals of the Study

The primary goal of the study is to test our hypothesis by performing experimental assessment of the effects of *partial fasciotomy* in the rat. It is aimed at describing how this intervention affects acutely muscle length-force characteristics as well as proximo-distal muscle force differences on the basis of epimuscular myofascial force transmission.

The secondary goal of the study is to test the role of increased recovery time for control measurements, on history effects.

2. METHODS

Surgical and experimental procedures were in strict agreement with the guidelines and regulations concerning animal welfare and experimentation set forth by Turkish law, and approved by the Committee on Ethics of Animal Experimentation at Boğaziçi University. Immediately after all experiments, animals were sacrificed using an overdose of urethane solution.

2.1 Surgical Procedures and Experimental Set-Up

Male Wistar rats ($n = 5$) with mean body mass = 298 gr (S.D. 7.84) were anaesthetized using intraperitoneally injected urethane solution (1.2 ml of 12.5% urethane solution/100 gr body mass). Extra doses were given if necessary (maximally 0.5 ml). During surgery and data collection, the animals were placed on a heated pad (Harvard Apparatus, Homoeothermic Blanket Control Unit) to prevent hypothermia (Fig 2.1). Body temperature of the animals were controlled with an integrated rectal thermometer and kept at approximately 37° C.

Figure 2.1 Experimental set up. FT indicates force transducer.

The anterior crural compartment (Fig 2.2) which envelopes tibialis anterior (TA), extensor digitorum longus (EDL) and extensor hallucis longus (EHL) muscles was exposed by removing the skin and biceps femoris muscle of the left hind limb. The retinaculae (i.e. the transverse crural ligament and the crural cruciate ligament) were removed by limited distal fasciotomy. Special care was taken to leave the connective tissue at the muscle bellies within the anterior crural compartment intact in order to maintain the physiological relations of intra-, inter- and extramuscular connections.

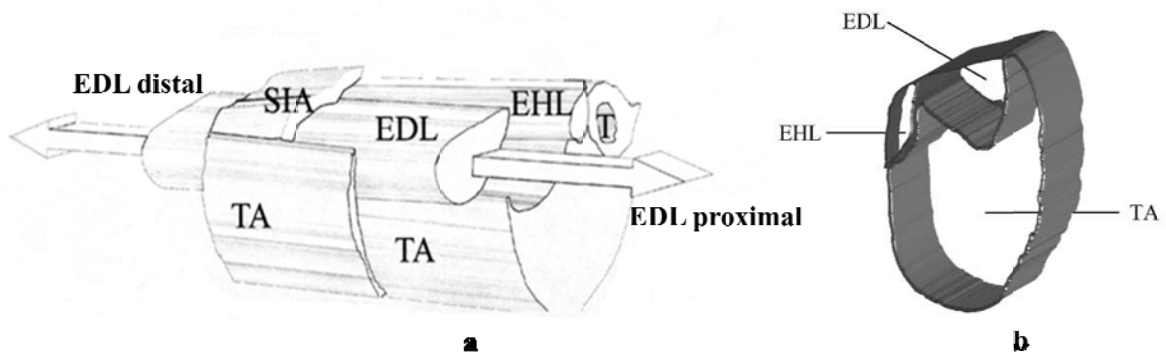


Figure 2.2 Schematic representation of the anterior tibial compartment: (a) medial view, (b) posterior view. Tibialis anterior muscle (TA), extensor digitorum longus muscle (EDL), extensor hallucis longus muscle (EHL), anterior intermuscular septum (SIA), tibia (T) are represented. Part (a) of the figure is modified from Huijing (2001) [26] and part (b) from Maas (2001) [27].

The femoral compartments were opened in order to attach a clamp for femur for fixation of animal and to reach the proximal tendon of EDL. For avoiding interference with the physiological relationship between length-force characteristics of the different heads of the EDL, the proximal tendon was cut as proximally as possible and tied to a Kevlar thread.

The rat was placed on the homoeothermic blanket and was mounted in the experimental set-up. The left foot of the animal was attached firmly to a foot plate whereas, the femur was fixed by a metal clamp. The position of the foot plate was manipulated to set a *reference position*: as *reference position*, a combination of knee and ankle angles of 120° and 100° respectively was selected. Note that the reference position corresponds to an in vivo position attained during the stance phase of the rats' gait. This allows the present experiments in situ to be performed in conditions closer to those in vivo.

Note also that the ankle angle was in maximal plantar flexion (180°) during the measurements.

At the reference position, two groups of distal tendons, (i) a combination of the four distal tendons of EDL muscle and (ii) the combined distal tendons of TA+EHL muscles) were tied separately by using Kevlar threads (Fig 2.3). Matching markers were placed on the distal tendons of EDL muscle and TA+EHL muscle complex, as well as on a fixed location on the lower leg. Subsequently, the distal tendon complexes were dissected as distally as possible and removed from their retinaculae near the ankle joint. Each Kevlar thread was connected to a force transducer (BLH Electronics Inc., Canton MA) separately. The sciatic nerve was dissected as proximally as possible, placed on a bipolar silver electrode and was prevented from dehydration by covering with a piece of latex (Fig. 2.4).

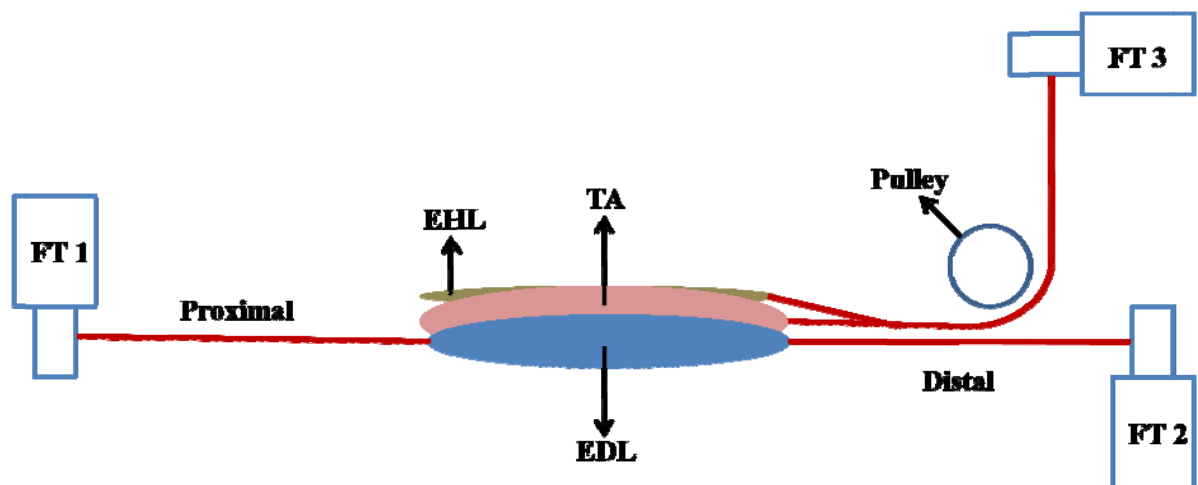


Figure 2.3 Schematic representation of the experimental set up. FT 1 indicates the force transducer connected to the proximal tendon of EDL muscle, FT 2 indicates the force transducer connected to the tied distal tendons of EDL muscle and FT 3 indicates the force transducer connected to the tied distal tendons of TA and EHL muscles. A pulley is used to guide the Kevlar thread from TA+EHL muscle complex to FT 3.

2.2 Experimental Conditions and Procedures

During the experiment, temperature of the room was kept at 22° C. Muscle and tendon tissue was further irrigated regularly by isotonic saline against dehydration. The experimental stimulation protocol (Biopac Systems stimulator, STMISOC) consisted of two twitches (square pulse with 0.1 ms, pulse train 200 ms, stimulation frequency 100 Hz) followed by a tetanus after 500 ms (constant current of 2 mA was used). 400 ms after the

tetanic contraction, another twitch was evoked. After each stimulation, the muscles were allowed to recover for 2 minutes at low muscle length, to minimize any effects of fatigue. Muscle passive forces were measured 100 ms after the second twitch; whereas, muscle total forces were measured during the tetanic plateau. Proximal and distal EDL forces as well as TA+EHL distal forces were measured simultaneously.

At the beginning of each experiment, EDL muscle and TA+EHL muscles were preconditioned by isometric contractions at low and reference length until proximally and distally measured isometric forces at low and reference length were reproducible in order to stabilize the effects of previous activity at higher muscle length.

For the actual collection of isometric muscle length-force characteristics, two conditions were studied: (1) EDL muscle length changes exclusively and (2) EDL and TA+EHL muscle length changes simultaneously. All isometric length changes were imposed distally.

(1) *EDL muscle length changes exclusively*: EDL forces were recorded at various muscle lengths, obtained by moving the force transducer by 1 mm increments, starting from below distal active slack length (the muscle length at which active muscle force equals zero) until 2 mm over EDL distal optimum length. Note that the distal tendon of TA+EHL muscle complex and the proximal tendon of EDL muscle were kept at the reference position at all times during the experiment.

(2) *EDL and TA+EHL muscle length changes simultaneously*: EDL and TA+EHL forces were recorded at various muscle lengths, obtained by moving the force transducer by 1 mm increments starting from below distal active slack length of EDL muscle until 2 mm over EDL distal optimum length. Note that the proximal EDL tendon was kept at the reference position at all times during the experiment.

2.3 Experimental Protocol

Isometric measurements of muscle forces were performed in two different conditions:

(1)

Figure 2.4 The *intact* anterior crural compartment. The target muscles and their myofascial connections at their muscle bellies were preserved. The EDL and EHL muscle bellies cannot be seen due to their anatomical locations (TA muscle covers them fully in intact condition).

(2)

Figure 2.5 After *partial fasciotomy*. The compartmental fascia that covers the EDL and TA+EHL muscles was cut longitudinally from the proximal end up to approximately 50% of the entire length of the fascia. Note that after this intervention proximal end of EDL muscle belly is visible whereas, EHL muscle belly is covered by the TA muscle.

(1) *Intact*: the target muscles and their myofascial connections at their muscle bellies were preserved (Fig 2.4).

(2) *After partial fasciotomy*: the compartmental fascia that covers the EDL and TA+EHL muscles was cut longitudinally from the proximal end up to approximately 50% of the entire length of the fascia (Fig 2.5).

Note that in each of these conditions the two subsequent conditions of (i) EDL length changes exclusively and (ii) EDL & TA+EHL length changes simultaneously were applied.

2.3.1 Control Contractions

To test the possible history effects, separate muscle force measurements (referred to as *the control contractions*) were performed subsequent to collection of each length-force data (1) at lower muscle length (i.e., at the reference position) and (2) at the optimum length of EDL muscle distally. Corresponding force values measured after control contractions and during the collection of actual length-force data were compared.

Note that in order to test time effect of recovery period on hysteresis, control measurements were performed after (1) our typical recovery period of 2 minutes and (2) an extended recovery period of 15 minutes, subsequently. These measurements were referred to as *the first control measurements* and *the second control measurements* respectively.

2.4 Treatment of Data and Statistics

Passive muscle length-force data were fitted with an exponential curve.

$$y = e^{ax+b}, \quad (1)$$

where, y and x represent passive muscle force, and muscle-tendon complex length respectively and a and b are fitting coefficients. Muscle total force data as was fitted by a polynomial

$$y = b_0 + b_1x + b_2x^2 + b_3x^3 + b_4x^4 + \dots + b_nx^n, \quad (2)$$

where, y and x represent muscle total force and muscle-tendon complex length respectively, and b_0 through b_n are fitting coefficients. Active muscle force data was estimated by subtracting passive muscle force from total muscle force at corresponding muscle-tendon complex lengths and were fitted also by a polynomial (equation 2). The mean of force values with standard errors (SE), optimal active force and optimum muscle tendon complex length were calculated from the fitted data.

In the muscle force fitting procedure, the order of polynomials used was determined by one-way analysis of variance (ANOVA): the power was increased from one to maximally six until no significant improvement to the description of changes of muscle length and force data was added. One-way ANOVA was also performed to test length effect on EDL and TA+EHL muscle forces. Two-way ANOVA was used to test for the effects of altered muscle length and lengthening condition on i) distal and proximal EDL forces, ii) the proximo-distal EDL force differences and iii) TA+EHL distal forces.

Differences were considered significant at $P < 0.05$. If significant main effects were found, Bonferroni post-hoc tests were performed to locate significant differences. Force values were plotted (mean + SE), and muscle length is expressed as a deviation of distal EDL optimum muscle length (i.e., for an interval of $-11 \leq \Delta l_{m+t} \leq 2$).

3. RESULTS

3.1 Control Contractions

3.1.1 EDL Lengthening Exclusively

3.1.1.1 First control measurements

At optimum length: TA+EHL muscle control forces were 1.25% and 7.12% lower than the actual data measured in intact and partial fasciotomy conditions respectively (Fig. 3.1).

EDL muscle control forces were distally 13.99% and 15.01% (Fig. 3.2a) and proximally 2.15% and 6.60% (Fig. 3.2b) lower than the actual data measured in intact and partial fasciotomy conditions respectively.

At lower muscle length: TA+EHL muscle control forces were 12.32% and 3.16% lower than the actual data measured in intact and partial fasciotomy conditions respectively (Fig. 3.1).

EDL muscle control forces were distally 78.53% and 60.27% (Fig. 3.2a) and proximally 41.53% and 5.70% (Fig. 3.2b) lower than the actual data measured in intact and partial fasciotomy conditions respectively.

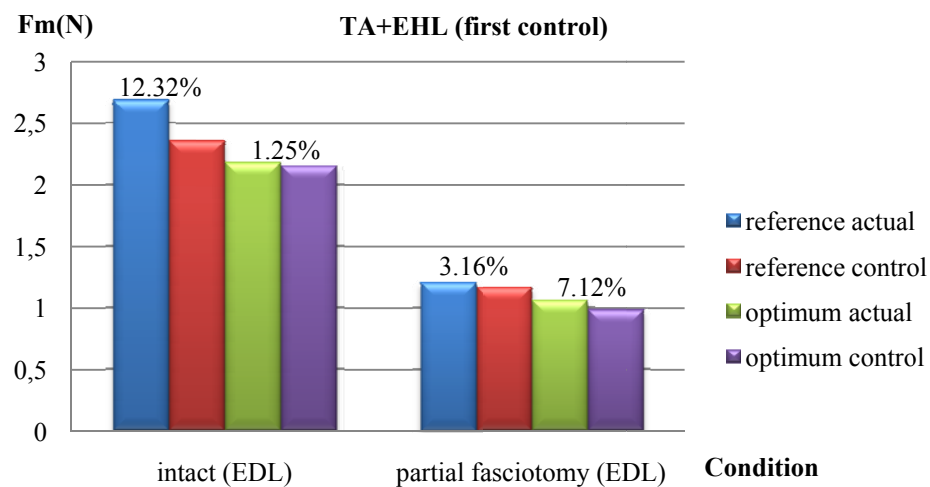


Figure 3.1 TA+EHL first control measurements at optimum and low length in intact and partial fasciotomy conditions.

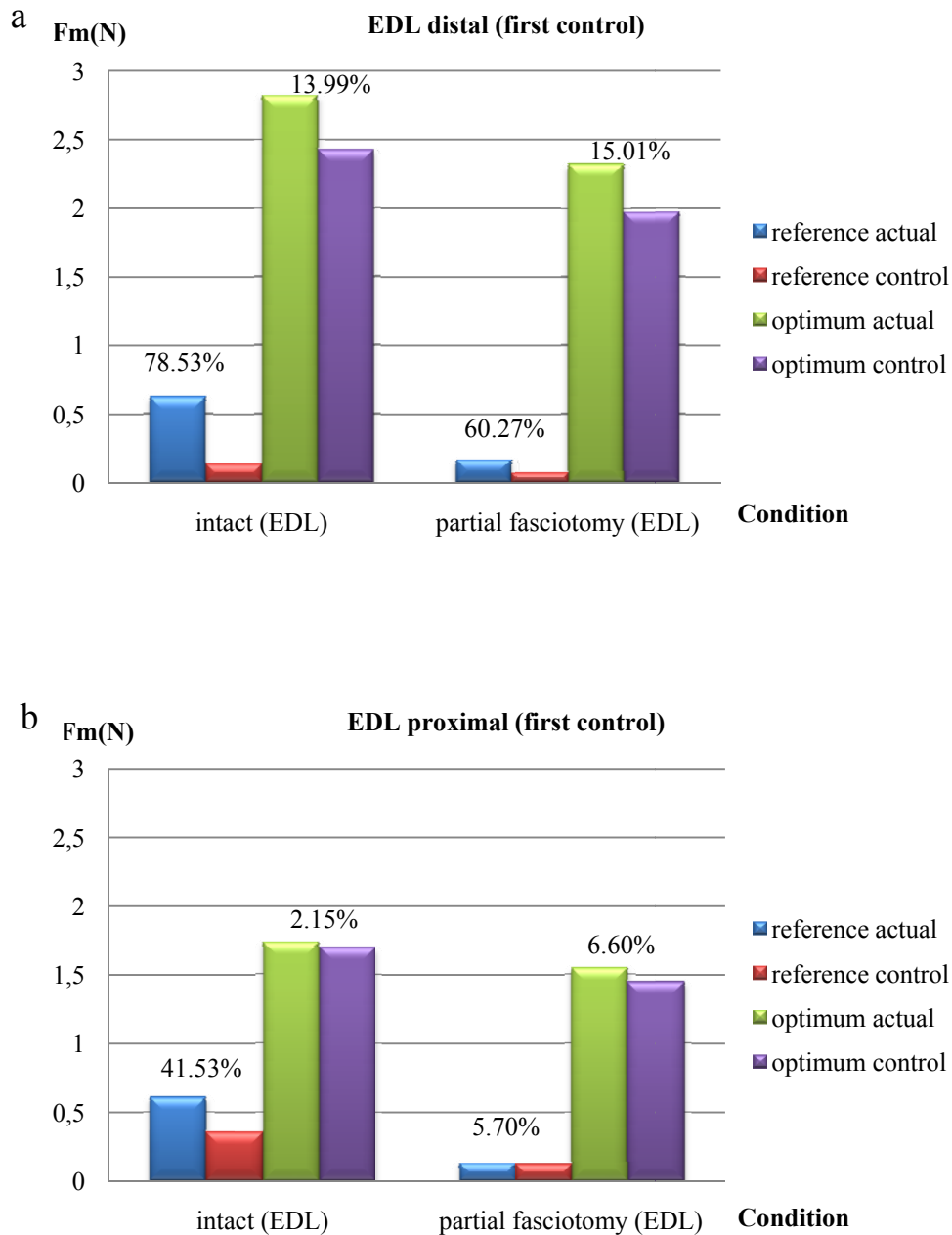


Figure 3.2 EDL muscle first control measurements at optimum and low length in intact and partial fasciotomy conditions (a) distally, (b) proximally.

It is concluded that (1) for both intact and partial fasciotomy conditions and for both muscle lengths, the difference between the control measurements and the actual data is rather limited for the restrained TA+EHL muscle complex. On the other hand, for the lengthened EDL muscle (2) such difference does not substantiate at the optimum length whereas, (3) it may reach very high levels at the lower (reference) muscle length studied.

3.1.1.2 Second control measurements

At optimum length: TA+EHL muscle control forces were 10.91% and 23.27% lower than the actual data measured in the intact and fasciotomy conditions respectively (Fig. 3.3).

EDL muscle control forces were distally 39.72% and 7.80% (Fig. 3.4a) and proximally 23.47% and 32.23% (Fig. 3.4b) lower than the actual data measured in the intact and fasciotomy conditions respectively.

At lower muscle length: During EDL muscle lengthening TA+EHL muscle control forces were 22.81% and 13.97% lower than the actual data measured in the intact and fasciotomy conditions respectively (Fig. 3.3).

EDL muscle control forces were distally 97.43% (Fig. 4.4a) and 84.50% and proximally 55.69% and 41.62% (Fig. 3.4b) lower than the actual data measured in the intact and fasciotomy conditions respectively.

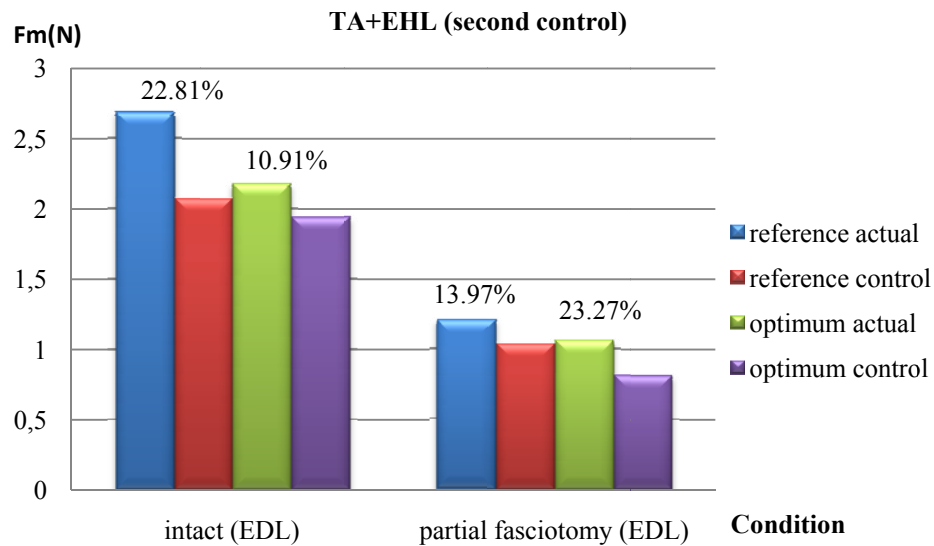


Figure 3.3 TA+EHL second control measurements at optimum and low length in intact and partial fasciotomy conditions.

It is concluded that (1) for both intact and partial fasciotomy conditions and for both muscle lengths, the difference between the control measurements and the actual data is

rather limited for the restrained TA+EHL muscle complex. On the other hand, for the lengthened EDL muscle (2) such difference does not substantiate at the optimum length whereas, (3) it may reach very high levels at the lower muscle length studied.

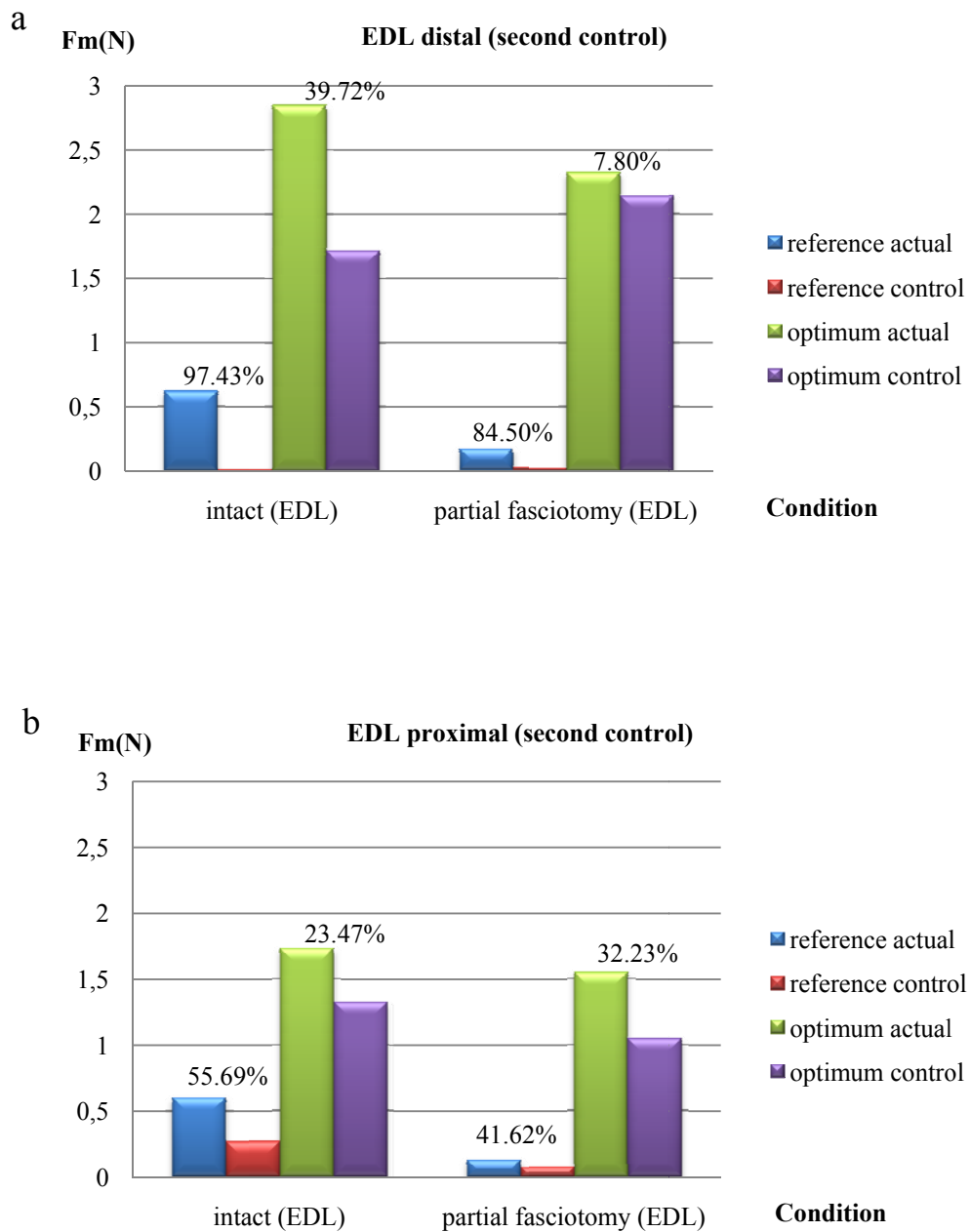


Figure 3.4 EDL muscle second control measurements at optimum and low length in intact and partial fasciotomy conditions (a) distally, (b) proximally.

It is also concluded that the difference between the control measurements and the actual data for both intact and partial fasciotomy conditions, for the restrained TA+EHL muscle complex and for the lengthened EDL muscle, both at the reference and the optimum lengths are higher in the second control measurements than those in the first control measurements which shows that the increase in recovery time increases history effect.

3.1.2 EDL & TA+EHL Lengthening Simultaneously

3.1.2.1 First control measurements

At optimum length: TA+EHL muscle control forces were 6.49% and 4.8% lower than the actual data measured in the intact and partial fasciotomy conditions respectively (Fig. 3.5).

EDL muscle control forces were distally 13.22% and 3.96% (Fig. 3.6a) and proximally 12.94% and 2.70% (Fig. 3.6b) lower than the actual data measured in the intact and partial fasciotomy conditions respectively.

At lower muscle length: TA+EHL muscle control forces were 57.28% and 31.90% lower than the actual data measured in the intact, partial fasciotomy conditions respectively (Fig. 3.5).

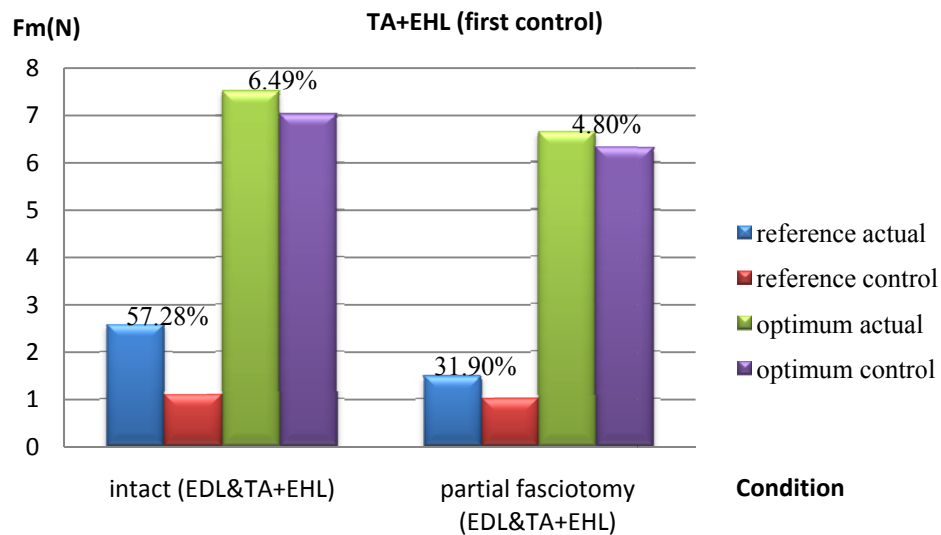


Figure 3.5 TA+EHL first control measurements at optimum and low length in intact and partial fasciotomy conditions.

EDL muscle control forces were distally 59.46% and 29.67% (Fig. 3.6a) and proximally 39.14% and 16.91% (Fig. 3.6b) lower than the actual data measured in the intact and partial fasciotomy conditions respectively.

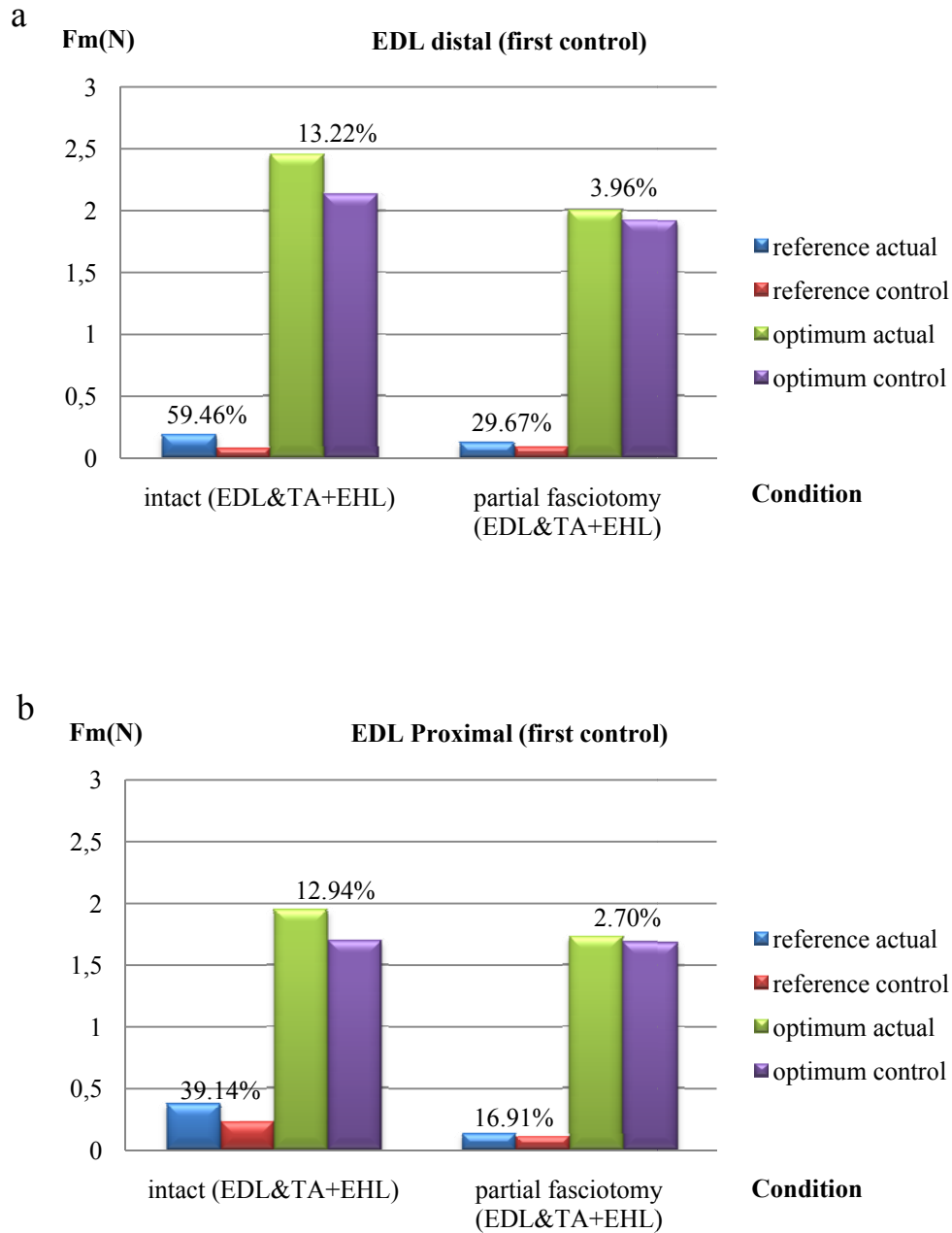


Figure 3.6 EDL muscle first control measurements at optimum and low length in intact and partial fasciotomy conditions (a) distally, (b) proximally.

It is concluded that regarding effects of history, TA+EHL muscle complex acts similar to EDL muscle if these muscles are lengthened simultaneously with EDL muscle:

for both intact and partial fasciotomy conditions and for both muscle lengths, the difference between TA+EHL control measurements and the actual data is (1) small at the optimum length whereas (2) such difference may reach very high levels at the lower muscle length studied.

For both intact and partial fasciotomy conditions and for both muscle lengths, the difference between EDL control measurements and the actual data both distally and proximally is (1) sizable at the optimum length whereas, (2) such difference may reach very high levels at the lower muscle length studied.

Note that, for EDL muscle distally, for both conditions and muscle lengths, the difference between control measurements and the actual data is lower after simultaneous lengthening of the synergistic muscles. However, for EDL muscle proximally such difference is lower only for the lower length in intact condition and for optimum length in fasciotomy condition.

3.1.2.2 Second control measurements

At optimum length: TA+EHL muscle control forces were 0.38% and 3.76% lower than the actual data measured in the intact and partial fasciotomy conditions respectively (Fig. 3.7).

EDL muscle control forces were distally 7.87% and 5.45% (Fig. 3.8a) and proximally 0.28% and 4.39% (Fig. 3.8b) lower than the actual data measured in the intact and partial fasciotomy conditions respectively.

At lower muscle length: TA+EHL muscle control forces were 68.26% and 54.62% lower than the actual data measured in the intact and partial fasciotomy conditions respectively (Fig. 3.7).

EDL muscle control forces were distally 76.06% and 69.55% (Fig. 3.8a) and proximally 50.13% and 61.63% (Fig. 3.8b) lower than the actual data measured in the intact and partial fasciotomy conditions respectively.

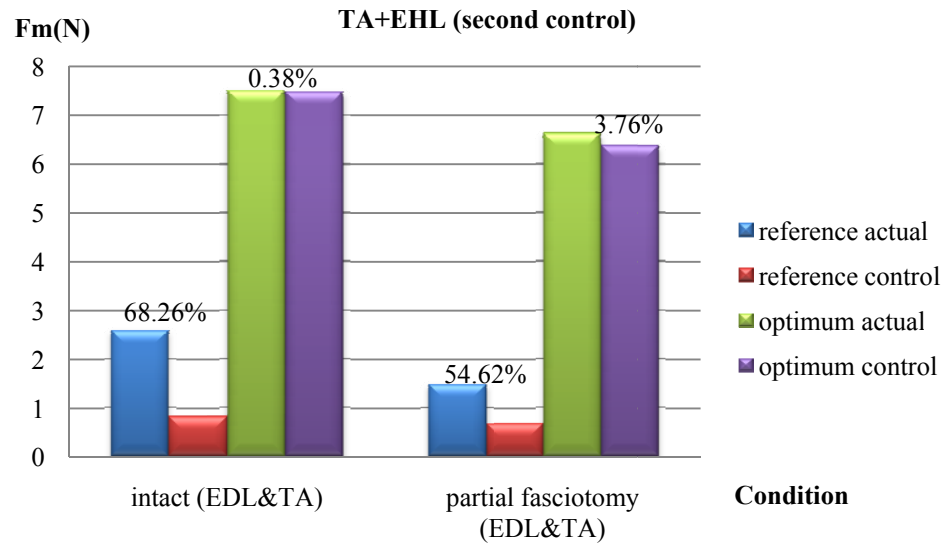


Figure 3.7 TA+EHL second control measurements at optimum and low length in intact and partial fasciotomy conditions.

It is concluded that also for the second control measurements, TA+EHL muscle complex acts similar to EDL muscle after lengthening of the synergistic muscles simultaneously: for both intact and partial fasciotomy conditions and for both muscle lengths, the difference between TA+EHL control measurements and the actual data is (1) fairly small at the optimum length whereas, (2) such difference may reach very high levels at the lower muscle length.

For both intact and partial fasciotomy conditions and for both muscle lengths, the differences between EDL control measurements and the actual data distally and proximally (1) rather limited at the optimum length whereas, (2) such difference substantiates at the lower muscle length.

If the second control forces for simultaneous lengthening of synergistic muscles and those for lengthening of EDL muscle exclusively are compared for EDL muscle distally, (for both conditions and muscle lengths), the difference between control and actual forces is lower for simultaneous muscle lengthening. The same applies for EDL muscle also proximally except for the lower length in partial fasciotomy condition.

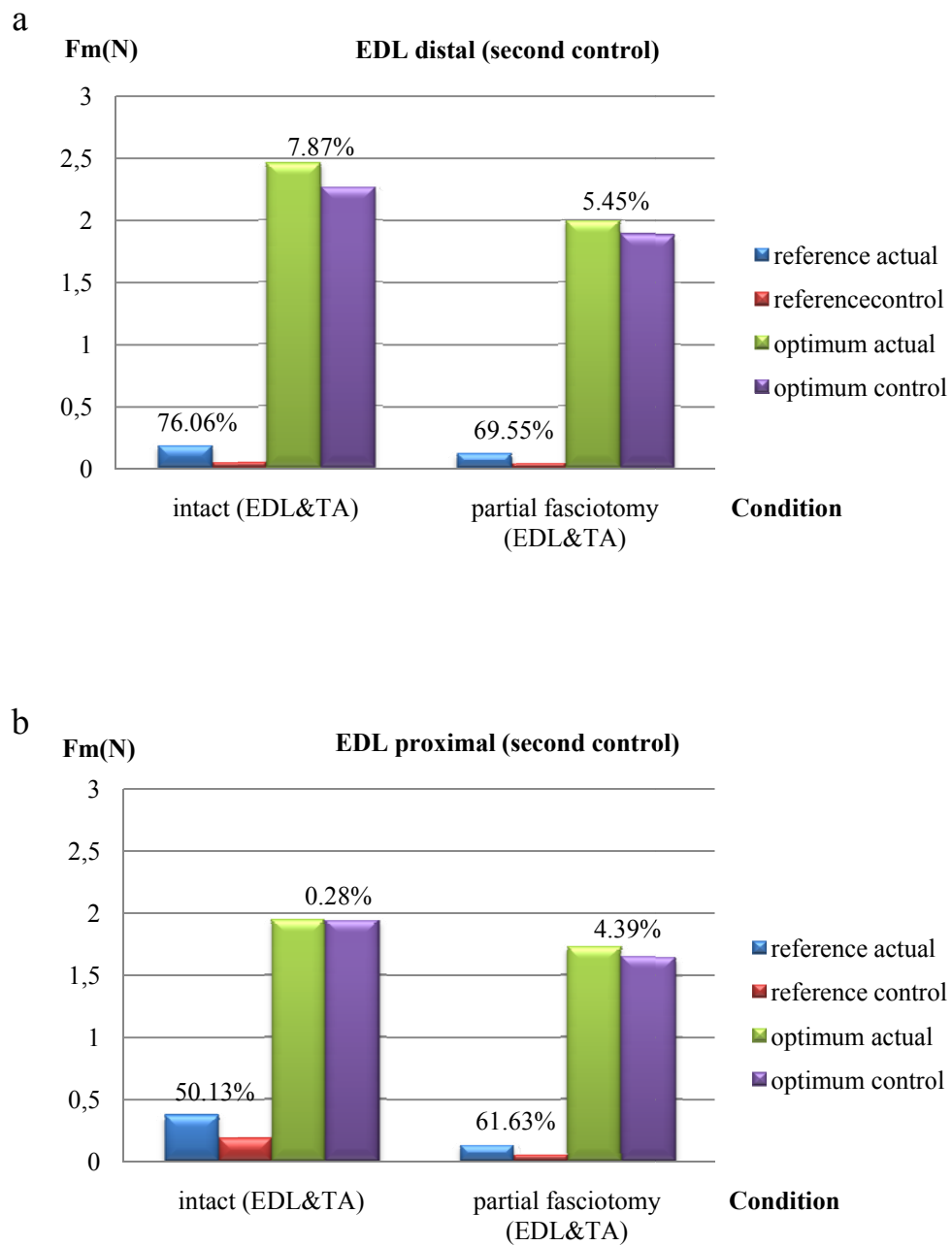


Figure 3.8 EDL muscle second control measurements at optimum and low length in intact and partial fasciotomy conditions (a) distally, (b) proximally.

3.2 Effects of Partial Fasciotomy on Muscle Length-Force Characteristics:

3.2.1 EDL Lengthening Exclusively

For TA+EHL, EDL distal and EDL proximal active forces, ANOVA showed significant effects of EDL lengthening in both intact and partial fasciotomy conditions.

Muscle length effects on TA+EHL, EDL distal and EDL proximal passive forces were also significant for both conditions.

EDL distal forces

The shape changes that partial fasciotomy caused in EDL length-active and passive force characteristics compared to intact condition were significant. As a result of partial fasciotomy, EDL distal active forces decreased substantially (Fig. 3.9) at most muscle lengths studied (i.e., for $\Delta l_{m+t} > -10$ mm). Moreover, the determinants of muscle length-active force characteristics were affected substantially by partial fasciotomy: (1) EDL muscle distal optimal force decreased (by 13.81%). (2) EDL distal optimum length shifted to a higher muscle length (by 0.7 mm).

Regarding passive EDL forces (Fig. 3.9), partial fasciotomy caused EDL distal passive forces to decrease especially at higher muscle lengths (e.g. by 46.35% at $\Delta l_{m+t} = 2$ mm).

It is concluded that disruption of the integrity of epimuscular connections even by partial fasciotomy has major effects on muscle length-active force characteristics distally. Partial fasciotomy causes: (1) shape changes leading to a substantial decrease in active and passive forces and (2) alterations in the determinants of muscle length-force characteristics including shifting of muscle optimum length to a higher length and decreasing of the optimal force.

Also proximally for EDL active and passive forces, shape changes that partial fasciotomy caused compared to intact condition were significant.

Partial fasciotomy caused active EDL proximal force to decrease (Fig. 3.10). Note that at lower muscle lengths, such force decrease was greater than that measured at higher

lengths (e.g., a force decrease of 27.28% and 16.31% was measured at $\Delta l_{m+t} = -5$ mm and $\Delta l_{m+t} = 0$ mm respectively).

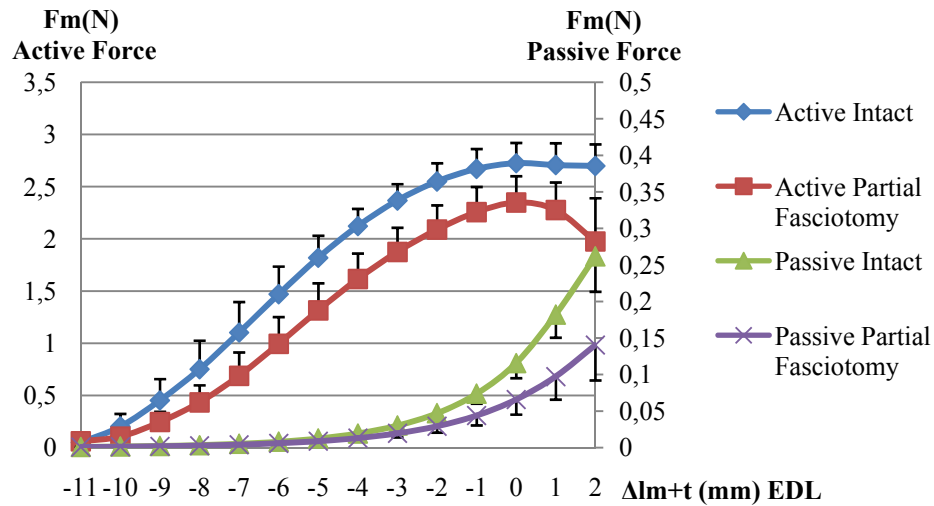


Figure 3.9 EDL distal length-active and passive force characteristics in intact and partial fasciotomy conditions for EDL muscle lengthening exclusively. EDL muscle tendon complex length is expressed as deviation (Δl_{m+t}) from optimum length. *EDL proximal forces*

Partial fasciotomy caused also EDL proximal passive forces to decrease (Fig. 3.10) for all lengths especially at higher muscle lengths (e.g. by 60.58% at $\Delta l_{m+t} = 2$ mm). Remarkably, EDL proximal passive forces were non-zero for almost all muscle lengths.

It is concluded that the intervention affects substantially muscle length-active force characteristics also proximally. Partial fasciotomy causes: (1) shape changes leading to a substantial decrease in active force primarily at intermediate and lower muscle lengths and in passive force (2) alterations in the determinants of muscle length-force characteristics including shifting of the muscle optimum to higher length (by 1.7 mm) and decreasing of the optimal force (by 16.31%).

ANOVA showed significant differences in total forces exerted at EDL distal and proximal tendons (Fig. 3.11).

In the intact condition, EDL total forces exerted proximally were higher than those exerted distally at lower muscle lengths. In contrast, at intermediate and higher muscle

lengths (i.e., for approximately $\Delta l_{m+t} > -8.5$ mm), the distal forces were higher than the proximal forces.

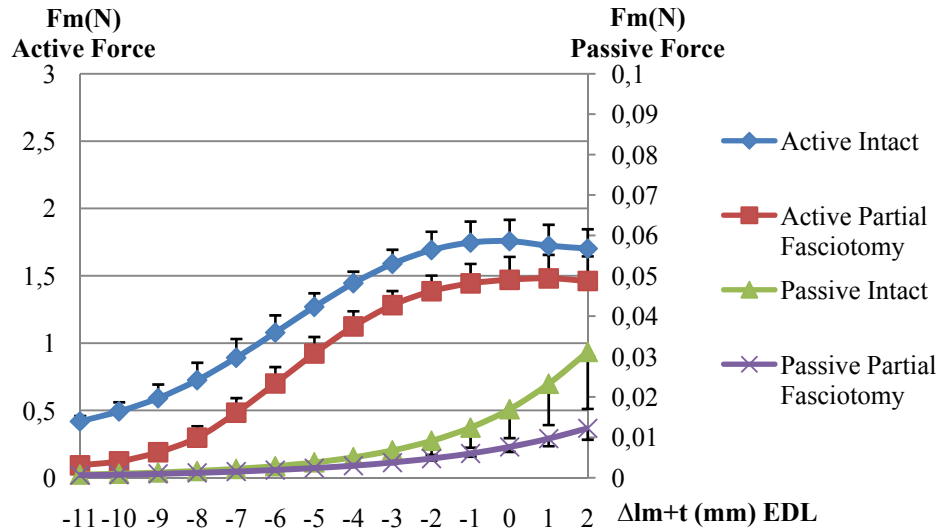


Figure 3.10 EDL proximal length-active and passive force characteristics in intact and partial fasciotomy conditions for EDL muscle lengthening exclusively. EDL muscle tendon complex length is expressed as deviation (Δl_{m+t}) from optimum length. *Proximo-distal EDL force differences*

It is concluded that a distally directed net epimuscular myofascial load acts on intact EDL muscle at lower muscle lengths however, as a function of increasing muscle length, the direction of such load is reversed.

After partial fasciotomy, the proximo-distal total force differences (Fig. 3.11) were positive for most muscle lengths (for $\Delta l_{m+t} > -10$ mm) studied.

It is concluded that partial fasciotomy removes almost fully the net distally directed epimuscular myofascial loads acting on EDL muscle.

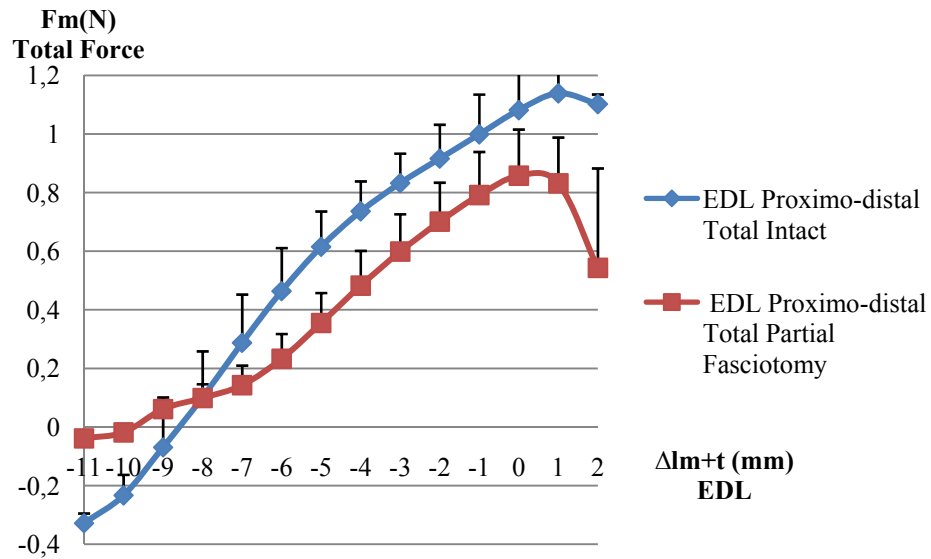


Figure 3.11 EDL proximo-distal total force differences ($F_{\text{distal}} - F_{\text{proximal}}$) in intact and partial fasciotomy conditions for EDL muscle lengthening exclusively.

TA+EHL forces

The shape changes that partial fasciotomy caused in TA+EHL length-active and passive force characteristics compared to intact condition (Fig. 3.12) were significant.

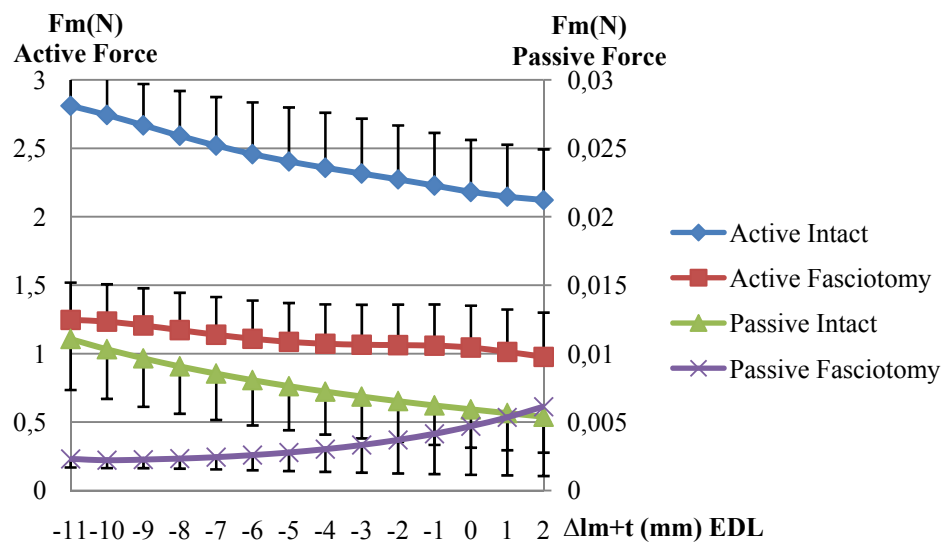


Figure 3.12 TA+EHL length-active and passive force characteristics in intact and partial fasciotomy conditions for EDL muscle lengthening exclusively. EDL muscle tendon complex length is expressed as deviation (Δl_{m+t}) from optimum length.

Partial fasciotomy caused TA+EHL active forces (Fig. 3.12) to decrease substantially (e.g. by 55.65% and 52.10% at $\Delta l_{m+t} = -11$ mm and $\Delta l_{m+t} = 0$ mm respectively compared to TA+EHL active forces measured in intact condition).

Note that, partial fasciotomy caused TA+EHL passive forces to decrease at all EDL lengths (Fig. 3.12) except for $\Delta l_{m+t} = 2$ mm: especially at lower muscle lengths such decrease was substantial (e.g. by 79.13% at $\Delta l_{m+t} = -11$ mm and by only 5.49% at $\Delta l_{m+t} = 1$ mm).

It is concluded that epimuscular connections, damaged by the intervention, affect muscle length-active force characteristics of restrained TA+EHL complex substantially. Partial fasciotomy causes: significant decrease both in active and passive TA+EHL force in response to increasing the length of the neighboring muscle exclusively.

3.2.2 EDL & TA+EHL Lengthening Simultaneously

For active muscle forces exerted at TA+EHL tied tendons as well as EDL muscles' distal and proximal tendons, ANOVA showed significant effects of synergistic muscle length changes in intact and partial fasciotomy conditions studied. Muscle length effects on exponentially increasing passive forces were significant for EDL muscle distally.

EDL distal forces

The shape changes that partial fasciotomy caused in TA+EHL length-active and passive force characteristics compared to intact condition were significant.

As a result of partial fasciotomy, EDL distal active forces (Fig. 3.13), decreased substantially which effect was more pronounced for $\Delta l_{m+t} > -7$ mm. Additionally, the effects of partial fasciotomy on the determinants of muscle length-force characteristics were sizable: (1) EDL muscle optimal force decreased substantially (by 18.46%) and (2) EDL optimum length shifted to a higher muscle length (by 0.3 mm).

Partial fasciotomy caused EDL distal passive forces (Fig. 3.13) to decrease especially at higher muscle lengths (i.e., $\Delta l_{m+t} > -9$ mm, e.g., by 22.15% at $\Delta l_{m+t} = 2$ mm). Note that the non-zero passive forces for almost all muscle lengths and in all conditions studied are remarkable.

It is concluded that damaging of epimuscular connections by partial fasciotomy has major effects on muscle length-active force characteristics distally also for simultaneous lengthening of the synergistic muscles. Partial fasciotomy causes: (1) shape changes leading to a substantial decrease in active and passive forces and (2) alterations in the determinants of muscle length-force characteristics including shifting of the muscle optimum length to a higher length and decreasing of the optimal force. Note that compared to EDL lengthening exclusively, EDL and TA+EHL simultaneous lengthening yields a higher decrease in optimal force but a lower shift in optimum length to higher muscle lengths.

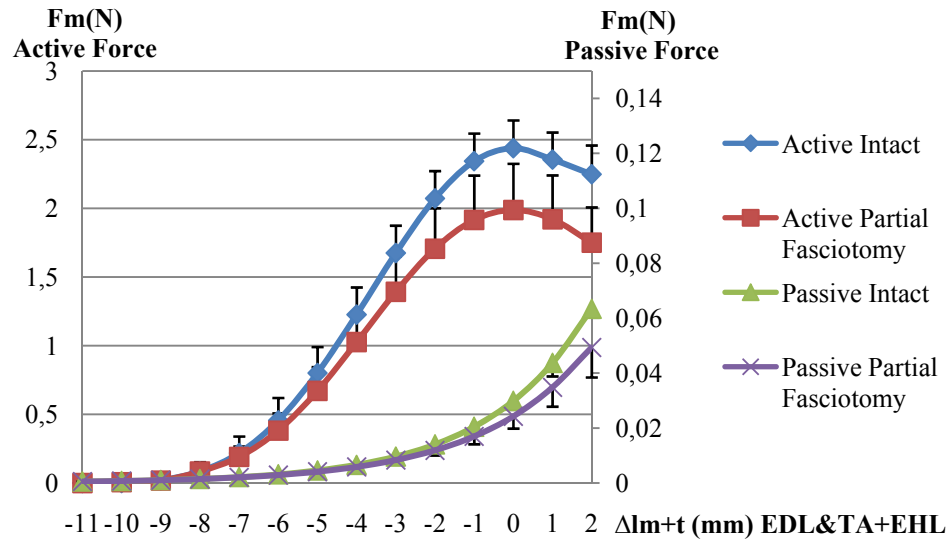


Figure 3.13 EDL distal length-active and passive force characteristics in intact and partial fasciotomy conditions for EDL&TA+EHL muscles lengthening simultaneously. EDL&TA+EHL muscle tendon complex length is expressed as deviation (Δl_{m+t}) from optimum length.

EDL proximal forces:

Proximally for EDL active forces, shape changes that partial fasciotomy caused compared to intact condition (Fig. 3.14) were significant.

After partial fasciotomy, the decrease in muscle active force was greater at lower lengths than that at higher lengths (proximally EDL active force decreased by 24.64% and 10.79% at $\Delta l_{m+t} = -5\text{mm}$ and at $\Delta l_{m+t} = 0\text{ mm}$ respectively).

For EDL proximal passive forces (Fig. 3.14), the shape change that partial fasciotomy caused compared to intact condition were not significant. Remarkably, EDL proximal passive forces were non-zero for almost all muscle lengths.

It is concluded that the intervention affects muscle length-active force characteristics proximally also for simultaneous lengthening of the synergistic muscles. Partial fasciotomy causes: (1) shape changes leading to a substantial decrease in active force primarily at intermediate and lower muscle lengths. (2) alterations in the determinants of muscle length-force characteristics including shifting of the muscle optimum to higher length (by 0.3 mm) and decreasing of the optimal force (by 10.79%).

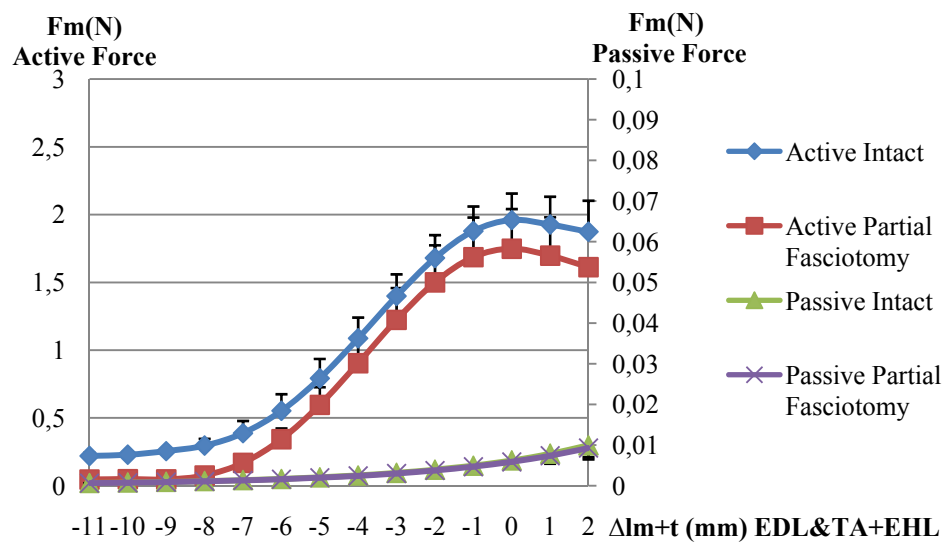


Figure 3.14 EDL proximal length-active and passive force characteristics in intact and partial fasciotomy conditions for EDL&TA+EHL muscles lengthening simultaneously. EDL&TA+EHL muscle tendon complex length is expressed as deviation (Δl_{m+t}) from optimum length.

Proximo-distal EDL total force differences

ANOVA showed significant differences in total force between EDL distal and proximal (Fig. 3.15).

In the intact condition, the total force exerted on the proximal tendon of EDL muscle was higher than that exerted on the distal tendon at lower muscle lengths (i.e., for $\Delta l_{m+t} <$

approx. -5 mm). In contrast, at higher muscle lengths the distal force was higher than the proximal force.

It is concluded that a distally directed net epimuscular myofascial load acts on intact EDL muscle at lower muscle lengths; whereas, such load is proximally directed at higher muscle lengths.

After partial fasciotomy, the proximo-distal force difference (Fig. 3.15) was positive for most muscle lengths (i.e., $\Delta l_{m+t} > \text{approx. } -8 \text{ mm}$).

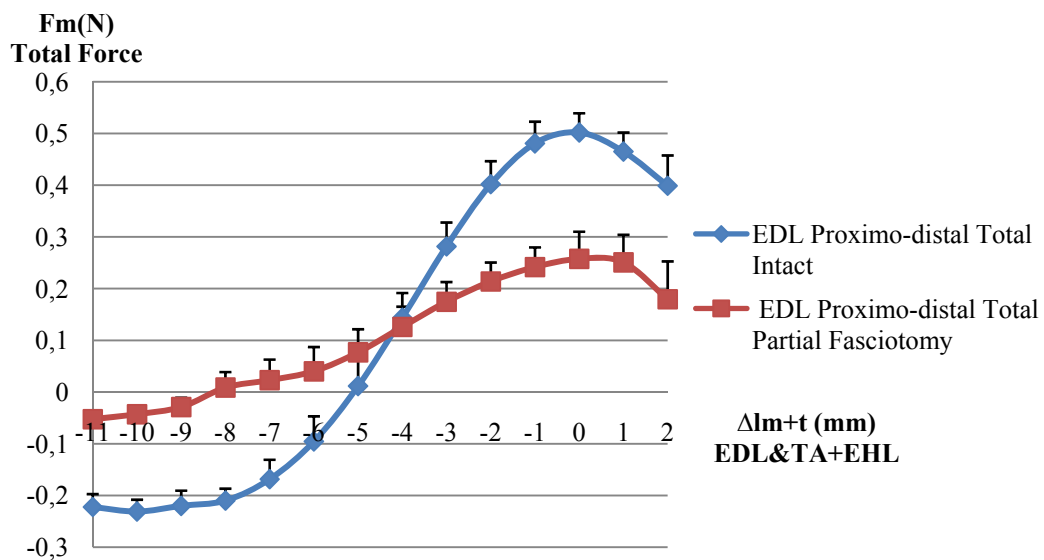


Figure 3.15 EDL proximo-distal total force differences ($F_{\text{distal}} - F_{\text{proximal}}$) in intact and fasciotomy conditions for EDL&TA+EHL muscles lengthening simultaneously.

It is concluded that partial fasciotomy removes almost fully the net distally directed epimuscular myofascial loads acting on EDL muscle also for simultaneous lengthening of the synergistic muscles.

TA+EHL forces

The shape changes that partial fasciotomy yielded in TA+EHL length-active force characteristics compared to intact condition were significant (Fig. 3.16).

Partial fasciotomy caused TA+EHL active forces (Fig. 3.16) to decrease substantially (e.g. by 15.74% and 12.2% at $\Delta l_{m+t} = -5$ mm and $\Delta l_{m+t} = 0$ mm respectively compared to TA+EHL active forces measured in intact condition).

The shape changes that partial fasciotomy caused in TA+EHL length-passive force characteristics compared to intact condition were not significant (Fig. 3.16). For TA+EHL passive forces ANOVA showed significant effects of altered synergistic muscle length after partial fasciotomy (for $\Delta l_{m+t} > -1$ mm) however, such effects were not significant in the intact condition.

It is concluded that disrupting the integrity of epimuscular connections by partial fasciotomy has major effects on length-active force characteristics of TA+EHL muscle complex after imposing length changes simultaneously with the synergistic EDL muscle: similar to the effects shown for EDL muscle, partial fasciotomy causes a sizable decrease in active TA+EHL force.

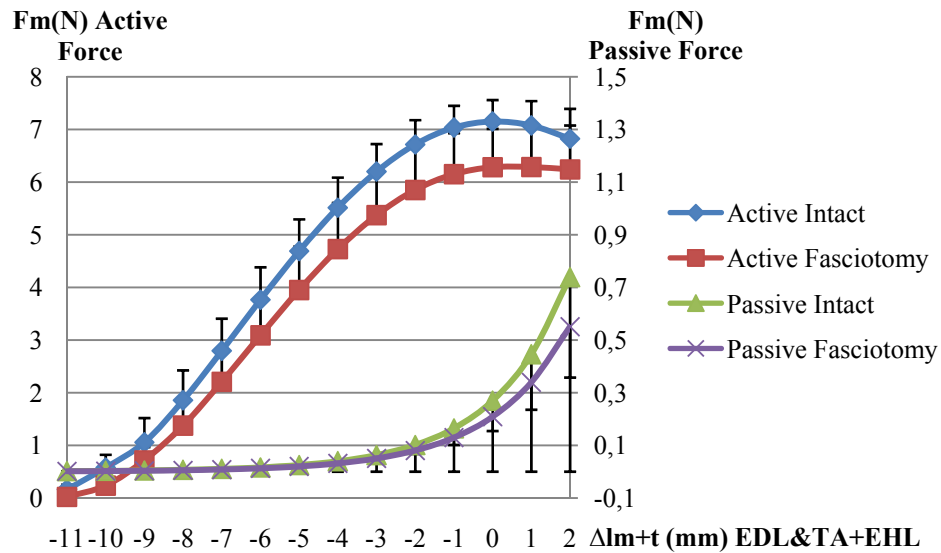


Figure 3.16 TA+EHL length-active and passive force characteristics in intact and partial fasciotomy conditions for EDL&TA+EHL muscles lengthening simultaneously. EDL&TA+EHL muscle tendon complex length is expressed as deviation (Δl_{m+t}) from optimum length.

3.3 Effects of Single Muscle Lengthening and Simultaneous Lengthening of Synergists on Muscle Length-Force Characteristics:

3.3.1 Intact Condition

3.3.1.1 EDL distal forces

In the intact condition, shape changes in EDL distal length-active force characteristics for lengthening of EDL exclusively compared to those for lengthening of EDL & TA+EHL simultaneously were significant (Fig. 3.17).

Simultaneous lengthening of synergists caused EDL distal active forces to decrease substantially at all muscle lengths studied (Fig. 3.17). Note that at lower muscle lengths such force decrease was greater than that measured at higher lengths (e.g. by 55.94% and 10.50% at $\Delta l_{m+t} = -5$ mm and at $\Delta l_{m+t} = 0$ mm respectively).

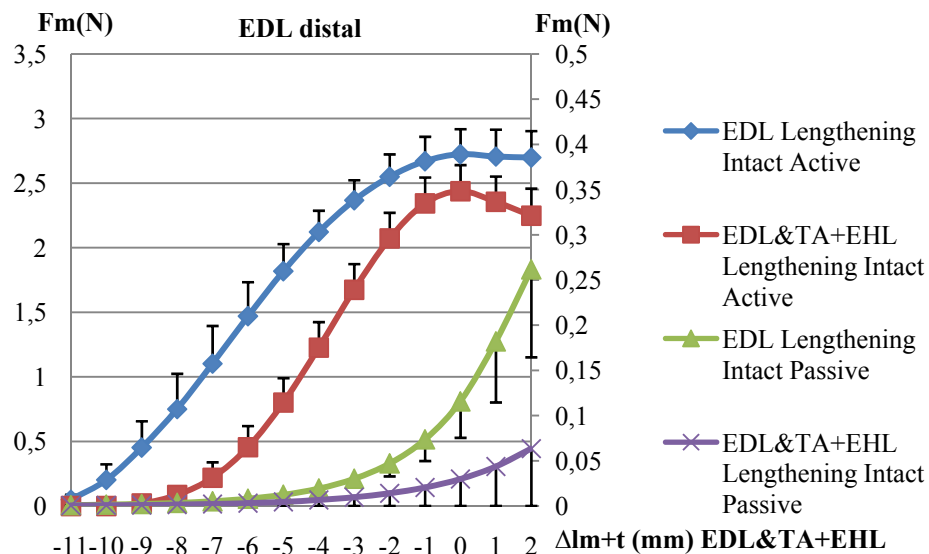


Figure 3.17 EDL distal length-active and passive force characteristics for lengthening of EDL muscle exclusively and lengthening of EDL & TA+EHL muscles simultaneously in intact condition. Synergists' muscle tendon complex length is expressed as deviation (Δl_{m+t}) from optimum length. It is concluded that in the intact condition, simultaneous lengthening of synergists causes: (1) shape changes leading to a substantial decrease in active and passive forces and (2) alterations in the determinants of muscle length-force characteristics including shifting of the muscle optimum length to a lower length (by 0.8 mm) and decreasing of the optimal force (by 10.50%) when compared to lengthening of EDL exclusively.

Regarding also passive EDL forces (Fig. 3.17), the shape changes due to the two lengthening conditions were significant. As a result of simultaneous lengthening of

synergists, EDL passive forces decreased substantially especially at higher muscle lengths (e.g. by 75.75% at $\Delta l_{m+t} = 2$ mm).

3.3.1.2 EDL proximal forces

In the intact condition, shape changes in EDL proximal length-active force characteristics for lengthening of EDL exclusively compared to lengthening of EDL & TA+EHL simultaneously were significant (Fig. 3.18).

EDL proximal active forces measured after EDL & TA+EHL lengthening simultaneously compared to forces of EDL muscle lengthening exclusively (Fig. 3.18) decreased substantially at lower muscle lengths (i.e., for $\Delta l_{m+t} < -2$ mm) in contrast to a sizable increase shown at higher muscle lengths (for $\Delta l_{m+t} > -2$ mm). Note that at lower muscle lengths, such force decrease was greater than that measured at higher (intermediate) muscle lengths (e.g. by 37.65% and 11.96% at $\Delta l_{m+t} = -5$ mm and at $\Delta l_{m+t} = -3$ mm respectively).

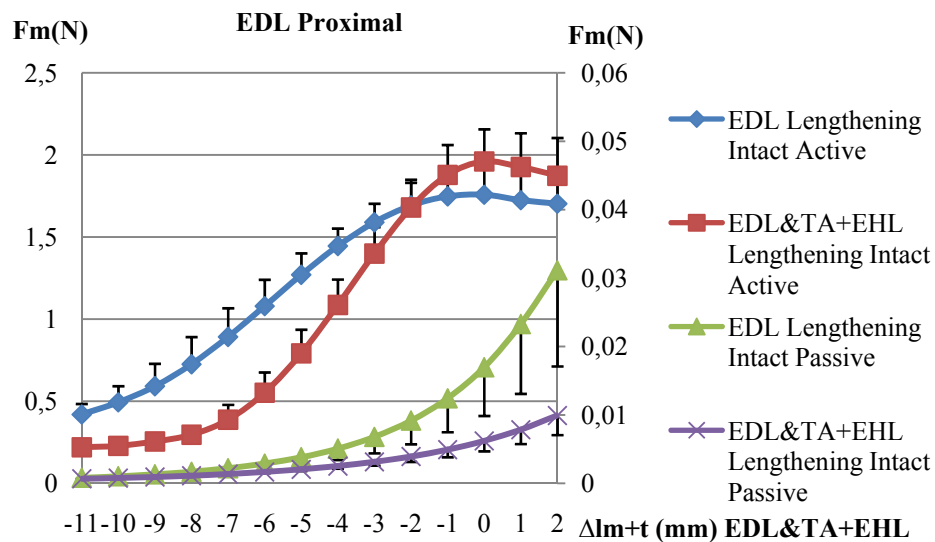


Figure 3.18 EDL proximal length-active and passive force characteristics for EDL muscle lengthening exclusively and EDL&TA+EHL muscles lengthening simultaneously in intact condition. EDL muscle tendon complex length is expressed as deviation (Δl_{m+t}) from optimum length. It is concluded that the, lengthening condition of synergistic muscles has major effects on muscle length-active force characteristics also proximally. Compared to EDL lengthening exclusively, simultaneous muscle lengthening causes: (1) major shape changes leading to a length dependent substantial decrease or increase in active forces and a sizable decrease in passive force (2) alterations in the determinants of muscle length-force characteristics including shifting of the muscle optimum length to a lower length (by 0.8 mm) and increasing of the optimal force by (11.52%).

Also for passive EDL forces, shape changes shown in EDL distal length-force characteristics due to the two muscle lengthening conditions were significant (Fig. 3.18). EDL passive forces decreased substantially especially at higher muscle lengths (e.g. by 68.14% at $\Delta l_{m+t} = 2$ mm).

Proximo-distal EDL total force differences

In the intact condition, EDL proximo-distal total force differences for EDL lengthening exclusively were higher than those measured for EDL & EDL+TA lengthening simultaneously for most muscle lengths (i.e., $\Delta l_{m+t} > -10$ mm).

The proximally directed net epimuscular myofascial load that acts on intact EDL muscle is encountered at higher muscle lengths for synergistic muscle lengthening simultaneously (i.e., the dominance of proximal load is compromised).

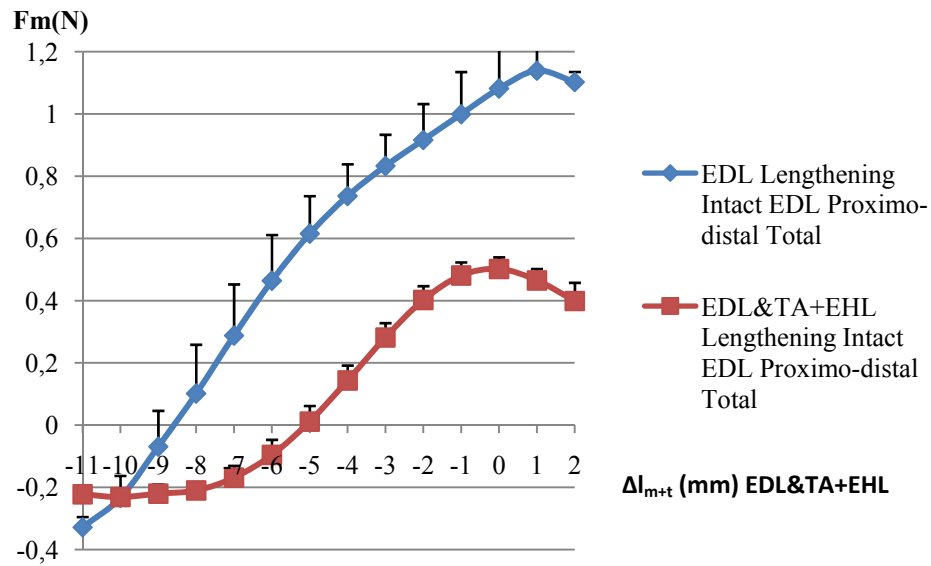


Figure 3.19 EDL proximo-distal total force differences ($F_{\text{distal}} - F_{\text{proximal}}$) for EDL muscle lengthening exclusively and EDL&TA+EHL muscles lengthening simultaneously in intact condition.

3.3.2 Partial Fasciotomy Condition

EDL distal forces

Also after partial fasciotomy, muscle lengthening condition caused significant shape changes in EDL distal length-active force characteristics (Fig. 4.20): EDL distal active

forces decreased substantially at all muscle lengths studied. Note that at lower muscle lengths, such force decrease was greater than that measured at higher lengths (e.g. by 48.95% and 25.33% at $\Delta l_{m+t} = -5$ mm and at $\Delta l_{m+t} = 0$ mm respectively).

Regarding also passive EDL forces, significant shape changes in EDL distal length-force characteristics were shown (Fig. 4.20): EDL passive forces decreased substantially especially at higher muscle lengths (e.g. by 64.82% at $\Delta l_{m+t} = 2$ mm).

It is concluded that also after partial fasciotomy, the lengthening condition affects substantially EDL length-active force characteristics distally. Simultaneous muscle lengthening causes: (1) shape changes leading to a substantial decrease in active and passive forces and (2) alterations in the determinants of muscle length-force characteristics including shifting of the muscle optimum length to a lower length (by 0.88 mm) and decreasing of the optimal force by (13.22%) when compared to EDL lengthening exclusively. Note that partial fasciotomy yields only a limited difference (of 0.08 mm) in the shift in optimum length.

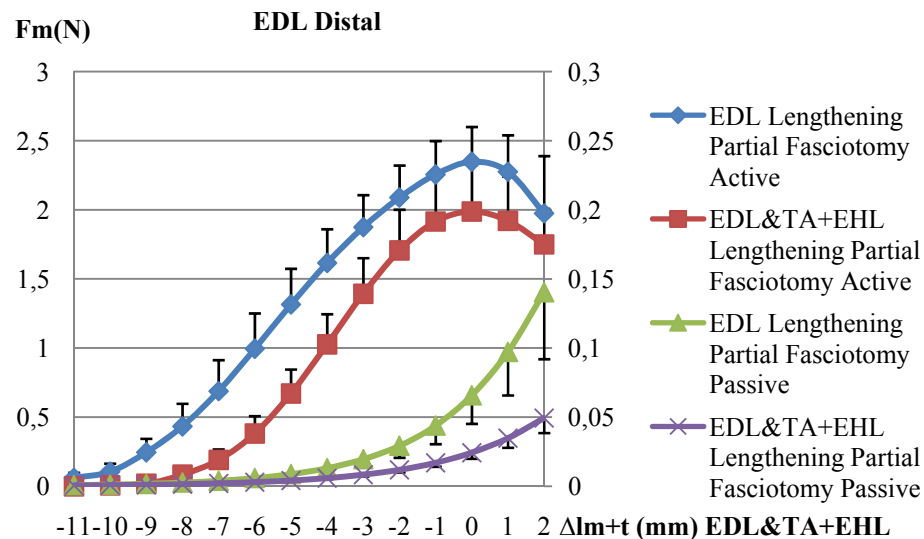


Figure 3.20 EDL distal length-active and passive force characteristics for EDL muscle lengthening exclusively and EDL&TA+EHL muscles lengthening simultaneously in partial fasciotomy condition. EDL muscle tendon complex length is expressed as deviation (Δl_{m+t}) from optimum length.

EDL proximal forces

After partial fasciotomy, the shape changes in EDL proximal length-active force characteristics in exclusive lengthening of EDL compared to simultaneous lengthening of EDL & TA+EHL were significant (Fig. 3.21).

EDL proximal active forces (Fig. 3.21), studied in simultaneous EDL & TA+EHL lengthening compared to forces in EDL muscle lengthening exclusively, decreased substantially at lower muscle lengths (for $\Delta l_{m+t} < -3$ mm) and increased considerably at higher muscle lengths (for $\Delta l_{m+t} > -3$ mm). Note that at lower muscle lengths, such force decrease was greater than that measured at higher lengths (e.g. by 35.39% and 4.61% at $\Delta l_{m+t} = -5$ mm and at $\Delta l_{m+t} = -3$ mm respectively).

Lengthening condition caused significant shape changes in EDL distal length-passive force characteristics (Fig. 3.21): EDL passive forces decreased substantially especially at higher muscle lengths (e.g. by 24.55% at $\Delta l_{m+t} = 2$ mm).

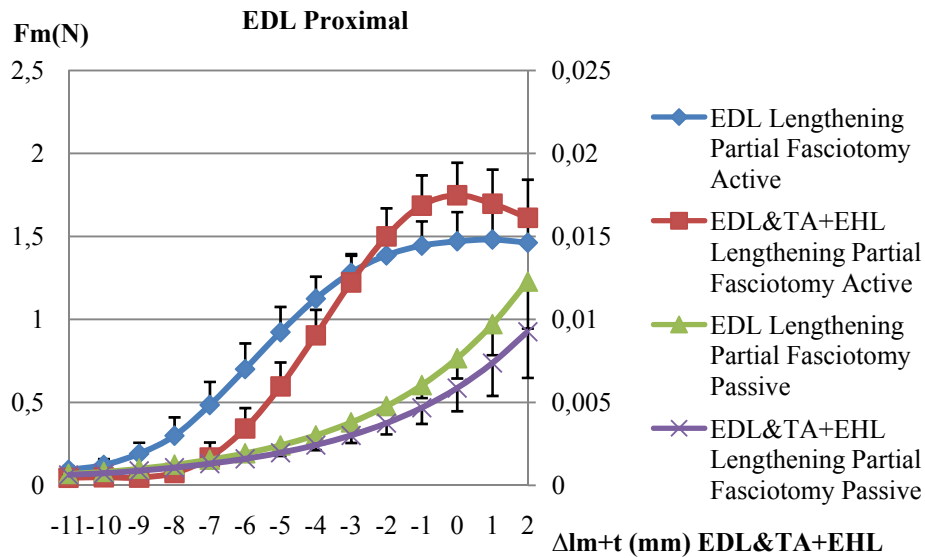


Figure 3.21 EDL proximal length-active and passive force characteristics for EDL muscle lengthening exclusively and EDL&TA+EHL muscles lengthening simultaneously in partial fasciotomy condition. EDL muscle tendon complex length is expressed as deviation (Δl_{m+t}) from optimum length.

Proximo-distal EDL total force differences

It is concluded that also after partial fasciotomy, the lengthening condition affects substantially EDL length-active force characteristics proximally. Simultaneous muscle lengthening causes: (1) major shape changes leading to a length dependent substantial decrease or increase in active forces and a sizable decrease in passive force (2) alterations in the determinants of muscle length-force characteristics including shifting of the muscle optimum length to a lower length (by 1.88 mm) and increasing of the optimal force by (18.88 %).

After partial fasciotomy, EDL proximo-distal total force differences for EDL lengthening exclusively were higher than those measured for EDL & EDL+TA lengthening simultaneously for most muscle lengths (i.e., $\Delta l_{m+t} > -10$ mm).

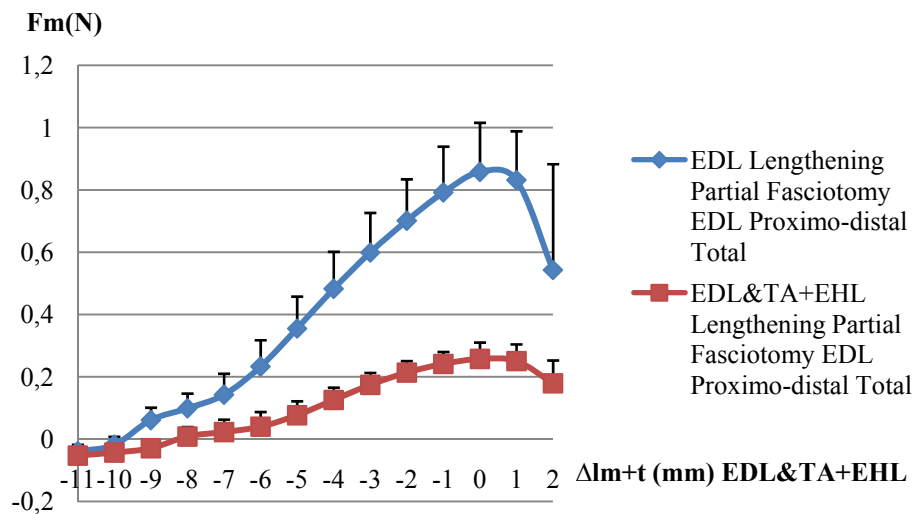


Figure 3.22 EDL proximo-distal total force differences ($F_{\text{distal}} - F_{\text{proximal}}$) for EDL muscle lengthening exclusively and EDL&TA+EHL muscles lengthening simultaneously in partial fasciotomy condition

The proximally directed net epimuscular myofascial load that acts on intact EDL muscle is encountered at higher muscle lengths for synergistic muscle lengthening simultaneously (i.e., the dominance of proximal load is compromised).

4. DISCUSSION

4.1 Effects of History

In an experimental study, measurement errors are always present. In order to minimize them controlled conditions are provided. Muscle tissue has viscoelastic properties and due to that, even under such controlled conditions, activity during the experiment may change the properties of the muscle such as architecture, tendon length, fiber length, contraction type, frequency of stimulation, amplitude of stimulation and recovery time, in a systematic way. History dependence of force production is the effect that the recent contractile conditions have on the force produced by a muscle. If this dependence is small, it usually does not interfere seriously with the purpose of the experiment.

In our present study, to test the role of increased recovery time for control measurements, on history effects, control measurements were performed subsequently i.e., after (1) our typical recovery period of 2 minutes and (2) an extended recovery period of 15 minutes. These measurements were referred to as *the first control measurements* and *the second control measurements*, respectively.

4.1.1 Control Measurements for EDL Distal, EDL Proximal and TA+EHL Forces in Intact and Partial Fasciotomy Conditions

4.1.1.1 EDL lengthening exclusively

4.1.1.1.1 First control measurements

For EDL lengthening exclusively for first control measurements it is concluded that (1) for both intact and partial fasciotomy conditions and for both muscle lengths, the difference between the control measurements and the actual data is rather limited for the restrained TA+EHL muscle complex. This finding shows that the history effects remain very limited for the restrained TA+EHL so the effects shown presently on muscle length-force characteristics are ascribable almost exclusively to different components of epimuscular myofascial force transmission.

For the lengthened EDL muscle, for both intact and partial fasciotomy conditions and for both muscle lengths (1) the difference between the control measurements and the actual data does not substantiate at the optimum length whereas, (2) it may reach quite high levels at the lower (reference) muscle length studied.

Limited force difference for optimum length shows similarity with the experimental results reported by Smeulders et al [23] for control measurements for flexor carpi ulnaris muscle of the rat. Such limited force difference indicates minimal history effect. Therefore, the effect of partial fasciotomy shown presently on muscle length-force characteristics at higher muscle lengths is also related largely to epimuscular myofascial force transmission.

However, at lower muscle lengths, our present results show considerable differences between the actual data and control forces. For example, in the intact condition, EDL muscle distal control force was 78.53% lower than the actual force at reference position. Therefore, a certain part of the changes in muscle force at lower muscle lengths does not seem ascribable to epimuscular myofascial force transmission.

Nevertheless, the history effects themselves are affected by epimuscular myofascial force transmission: the force difference between control and actual data becomes less pronounced after surgical dissections (e.g. for EDL distal force, force decrease of 78.53% was reduced after partial fasciotomy to 60.27%).

The mechanisms of history effects are obscure. A highly likely source may be the time dependent viscoelastic properties of muscle tissue e.g., stress relaxation. However, in our experiment the history effects for the restrained muscle group which is the synergistic of the target muscle were shown to be minor. This suggests that stress relaxation may not be the dominant mechanism.

On the other hand, previous activity at high muscle lengths was shown to cause decreased active force exerted at low muscle lengths [28] and repeated activity at low length subsequent to that at high length was shown to cease such reduction of active force [7]. The nature of such procedure involves a loading and unloading cycle for the muscle tissue indicating that hysteresis may be responsible with the history effects. In our study, the conditions for collecting actual and control data were different due to the experimental protocol: loading cycle (for actual measurements) involves increasing muscle length from

active slack length to higher lengths in *multiple steps* of 1 mm. Unloading cycle (for control measurements) involves shortening of muscle from $\Delta l_{m+t} = 2$ mm to the reference length (approximately $\Delta l_{m+t} = -6$ mm) in *a single step*. This causes sizable differences in the loading and unloading cycle and may employ a different history mechanism, which may be responsible with the differences between actual and control data.

Note that, the history effects being much less pronounced at higher muscle lengths may simply be because of a highly similar loading and unloading cycle to that applied in measuring of the actual data: control forces at high length were measured after one more contraction subsequent to the actual force measurement. In our view, comparisons between the actual data after surgical dissections are consistent since the loading and unloading path is no different.

4.1.1.1.2 Second control measurements

For EDL lengthening exclusively for second control measurements our conclusions were same with that of the first control measurements: force difference between the control measurements and the actual data is rather limited for the restrained TA+EHL muscle complex, for the lengthened EDL muscle such difference does not substantiate at the optimum length whereas, it may reach quite high levels at the lower (reference) muscle length studied.

A comparison between the second control measurements and the first control measurements shows that increase in recovery time increased the differences between control and actual forces. This is valid for both intact and partial fasciotomy conditions, for the restrained TA+EHL muscle complex and for the lengthened EDL muscle and both at the reference and the optimum lengths. Such more pronounced effect of added time shows that viscoelastic muscle properties play an important role in the history effects. We suggest that stress relaxation becomes a dominant mechanism only if recovery time is increased in a muscle mechanics experiment.

4.1.1.2 EDL & TA+EHL lengthening simultaneously

4.1.1.2.1 First control measurements

For EDL & TA+EHL lengthening simultaneously our results showed that regarding

effects of history, TA+EHL muscle complex acts similar to EDL muscle if these muscles are lengthened simultaneously with EDL muscle: for both intact and partial fasciotomy conditions, the force difference between TA+EHL (also for EDL forces) control measurements and the actual data is (1) small at the optimum length whereas (2) such difference may reach quite high levels at the lower muscle length studied. Note that, for EDL muscle distally, for both conditions and muscle lengths, the difference between control measurements and the actual data is lower after simultaneous lengthening of the synergistic muscles. Such decrease of history effects after simultaneous muscle lengthening may be explained by the decrease of the epimuscular myofascial load (exerted by TA+EHL muscle complex to EDL muscle) due to decrease in relative position difference between the anterior crural muscles.

4.1.1.2.2 Second control measurements

Also for the second control measurements, TA+EHL muscle complex acts similar to EDL muscle after lengthening of synergistic muscles simultaneously: for both intact and partial fasciotomy conditions, the difference between TA+EHL (also for EDL forces) control measurements and the actual data is (1) fairly small at the optimum length whereas, (2) such difference reaches high values at the lower muscle length.

As for the first control measurements, also for the second control measurements for EDL muscle distally forces for simultaneous lengthening of synergistic muscles are lower than those for lengthening of EDL muscle exclusively.

A comparison between the second control measurements and the first control measurements shows that increase in recovery time increased the differences between control and actual forces. This is valid for both intact and partial fasciotomy conditions, for the lengthened TA+EHL muscle complex and EDL muscle at the reference lengths but not relevant for optimum lengths. This can be explained by the decrease of the epimuscular myofascial load (exerted by TA+EHL muscle complex to EDL muscle) due to decrease in relative position difference between muscles by simultaneous lengthening. Therefore, increase in history effect by the time component seems compensated by the decrease in history effect by epimuscular myofascial load component. As muscle function in vivo involves typically such simultaneous length changes of neighboring muscles and not extended periods time between contractions, it is conceivable that the effects of

epimuscular myofascial force transmission may be substantial and much less affected by history effects.

4.2 Effects of Different Components of Epimuscular Myofascial Force Transmission on Muscular Mechanics:

For a muscle with its epimuscular connections intact, it has been shown that force measured at the origin of a muscle is mostly not equal to the force exerted at its insertion [7] which is a strong evidence for myofascial force transmission.

The concept of myofascial force transmission is based on the transmission of force between muscle fibers and fascial connective tissues. If the force is transmitted from muscle via its epimysium, force transmission is referred to as *epimuscular myofascial force transmission* [29].

There are two pathways for epimuscular myofascial force transmission: (1) by direct connections between the intramuscular stromata of two adjacent muscles which is referred as *intermuscular myofascial force transmission* [15, 26] (2) by collagenous connections between the intramuscular stromata and extramuscular connective tissue structures, such as connective tissues reinforcing nerves and blood vessels, intermuscular septa, the interosseal membrane, compartmental fascia and epitendinous tissues which is referred as *extramuscular myofascial force transmission* [7, 30].

4.2.1 Experimental Conditions:

In our study to provide the experiments with conditions close to those in vivo, the knee and ankle joint angles comprising the reference position were selected from the data determined by Grunner et al [32] corresponding to an in vivo posture of rat in the beginning of the stance phase during treadmill stepping. Therefore, lengths of EDL and TA+EHL muscles at reference position are representative of foot contact for gait of the animal in vivo.

So far, certain experimental studies showed the mechanical interaction between muscles of anterior crural compartment via myofascial pathways [15, 27, 31] but the experimental conditions imposed do not represent in vivo conditions. This is because in those studies, EDL muscle or TA+EHL muscles were lengthened exclusively whereas, the

neighboring synergistic muscles were kept at a constant length. In vivo movement involves simultaneous lengthening of a group of synergistic muscles. Therefore, in our present study we investigated the effects of lengthening of the whole anterior crural muscle group and compared the results to those measured in lengthening of EDL exclusively. Such more representative approach still showed substantial effects of epimuscular myofascial force transmission on muscular mechanics.

The compartmental fascia is a continuous structure throughout the anterior crural compartment and recent experiments implied that the distal part of it is stiffer (*referred to as distal fasciae*, [37]). Neurovascular tract connects to the EDL muscle belly longitudinally along the entire muscle length (for pictures see [7, 26, 27, 28, 30]). However, it was shown that approximately the proximal third of this structure (for a picture see [5]) is much stiffer than the remainder [30]. Our present study analyses the effects of partial fasciotomy (approximately by 50%) of the lateral aspect of the anterior crural compartment proximally on muscular mechanics. Note that the presently applied fasciotomy interferes directly with the fascial component of extramuscular connections exclusively: the neurovascular tract to EDL muscle still remains intact.

4.3 For EDL Lengthening Exclusively

4.3.1 Changes in Proximo-Distal Force Difference after Partial Fasciotomy

Our present results show that in both intact and fasciotomy conditions, proximally and distally measured EDL muscle total forces were unequal for most of the muscle lengths studied. Such proximo-distal force difference was reported by Huijing and Baan [26] for proximal and by Yucesoy [34] for distal EDL lengthening. Note that the proximo-distal total force difference at each muscle length equals the net value of the epimuscular loads acting on different parts of EDL muscle as determined by variations in the stiffness of epimuscular connections and the relative position of muscle.

Muscle relative position is a major determinant of epimuscular myofascial force transmission. As the length of the target muscle increases, the direct collagenous intermuscular connections of adjacent muscles are stretched. This will increase the epimuscular load to be exerted on the connective tissue stroma of the muscles. Any length change will change the position of a muscle with respect to the fixed bony structures and

cause loading of extramuscular connections. These loads are seen as determinants of sarcomere lengths.

Lengths of sarcomeres within muscle fibers show major heterogeneity due to epimuscular myofascial force transmission. It is well known that the sarcomeres arranged in series within a muscle fiber are in mechanical interaction. Intracellular and extracellular matrices are connected mechanically to muscle fibers with complex structures such as trans-sarcolemmal molecules. Therefore, lengths of sarcomeres cannot be determined exclusively by the interaction between the sarcomeres of the same fiber. Not only the forces exerted on it by the fiber reinforced extracellular matrix but also the forces of the sarcomeres located in neighboring muscle fibers should be taken into consideration. Moreover, due to the connections between intramuscular connective tissue and epimuscular connective tissues also the epimuscular loads are expected to take part in the balance of forces and therefore in determining the sarcomere length. It should be noted that such a net epimuscular force is not distributed uniformly because of non-uniform distribution of epimuscular tissues, such as neurovascular tracts, which affect the stiffness of the adjacent tissues or muscles. Presently, for EDL lengthening exclusively in the intact condition, a distally directed net epimuscular myofascial load acts on EDL muscle at lower muscle lengths. Remarkably, after partial fasciotomy, the distal load at lower lengths was removed because of the destruction of the proximal fascial connections between EDL and TA+EHL muscles, which are the producers of distal load.

For intermediate and high lengths of EDL muscle, as a function of increasing muscle length, the direction of epimuscular load was reversed such that the net epimuscular load was directed proximally. Although proximo-distal force difference decreases after partial fasciotomy such proximal load was still prominent since: (1) the neurovascular tract which gets stiffer on EDL muscle lengthening and despite (2) distal part of the compartmental fascia which connects EDL muscle distally to TA+EHL muscle still remains intact.

We conclude that partial fasciotomy alters substantially the epimuscular loads acting on EDL muscle which strongly indicates a major influence of this surgical intervention on the muscular mechanics (affecting sarcomere lengths) and function.

4.3.2 Shifts in EDL Optimum Length after Partial Fasciotomy

A major result of our present study is that after partial fasciotomy, the optimum length of EDL muscle shifts to higher muscle lengths distally. This suggests that disruption of different components of epimuscular connections causes an increased heterogeneity of mean sarcomere lengths of different fibers (a parallel distribution of sarcomere lengths). Such increased heterogeneity of mean sarcomere length of different fibers was shown to enhance muscle length range of force exertion [36]. For EDL muscle with extramuscular connections exclusively [30, 34, 35] or with inter- and extramuscular connections [15] and for extramuscularly connected EHL muscle [29] previous finite element modeling coupled with experiments showed that different components of epimuscular myofascial force transmission alter substantially the distribution of sarcomere lengths. Moreover, Yucesoy et al [30] showed that a shift in optimum length of epimuscularly connected EDL muscle to a higher length is correlated positively with increased parallel distribution of sarcomere lengths. However, in contrast to our present results, these authors showed that optimum length of EDL muscle shifts to higher lengths if its epimuscular connections are left intact. Such contradiction between the two studies may be explained with the relative position differences of muscles imposed by the experimental conditions: in our study the knee and ankle joint angles were set to 120° and 100° respectively while these angles were 90° for both joints in the study of Yucesoy et al. Also they shortened EDL muscle by 2mm proximally. All these reference position differences are conceivable to change the epimuscular loads on muscles yielding a complex mechanism of sarcomere length distributions. Note that in our present study, partial fasciotomy caused shifting of also the proximal optimum length of EDL muscle to a higher muscle length sustaining the indication of increased heterogeneity of mean fiber sarcomere lengths.

4.3.3 Reduction of EDL Forces after Partial Fasciotomy

Partial fasciotomy was shown presently to cause EDL active distal and proximal forces to decrease substantially. This is ascribable to (1) altered sarcomere length distributions and (2) the decrease in active force transmitted from the TA+EHL muscle complex to the EDL muscle via the extramuscular connections.

For EDL distal force: We suggest that both mechanisms are responsible with the reduction in active force. A reduction in muscle optimal force is caused by a more

heterogeneous parallel distribution of sarcomere lengths was shown previously [17, 36]. The presently measured shifts in muscle optimum length after partial fasciotomy and the simultaneous reduction in muscle optimal force indicate the important role of altered sarcomere length distribution in muscle force reduction distally. In addition, it was shown that some of TA+EHL active force is exerted at the distal EDL tendon for intact EDL muscle (e.g. [15, 27, 31, 37]). Therefore, the reduction in EDL active distal force shown presently after partial fasciotomy beside sarcomere length heterogeneity is also ascribable to interfering with the force transmitted from TA+EHL muscle complex to EDL distal tendon.

A study also involving partial fasciotomy (the *distal part* of the antebrachial compartmental fascia was incised longitudinally over two-thirds of muscle length) on rat flexor carpi ulnaris (FCU) muscle, in which FCU was lengthened distally, showed similar results at lower muscle lengths, however not for higher lengths [23]. This indicates that a different epimuscular myofascial force transmission mechanism is present within different compartments; however, the sizable mechanical role of compartmental fascia becomes confirmed.

For EDL proximal force: In our present study, partial fasciotomy causes a substantial reduction of also EDL proximal force however; such effect is more pronounced at lower muscle lengths. We suggest that the predominant mechanism of such force reduction is the altered sarcomere length distributions: our results indicate that at lower muscle lengths, disruption of different components of epimuscular connections remove gradually the epimuscular loads exerted on the muscle which loads must be responsible with limiting sarcomere shortening and therefore reduction of muscle force.

Additionally, shift of the length-active force profile to a higher length after dissection, partly explains the decrease in force output specifically at low muscle length, since such a shift has the greatest effect at the steepest part of the profile. Because after dissection the curvature changes to an even steeper profile, the decline of the force at low muscle length is enhanced. In addition to that a steeper curvature after dissection implicates a decreased active length range of the muscle after dissection.

Regarding the rather limited force reduction at higher lengths a plausible explanation is that the neurovascular tract gets stretched applying a proximally directed load on the

proximal ends of muscle fibers. Such load conceivably keeps the sarcomeres at lengths favorable for force production.

Based on previous work in intact condition, increasing EDL length distally causes transmission of some of EDL proximal force onto TA+EHL muscle complex: (1) finite element modeling [30].showed that the proximal force of restrained synergist (representing TA+EHL muscle complex) increased (2) earlier experiments showed that the force exerted onto the tibia (the origin of some muscle fibers of TA) increased as a function of EDL muscle length. Therefore, partial fasciotomy is likely to reduce such force transmission from EDL muscle.

For EDL passive forces: For a truly isolated muscle, passive force is due to the tensile resistance of the muscle tissue only. However, for muscle with extramuscular connections, Yucesoy et al [15] showed that distally passive forces start building up already at lengths lower than optimum muscle length. This happens because the extramuscular connections cause a certain passive resistance even at those lengths.

It is also interesting that while the distal EDL passive force increases at all lengths, the proximal passive force increases only at higher muscle lengths. This shows that any tensile loading of the proximal part of the passive muscle at lower lengths is prevented by the extramuscular connections.

Presently, after partial fasciotomy both distally and proximally passive EDL forces decreased considerably, in which force reduction was higher proximally than distally. This is explained by the decreased epimuscular connections, especially proximally, due to proximal fasciotomy.

4.3.4 Reduction of TA+EHL Force after Partial Fasciotomy

Our present results show alteration of also TA+EHL force after partial fasciotomy and due to EDL lengthening. Such effect of neighboring muscle lengthening was reported also in earlier experiments [15, 33, 37]. Additionally, the present study shows that partial fasciotomy lowers the percentage of decrease of TA+EHL force during distal lengthening of EDL muscle: distal lengthening of EDL muscle becomes less effective on TA+EHL muscle complex force. This indicates that, both inter and extramuscular connections are

active on myofascial force transmission mechanism and diminishing these connections lessens the force transmission from TA+EHL muscle complex to EDL muscle and other non-muscular structures.

Also TA+EHL passive forces decreases after fasciotomy since the stiffness of epimuscular connections are reduced due to disrupted integrity of anterior crural compartment.

4.4 For EDL & TA+EHL Lengthening Simultaneously

In first part of our study, in the anterior crural compartment, EDL muscle was lengthened exclusively whereas, the neighboring synergistic muscles were kept at constant length. This approach is sufficient to show the substantial effects of epimuscular myofascial force transmission. However, such highly asymmetric length changes of neighboring synergistic muscles are not likely during joint motion *in vivo*: muscles within the same compartment often undergo simultaneous length changes. In the view of this, EDL and TA+EHL muscles were lengthened simultaneously in the second part of our study. This simultaneously imposed length changes to all synergistic muscles limits the major determinant of myofascial force transmission effects i.e., the changes in muscle relative position (e.g. [35, 38]).

Simultaneous length changes of TA+EHL and EDL muscles represent ankle dorsiflexion performed together with extension of the toes respectively. Although this combined joint motion is not a part of gait motion it can be seen in passive warming up exercises. Nevertheless, our present approach represents the principles of simultaneous length changes of synergistic muscles (e.g. shortening of all hamstrings during knee flexion) and the results shown confirm that effects of epimuscular myofascial force transmission are conceivable also *in vivo*.

On the other hand, our approach still has important differences compared to the condition *in vivo* primarily because the ankle joint was kept at a fixed angle (in maximal plantar flexion) during the experiments. In general, for activity *in vivo*, length changes of TA muscle would alter ankle angle and hence the lengths of the antagonists (e.g. triceps surae muscles) too. Recent studies showed sizable epimuscular myofascial force transmission between antagonistic muscles (e.g. increasing TA+EHL complex length was

reported to decrease triceps surae force [39]). Therefore, the epimuscular interaction between the muscles of the lower leg is expected to be much more variable in vivo than tested presently. Regarding the present reference position in particular, maximal plantar flexion instead of ankle angle=100° causes the antagonists (e.g. triceps surae muscles) of the target muscle group to be active at shorter lengths during the experiment than their lengths would be at the reference position. This is conceivable to elevate the difference between the relative positions of the anterior crural muscles with respect to their antagonists. Therefore, more epimuscular myofascial interaction between these muscles is likely compared to the condition in vivo.

4.4.1 Effects of Partial Fasciotomy on EDL and TA+EHL Muscles

In the intact condition, the total force exerted on the proximal tendon of EDL muscle was higher than that exerted on the distal tendon at lower muscle lengths. In contrast, at higher muscle lengths the distal force was higher than the proximal force. Such proximo-distal total force difference at each muscle length equals the net value of the epimuscular loads acting on EDL muscle. Therefore, it is concluded that a distally directed net epimuscular myofascial load acts on intact EDL muscle at lower muscle lengths; whereas, such load is proximally directed at higher muscle lengths. In contrast to our findings, Meijer et al. [37] showed that a distally directed net epimuscular load acts on EDL muscle for all muscle lengths. Note however that these authors reported active instead of total force differences. Total proximo-distal force differences would approximate proximal loads for high lengths of EDL muscle. A major determinant yet is the differences in experimental conditions between the two studies: (1) Meijer et al. [37] set the reference knee angle to 110° and shortened EDL muscle by 2 mm proximally, prior to any length changes imposed distally. Consequently, EDL muscle in the present study should be longer proximally. (2) The peroneal muscles were set to an intermediate length. This is in contrast to the very short peroneal muscle length imposed presently by maximal plantar flexion. Such condition differences conceivably caused sizable relative position differences: the former between the proximal end of EDL and synergistic TA muscle and the latter between the antagonistic anterior crural and peroneal muscles. The relative position effects between the antagonists must become more prominent especially at higher muscle lengths. This is plausible to cause the presently measured higher proximal epimuscular loads that act on EDL muscle. We conclude that relative position differences are not only important for

synergistic muscles but they have a substantial role in determining the effects of epimuscular myofascial force transmission between antagonistic muscles as well.

After partial fasciotomy, the distal load at lower lengths was removed because of the destruction of the proximal fascial connections between EDL and TA+EHL muscles, which is a source of such distal load.

For intermediate and high lengths of EDL muscle, net epimuscular load were directed proximally. Although proximo-distal force difference decreases after partial fasciotomy proximal load is still prominent primarily because the neurovascular tract which becomes stiffer when EDL muscle lengthened still remains intact. On the other hand, distal part of the fascia which provides certain connection between EDL muscle distally and TA+EHL muscle still remains intact. Although the effect of this structure for producing a distal load is decreased due to simultaneous muscle lengthening, it cannot be ruled out.

We conclude that partial fasciotomy alters substantially the epimuscular loads acting on EDL muscle also in more physiological conditions (i.e., after simultaneous muscle lengthening).

Moreover, for both active and passive forces of EDL partial fasciotomy causes: (1) shape changes leading to a substantial decrease in active and passive forces and (2) alterations in the determinants of muscle length-force characteristics including shifting of the muscle optimum length to a higher length and decreasing of the optimal force. Both optimal force decrease and optimal shift designated to EDL distal and proximal indicate increased heterogeneity of mean fiber sarcomere lengths. For TA+EHL partial fasciotomy caused active forces to decrease substantially.

It is therefore concluded that disrupting the integrity of epimuscular connections by partial fasciotomy has major effects on length-active force characteristics of TA+EHL muscle complex after imposing length changes simultaneously with the synergistic EDL muscle: similar to the effects shown for EDL muscle, partial fasciotomy causes a sizable decrease in active TA+EHL force.

4.5 Effects of Single Muscle Lengthening or Simultaneous Lengthening of Synergists on Muscle Length-Force Characteristics

4.5.1 Intact Condition

The main factor that forms differences between EDL lengthening exclusively and simultaneous lengthening of EDL and TA+EHL is the decrease in relative position of TA+EHL muscles according to EDL muscle. Previous studies showed that distal lengthening of the EDL muscle, as well as distal lengthening of synergistic EDL and TA+EHL muscles produce proximo-distal force differences which are indicative of epimuscular myofascial force transmission [17, 26]. The present results are in agreement with previous studies. However our present study is a novel demonstration of the effects of length of a whole muscle group of synergistic muscles on epimuscular myofascial force transmission between synergistic muscles after partial fasciotomy. In the intact condition, both the magnitude and the direction of the net epimuscular force on EDL are affected after the added lengthening of TA+EHL. For lengthening of EDL exclusively the proximo-distal total force difference reverses from a negative value at low lengths to a positive value at intermediate and high muscle lengths. The added lengthening of TA+EHL shifts the whole curve downwards (except at very low lengths). Although distally directed net epimuscular load was produced only at low lengths for exclusive lengthening, for simultaneous lengthening distal load was produced also at intermediate lengths. These results indicate that the proximally directed net epimuscular myofascial load that acts on intact EDL muscle is encountered at higher muscle lengths for synergistic muscle lengthening simultaneously. This is ascribable to changes in relative position between TA+EHL and EDL and concomitant length and stiffness changes in their intermuscular connections. After the added lengthening of TA+EHL, such changes in relative position between TA+EHL and EDL are absent and as result the dominance of proximal load is decreased but compromised.

4.5.2 Fasciotomy Condition

After partial fasciotomy, EDL proximo-distal total force differences for EDL lengthening exclusively were higher than those measured for EDL & EDL+TA lengthening simultaneously for most muscle length. The proximally directed net epimuscular myofascial load that acts on intact EDL muscle is encountered at higher

muscle lengths for synergistic muscle lengthening simultaneously (i.e., the dominance of proximal load is compromised).

It is concluded that also after partial fasciotomy, the lengthening condition affects substantially EDL length-active force characteristics distally. Simultaneous muscle lengthening causes decreasing of active and passive forces, shifting of the muscle optimum length to a lower length and decreasing of the optimal force when compared to EDL lengthening exclusively. A plausible explanation is reduced sarcomere length heterogeneity because of (1) reduced change in muscle relative position due to simultaneous muscle lengthening and (2) reduced stiffness of epimuscular connections after fasciotomy.

4.6 Fasciotomy as a Corrective Surgical Intervention

In most orthopedic surgeries related to muscle diseases fasciotomy (commonly partially) is widely applied. It is a preliminary step in musculo-skeletal system surgeries which effects mechanical interaction of muscle fibers and connective tissues.

In surgical operations such as tendon transfers, improved movement range is aimed at by altering the action of a muscle. However postoperative success is not observed in all patients (e.g. Askawa et.al [40]). These authors proposed that formation of scar tissue restricts muscle motion and limits the exertion of the desired force. Lieber [40] linked the same problem to an imperfect choice of muscle length for tendon reattachment. In contrast to studies that support major inhomogeneity in lengths of sarcomeres [15, 29, 36], Lieber made use of a single sample of sarcomere length as being representative of the entire muscle. However, taking the muscle out of its normal alignment to a new route changes the sarcomere distribution as a result of this new alignment. Therefore, myofascial force transmission was not accounted for however, without it our present results and the earlier findings of our research groups suggest strongly that the explanations will be incomplete.

Recently, Smeulders et al [23] studied the effect of progressive surgical dissection for tendon transposition on length-force characteristics of rat flexor carpi ulnaris muscle. These authors showed that partial fasciotomy performed distally alone caused an active force decrease approximately by 40% at low lengths compared to the intact situation providing strong evidence on the role of fascia in muscular force transmission.

To date, the surgeon's subjective estimation of passive tension of the muscle is the only guideline to qualify muscle function. In our present study, decrease in passive forces were seen mostly at high muscle lengths, whereas active forces decreased significantly at all muscle lengths. This suggests that the surgeon's estimation on such base only may not be accurate for muscular activity.

Compartment syndrome which is produced by increased pressure usually occurs as an overuse type of injury in athletes, resulting in a chronic affliction. If symptoms have persisted for longer than 6 months a complete fasciotomy is indicated as a treatment. Eventhough fasciotomy is clinically very successful regarding decompression; our present results indicate sizable muscle weakness. Garfin et al [22] raised a cost-benefit comparison by reporting force reduction in dog hindlimb after complete fasciotomy. The effect of such changes on muscular performance in the athlete should be considered in the decisions about therapy.

Fascia is a functionally important pathway for force transmission in surgeries. The effects of total fasciotomy on muscle mechanics have been studied recently [6, 26, 28] however, the effects of partial fasciotomy which intervention is routinely used in for example aponeurotomy surgeries in spasticity treatments have not been investigated especially in simultaneous lengthening of synergistic muscles. Based on our present findings and taking into account the earlier findings on the substantial role of epimuscular myofascial force transmission, we suggest that partial fasciotomy alone has major effects on muscular mechanics which should be considered by the surgeons for a full control over the desired and actual outcome of an operation.

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