

REVIEW | Synthesis

Not merely a protective packing organ? A review of fascia and its force transmission capacity

 Jan Wilke,¹ Robert Schleip,² Can A. Yucesoy,³ and Winfried Banzer¹

¹Department of Sports Medicine, Goethe University, Frankfurt am Main, Germany; ²Fascia Research Group, Neurosurgical Clinic Guenzburg of Ulm University, Ulm, Germany; and ³Institute of Biomedical Engineering, Bogazici University, Istanbul, Turkey

Submitted 20 June 2017; accepted in final form 28 August 2017

Wilke J, Schleip R, Yucesoy CA, Banzer W. Not merely a protective packing organ? A review of fascia and its force transmission capacity. *J Appl Physiol* 124: 234–244, 2018. First published November 9, 2017; doi:10.1152/jappphysiol.00565.2017.—Recent research indicates that fascia is capable of changing its biomechanical properties. Moreover, as it links the skeletal muscles, forming a body-wide network of multidirectional myofascial continuity, the classical conception of muscles as independent actuators has been challenged. Hence, the present synthesis review aims to characterize the mechanical relevance of the connective tissue for the locomotor system. Results of cadaveric and animal studies suggest a clinically relevant myofascial force transmission to neighboring structures within one limb (e.g., between synergists) and in the course of muscle-fascia chains (e.g., between leg and trunk). Initial in vivo trials appear to underpin these findings, demonstrating the existence of nonlocal exercise effects. However, the factors influencing the amount of transmitted force (e.g., age and physical activity) remain controversial, as well as the role of the central nervous system within the context of the observed remote exercise effects.

epimuscular; fascia; force transmission; myofascial chains

INTRODUCTION

Fascia, the fibrous connective tissue surrounding the skeletal muscles, has traditionally been characterized as a passive-enveloping sheath with limited significance for the movement system (86). Tittel's (83) atlas on functional and descriptive anatomy dedicated only seven lines to the characterization of fascia, and Wirhed (94) mentioned the terms fascia or myofascia in his entire textbook on sports anatomy as few as three times. However, during the last decades, the muscular connective tissue has aroused increasing interest from researchers and practitioners (Fig. 1). Besides possessing a potential role in proprioception and pain perception (91), fascia has been demonstrated to connect mechanically the muscles of the human body (31, 89, 98), which challenges the classical concept of muscles as being morphologically independent actuators.

Myofascial continuity may have significant implications for health, disease, and injury. For example, as claimed by some therapists, a mechanical force transmission across the muscle-fascia connections could explain the development of musculo-skeletal pain conditions on the one hand or increased performance during multijoint movements on the other hand (54). The present synthesis paper reviews recent histological and

experimental findings aiming to delineate the functional relevance of the fascial system in exercise and locomotion, with a special emphasis on myofascial force transmission.

CHANGES OF TISSUE STIFFNESS

Fascia alters its stiffness (the resistance to external deformation) via two mechanisms: cellular contraction and the modification of the fluid characteristics.

Cellular contraction. In vitro experiments have revealed a characteristic strain-hardening effect of fascia upon stretching. Whereas initially decreasing in response to this mechanical stimulus, tissue stiffness recovers during subsequent rest and may even rise above its original level (65, 96) (Fig. 2). It has been speculated that cellular contraction represents the moderating mechanism of the stiffness increase (96). Indeed, the presence of contractile cells has been confirmed for the plantar, lumbar, and crural fasciae and fascia lata and the fascia of the gastrocnemius muscle (9, 67, 70). In most cases, the detected contractile cells were myofibroblasts. They represent an intermediate type between fibroblasts and smooth muscle cells whose activity and differentiation are regulated by the mechanical loading of the tissue (29). The contractile force of myofibroblasts is two times higher than that of fibroblasts, which is due to the expression of alpha-smooth muscle actin in stress fibers (Fig. 3) (29, 95); whereas a single fibroblast contracts the extracellular matrix with 2 μ N, myofibroblasts reach a con-

Address for reprint requests and other correspondence: J. Wilke, Dept. of Sports Medicine, Goethe Univ. Frankfurt am Main, Ginnheimer Landstrasse 39, 60488 Frankfurt am Main, Germany (e-mail: wilke@sport.uni-frankfurt.de).

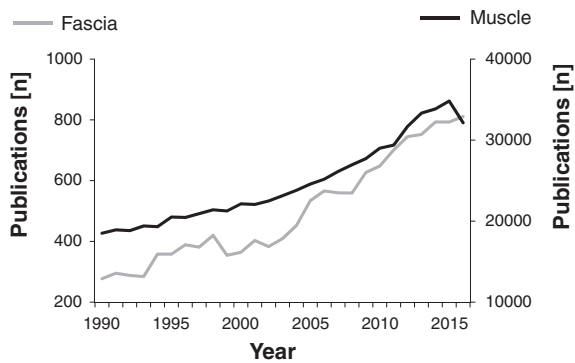


Fig. 1. Papers published on the topics of fascia and muscle since 1990. Depicted are total counts (PubMed search with terms “fascia” and “muscle”).

tractile force of $4.1 \mu\text{N}$ per cell (95). As myofibroblasts are interconnected via gap and adherence junctions (24, 84), they are capable of synchronizing their contraction, further increasing total mechanical impact.

The relevance of cellular contraction for the movement system is a matter of debate. Some authors assume that contractile cell activity creates a fascial tone (66, 70). According to calculations, the superficial lamina of the lumbar fascia at the level of L3 can contract with a force of up to 38 N (66). Such force production might be sufficient to influence musculoskeletal dynamics. Rat experiments suggest that the maximal contractile force of myofibroblasts in the lumbar fascia is reached 1 h after stimulation with mepyramine, a first-generation antihistamine (30). Cellular activity might hence be responsible for long-term rather than acute changes in connective tissue stiffness. This hypothesis is supported by data indicating that chronic excessive myofibroblast activity causes tissue fibrosis, which occurs in associated diseases, e.g., Dupuytren’s contracture or frozen shoulder (29).

In addition to exogenous pharmacological agents, such as mepyramine, cellular contraction in fascia is mediated by endogenous cytokines. Stimulation of the sympathetic nervous system has been demonstrated to influence the expression of the transforming growth factor $\beta 1$, a polypeptide promoting collagen synthesis (10). Transforming growth factor $\beta 1$ secre-

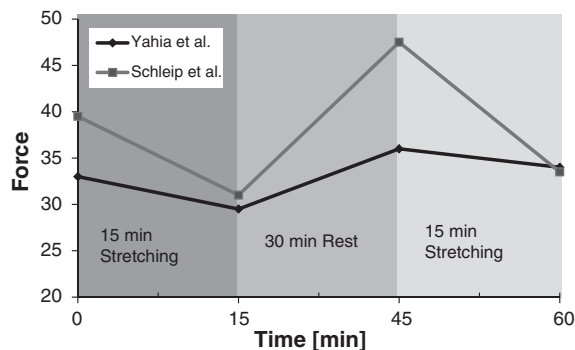


Fig. 2. Strain hardening of fascia: isometric lengthening of the tissue leads to a force decrease, indicating lower stiffness, which during subsequent rest, is followed by a supercompensation-like increase of fascial stiffness. Data from Schleip et al. (65) and Yahia et al. (96). Note that the strain-hardening effect was observed at higher (5 and 6%) but rarely at lower strain rates.

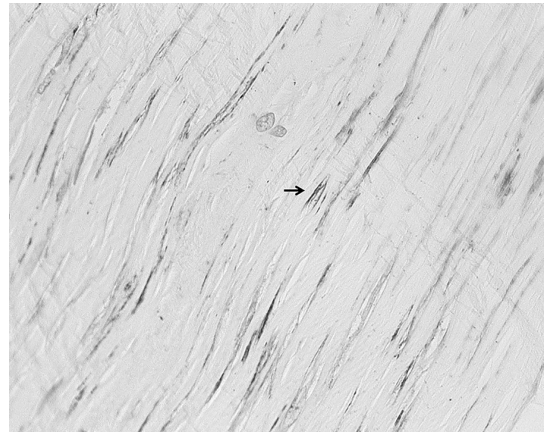


Fig. 3. Histological section of the posterior layer of the human thoracolumbar fascia, taken at the height of L4. alpha-smooth muscle actin stress fiber bundles (arrow)—a marker for myofibroblasts—are shown as darker.

tion, in turn, upregulates both myofibroblast differentiation and contractile activity (29, 84). Thus chronic shifts in the autonomic nervous system may affect fascial stiffness, thereby, inter alia, contributing to the development, prevention, and treatment of musculoskeletal pain conditions. Finally, another pathway influencing myofibroblast differentiation involves mechanical tissue loading, e.g., passive lengthening (37, 69, 84). However, it is unclear how these processes, mostly observed in the dermal tissues of animals, translate into humans.

Changes in the fluid characteristics. In contrast to chronic alterations, short-term fascial stiffness changes are unlikely to be driven predominantly by cell contraction. In their experiments, Schleip et al. (65) stretched porcine thoracolumbar fasciae after rendering the myofibroblasts unviable. Still, the tissue provided a strain-hardening response, which apparently, was not caused by the cells. In the absence of myofibroblast activity, the water content initially decreased and subsequently increased above its initial level, thereby resembling the strain-hardening curve. It can thus be inferred that the amount of water bound in the tissue substantially manipulates mechanical stiffness. This hypothesis is corroborated by other studies, demonstrating the influence of changes in water content on the viscoelastic behavior of the connective tissue (16, 27, 80). Its impressive dynamic adaptability is most obvious in the case of trauma: after only a few minutes, local fluid flow can increase by several hundred times (63). Whereas the relative contributions of cell contraction and changes in fluid content to the state of tissue stiffness cannot be quantified exactly, it is most plausible that both mechanisms act in concert. An increased interstitial fluid flow (e.g., following manual treatments) triggers both myofibroblast differentiation and the realignment of collagenous fibers (55). Hence, acute stiffness changes, induced by alterations in the water content, might favor the occurrence of long-term contractile activity increases.

Histochemical experiments have revealed the presence of hyaluronic acid (HA) between the fibrous layers of the myofascia. It provides a smooth, gliding lubricant and allows for high adaptability to motion of the underlying muscle (78). Similarly to other fluids, HA is sensitive to mechanical loading, and its concentration increases postexercise (61). Although

physiological amounts of the substance can be expected to facilitate movement, the thixotropic behavior of HA at higher concentrations may also cause restrictions (60). In the absence of mechanical loading, e.g., during physical inactivity and immobilization, HA becomes more viscous, and the mechanical result of this process might be a higher stiffness in the fascia.

MYOFASCIAL CONTINUITY

The connective tissue and the underlying muscle can influence each other via the mutual mechanical interaction between the contractile elements and the muscle-related fascial structures. Varela and Frenk (87) and Findley et al. (23) proposed a radial transmission of muscle force onto the enveloping fascia. During contraction, the shortened muscle increases its diameter, which in turn, stretches the epimysium. However, several anatomic details suggest that the mechanical interactions between muscular and connective tissue are well beyond that. Within the muscle belly, the contractile apparatus and the fascia, comprising the extracellular matrix, are interconnected. Muscle fibers and the endomysium not only fuse at the ends but also along the full peripheral length of the muscle fiber (8). Furthermore, intramuscular fasciae, including endomysium, perimysium, and epimysium, are continuous with collagen-reinforced structures, such as neurovascular tracts, intermuscular septa, compartmental fasciae, and interosseous membranes (31, 99). Finally, in some cases, direct insertions of skeletal muscles into the myofascia have been observed. For instance, the *Musculus deltoideus*, *M. latissimus dorsi*, and *M. pectoralis* display fibrous expansions connecting to the brachial fascia (72, 74, 77). It is assumable that the insertions allow for selective tensioning of the fascia, which in turn, supports and facilitates muscle activity via muscle and fascia mechanical interactions. A similar construction exists in the lower limb: the extensor hallucis longus muscle in the anterior crural compartment and the muscles of the peroneal compartment originate from the anterior intermuscular septum (100). This structure is continuous with the lateral collateral ligament, suggesting that muscle forces acting directly on the fascial system via muscle-fiber attachments or indirectly via the continuity described above can manipulate not only muscle function but also proprioception.

Structural continuity is not limited to the linkages between the fascia and the muscle. The connective tissue enveloping the adjacent compartmental muscles of the lower limb has been demonstrated to be tightly fused (33, 48). Likewise, there is also evidence for myofascial continuity in an in-series arrange-

ment: a fascial band connects the proximal end of the *M. gastrocnemius* to the distal *M. semitendinosus* (85). In view of the intimate morphological relationship between muscles and associated connective tissues, the effects of local stiffness changes and altered local muscular forces might affect both the tissue of origin and the surrounding areas. Two topics have therefore been the subject of recent research: myofascial force transmission 1) within limbs (e.g., between the adjacent muscles of the lower leg) and 2) in a series across myofascial chains (e.g., between the muscles of the leg and the trunk).

INTRALIMB MYOFASCIAL FORCE TRANSMISSION

The sarcomere is the basic functional unit of the skeletal muscle, and its length represents the key determinant of muscular force production and excursion (35). Taking this into account, mechanical interactions between the contractile elements and the muscle-related fascial structures, i.e., myofascial force transmission, have major functional significance, as they affect the force balance determining the length of a sarcomere. The muscle fiber's mechanical connections to the epimysium, along its full peripheral length, indicate that it cannot be considered as a mechanical element, which is connected to the extracellular matrix exclusively at the ends. That would mean that the force along the entire muscle-fiber length is identical, causing the sarcomeres arranged in a series within the muscle fiber to attain the same length. In contrast, as the muscle fiber has other connections to the extracellular matrix along its periphery, there must be myofascial loads acting on it. These loads include forces exerted by the endomysium, as well as forces produced in the neighboring muscle fibers. As a consequence, due to mechanical force transmission, force variations in both structures will mechanically influence their surroundings. This can even involve adjacent muscles: through the connective tissue linkages between them, strain applied to one muscle might be suspected to affect its neighboring synergists or antagonists directly (Fig. 4).

Evidence from cadaveric and animal studies. Upon passive proximal lengthening of the rat extensor digitorum longus muscle, Huijing and Baan (32) observed a force difference of up to 25% to occur between the proximal and distal tendon. The removal of the muscle's fascial linkages to the other muscles of the compartment almost eliminated the force difference, which indicates a mechanical force transmission through compartmental connective tissues. Several other studies have corroborated the occurrence of proximo-distal muscle force differences as the characteristic effect of intralimb myofascial force transmission [e.g., Maas et al. (46) and Yucesoy

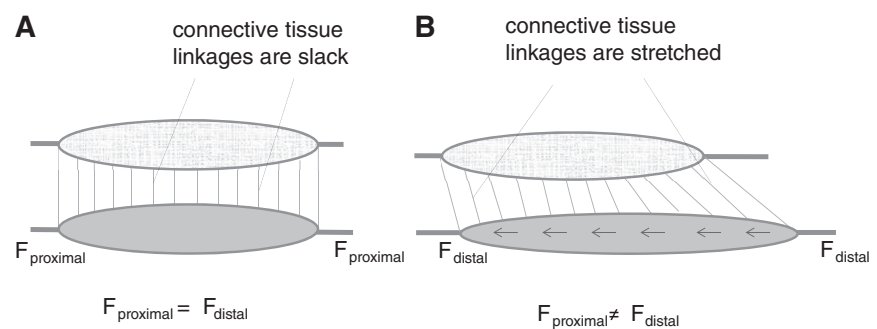


Fig. 4. Schematic illustration of the possible mechanical interaction between 2 adjacent skeletal muscles during rest (A) and isolated lengthening of 1 muscle (B). Based on Maas et al. (46a).

et al. (103)] (Fig. 5). Notably, these differences reflect the net amount and direction of epimuscular myofascial loads acting on the muscle, which conceivably create loads in various magnitudes and directions at different parts of the muscle (98). According to finite element modeling, such loads cause changes in sarcomere length and stress distributions along the fascicles (a measure of a muscle's force production), corresponding to the proximo-distal force differences (47). Another remarkable discovery is that intralimb myofascial force transmission can yield changes to the shape of the muscle's length-force characteristics (100), including a shift in the muscle's length range of force exertion, i.e., its excursion (103). Other calculations (93) confirm that the heterogeneity of the sarcomere lengths along and across muscle fascicles, as the mechanism of such change, is caused by myofascial loads and indicate that this can occur *in vivo*.

In experiments involving multiple compartments, Huijing et al. (33) studied the interaction between the various lower-leg muscles of the rat. Distal lengthening of the peronei muscles caused the active force of the *M. tibialis anterior* to decrease by 25%. Expanding on this finding, Yucesoy et al. (99) demonstrated epimuscular myofascial force transmission to affect the entire lower leg of the rat. Animal experiments and modeling show major effects of epimuscular myofascial force transmission on muscular mechanics with major functional implications and implications for *in vivo* muscle function (31, 98, 101, 102).

Evidence from *in vivo* studies. In addition to the large body of evidence derived from cadaveric/animal studies, which supports the relevance of intralimb myofascial force transmission, there are solid data describing its role in humans and under *in vivo* conditions. Bojsen-Møeller et al. (13) showed that the electrical percutaneous stimulation of the *M. gastrocnemius* induces a simultaneous displacement of the *M. soleus* and concluded on a possible force transmission between those muscles. Their observation was confirmed by the experiments of Huijing et al. (34), who used MRI to study the muscle strains of the lower limb during passively imposed knee motion. Considerable strains (on average, 9%, with local strains several times greater) were encountered in the *M. soleus*. As it does not cross the knee, and the ankle position was fixed, this finding is indicative of a myofascial force transmission from the gastrocnemius, which did undergo length changes. In a similar experiment (97), such mechanical interaction was found for other deep flexors in the lower limb and even antagonistic muscles, such as the peronei. Finally, Pamuk et al. (57) and Karakuzu et al. (39) demonstrated that knee extension imposed major strain heterogeneity along medial gastrocnemius fascicles, which

confirmed previous anticipations based on modeling (Fig. 6) (102).

Practical implications. In cerebral palsy (CP), limited joint mobility is often associated with higher forces of spastic muscles; higher force production, in particular, joint positions (typically flexed); and a narrow joint range of force production. Hence, the length-force curve of the muscle is shifted: its optimal force is encountered at shorter muscle lengths, and the muscle is incapable of producing active force at longer muscle lengths. Such altered characteristics of spastic muscle are typically explained by a physical shortening of the muscle, e.g., due to contractures. They cause a decreased number of serially arranged sarcomeres within the muscle fibers so that the peak force is attained earlier, and the myofilament overlap becomes exceeded upon stretching (51). In contrast, there are studies demonstrating no such adaptation (49). Recent intraoperative tests showed that spastic gracilis (3), semitendinosus (3), and semimembranosus (unpublished data) muscles do not necessarily have a profound force production in flexed knee positions and a narrow joint range of force exertion if they are stimulated alone. Moreover, the muscles were shown to produce a very large portion (above 80%) of their peak forces in a fully extended knee position. This indicates that the knee flexors of CP patients may not be exposed to a major physical adaptation in at least some cases. It also demonstrates that in the passive state of lower-leg muscles, the mechanical interactions between those muscles and the tested spastic muscle were not capable of substantially affecting its mechanics. However, in a different study, the simultaneous coactivation of a knee extensor did considerably affect the forces of the spastic gracilis muscle (4). For most of the tested participants, the muscle's higher force production (including the peak force) was encountered in flexed knee positions. Epimuscular myofascial force transmission should therefore be considered as a determinant of the pathological knee-joint condition in CP, and tissue adaptations might occur in the fascial structures rather than in the muscle contractile apparatus. This has considerable implications for surgical treatments (101) and spasticity management of CP patients using botulinum toxin [e.g., Ateş and Yucesoy (5)]. The latter was shown to compromise epimuscular myofascial force transmission among rat muscles exposed to it (104). If a similar process occurs in CP patients, then existing treatment approaches should be rethought.

Besides CP, intralimb myofascial force transmission may play a crucial role in sports performance, as it is capable of changing the muscular force production and excursion, both of which affect joint moments and range of motion (ROM). In

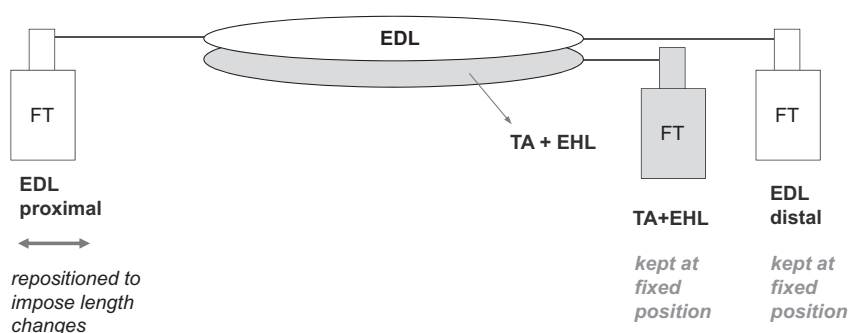


Fig. 5. Typical experimental setup assessing epimuscular myofascial force transmission in animals [based on the work of, e.g., Huijing and Baan (32)]: the extensor digitorum longus (EDL) proximal and distal tendons of the tibialis anterior (TA) and extensor hallucis longus (EHL), are connected to force transducers (FT). All muscles of the compartment are maximally excited at the same time. Imposed length changes of the EDL cause proximo-distal EDL force differences and changes to TA + EHL forces (despite their fixed length) as characteristic effects of epimuscular myofascial force transmission.

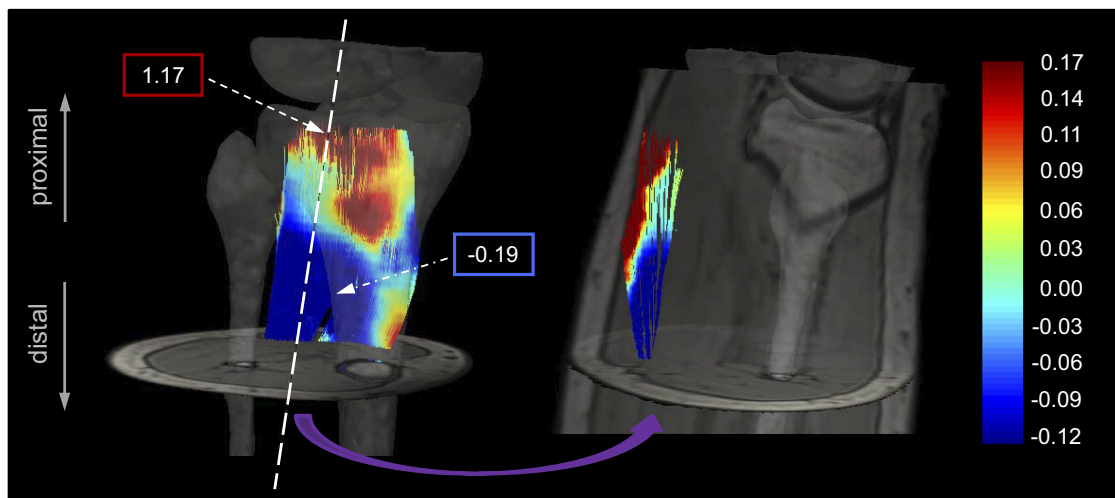


Fig. 6. Muscle fiber direction strains due to passive knee extension in human medial gastrocnemius in vivo. Strains calculated using MRI analyses [Huijing et al. (34) and Yaman et al. (97)] are projected on tracked medial gastrocnemius fascicles obtained using diffusion tensor imaging analyses [Pamuk et al. (57)]. The color bar indicates heterogeneity of strain along the fascicles: 0.17 and -0.12 represent 17% local lengthening and 12% local shortening, respectively. The peaks of local lengthening and shortening are shown separately in red and blue boxes, respectively (*left*). The white dashed line (*left*) corresponds to the sagittal slice (*right*). Local shortening accompanied by local lengthening along the same fascicles indicates the effects of epimuscular myofascial force transmission.

healthy individuals and athletes, an understanding of intermuscular mechanical interactions can help to optimize and restore performance. Adaptations in the fascial structures (both intra- and intermuscularly) potentially cause the same muscles to function differently. For instance, due to myofascial force transmission through the connective tissue linkages, the pathologically increased stiffness (stemming from training overload, disease, or injury) of a muscle can restrict the extensibility of synergists and antagonists.

Under physiological conditions, intralimb myofascial force transmission seems to be of relevance during eccentric contractions and stretching interventions. Eccentric contractions—a hallmark of athletic movement—impose high mechanical stresses on the affected muscle. Possibly, myofascial force transmission to neighboring muscles represents a mechanism protecting the target muscle against overload. Stretching, so far, has been used primarily to alter the neurophysiological and biomechanical function of the lengthened muscle. However, due to the morphological connections, it might as well affect synergists and antagonists, thereby modifying sports performance.

In sum, future research is needed to address the hypothesized relevance of intralimb myofascial force transmission for musculoskeletal disorders and sports performance. Besides movement-based interventions, it might be interesting to elucidate the effects of soft-tissue treatments on the degree of mechanical interaction. Self-myofascial release using a foam roller and manual therapy could be capable of manipulating force transmission and thus facilitate or limit movement and power output. Early evidence suggests that small forces might be sufficient to induce mechanical interactions between compartmental muscles. In a recent experiment, the use of Kinesio Taping caused strain distributions within the targeted and nontargeted adjacent muscles of the human lower leg, which is indicative of in vivo myofascial force transmission (57).

Limitations and perspectives. Some authors have questioned the relevance of intralimb myofascial force transmission for

physiologically representative or in vivo conditions [e.g., Herbert et al. (28)]. Maas and Sandercock (48) examined the influence of *M. gastrocnemius* and *M. plantaris* length changes on the soleus ankle moment in the cat. Despite strong structural continuity between the muscles, no substantial mechanical interaction was shown. In a similar experiment, only small amounts of myofascial force transmission were found between the lateral gastrocnemius/soleus and the medial gastrocnemius (64). Likewise, a study with living rats showed that different knee angles, between 60 and 90°, have no influence on soleus ankle moment (82). Although they cannot be directly extrapolated to humans, those findings suggest that intralimb myofascial force transmission may have limited effects on muscle force under physiological conditions. This hypothesis is, however, contrasted by data from Bernabei et al. (7), who found a substantial mechanical interaction between the rat soleus and the lateral gastrocnemius and plantaris complex.

Tian et al. (81) studied intersynergistic force transmission between the gastrocnemius and the soleus in humans in vivo. Knee flexion, at a constant ankle position, did induce myofascial force-transmission effects, indicated by soleus length changes. However, this effect was partly ascribed to the shortening of the common Achilles tendon. Hence, it is of particular interest to delineate more precisely the relative contribution of myotendinous mechanical interactions among muscles that share a common tendon.

In conclusion, limited data suggest that intralimb myofascial force transmission is paramount in pathological conditions (e.g., spastic paresis) but has a smaller yet potentially relevant role under physiological conditions if muscle forces are considered. However, recent data provide evidence that myofascial force transmission manipulates local muscle tissue lengths (34, 57, 58, 97). This means that even for joint positions at which muscle force is not directly affected, there may be effects on mechanoreceptors, sensory organs, and sarcomeres. Therefore, potential effects of myofascial force transmission on, e.g., pain,

joint position sense, proprioception, and joint ROM are highly plausible.

MYOFASCIAL FORCE TRANSMISSION ACROSS MYOFASCIAL CHAINS

Concepts of myofascial chains suggest that mechanical force can be transferred, not only within one limb between synergists or antagonists but also between muscles arranged in series. One of the most popular approaches encompasses a system of 12 muscle-fascial lines connecting the muscles of the human body (54) (Fig. 7). Although myofascial continuity is not limited to the components incorporated in these chains, evidence from cadaveric studies has verified their existence in, at least, several aspects (89) (Table 1). It has been argued that a potential mechanical force transmission between components of myofascial chains mainly occurs in the longitudinal (e.g., proximo-distal) direction. Histological studies solidify this the-

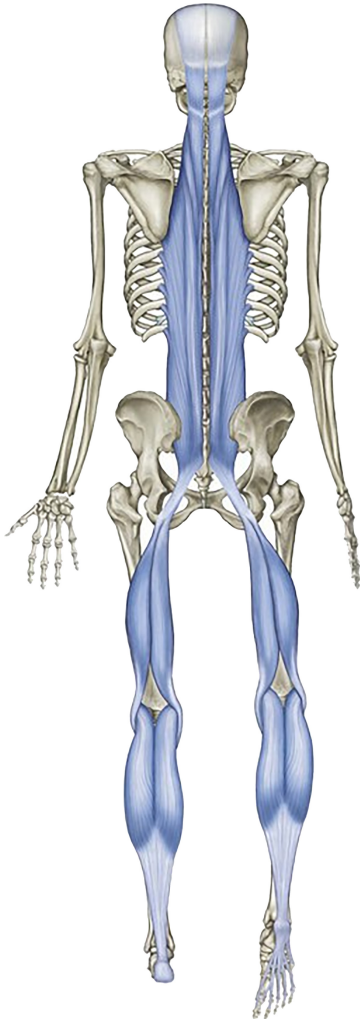


Fig. 7. Example of a myofascial chain: it consists of the plantar aponeurosis, Achilles tendon, gastrocnemius muscle, hamstring muscles, sacrotuberous ligament, and the lumbar fascia/erector spinae muscle. Note the longitudinal in-series arrangement of the components, suggesting direct continuity between head and toes [with permission of Myers 2009 (53a)].

ory. The arrangement of the collagenous fibers within the connective tissue is dependent on load application; as tendons and ligaments are primarily designed to transfer and counteract lengthening forces, the collagenous fibers are mostly aligned to the morphology of the structures (56). The collagen of the myofasciae displays a lattice-like arrangement: the fibers display a crossing angle of $\sim 80^\circ$, which corresponds to the muscular lines of action (6, 21). Although the bidirectional arrangement of the collagen allows lengthening in the longitudinal and transversal plane, the maximal loading capacity in the longitudinal direction is almost five times higher for the crural fascia (21, 75) and three times higher for the fasciae of the abdominal wall (42). Surprisingly, despite its bidirectional arrangement, the fascia lata of the thigh exhibits similar material properties as the unidirectional patellar tendon (14).

Evidence from cadaveric studies. A few studies have examined a potential force transmission between the components of myofascial chains in human cadavers (Table 1). Although the experimental methods vary considerably, a systematic review concluded that force applied to a local structure can substantially affect neighboring connective tissues and muscles (43). Among the studied muscle-fascia lines, moderate evidence was found for a mechanical force transmission across all transitions of the posterior myofascial chain, consisting of the plantar aponeurosis, gastrocnemius muscle/fascia, hamstring muscles/fasciae, sacrotuberous ligament, and lumbar fascia/erector spinae muscle. Partial evidence is available for two diagonal lines on the dorsal (*M. latissimus dorsi*, lumbar fascia, contralateral *M. gluteus maximus*, *M. vastus lateralis*) and ventral (*M. pectoralis major*, *M. rectus abdominis*, contralateral *M. adductor longus*) side of the body. Whereas the findings from cadaveric studies appear to provide a proof of principle regarding myofascial force transmission, two issues remain a matter of debate. As the degree of myofascial continuity (related to the proportion of connecting fibers) is likely to be paramount for the magnitude of transmitted force, the role of physical activity and aging should be investigated with reference to myofascial strain transfer. Cadaveric research is mostly carried out using specimens of older age, which might represent a selection bias.

Evidence from in vivo studies. Data gathered in cadaveric research do not necessarily imply functional relevance for the locomotor system. In contrast, in vivo studies conducted in clinical settings provide valuable hints regarding the relative contribution of myofascial force transmission to the proper functioning of the movement system. In almost identical experiments, increasing hip flexion has been demonstrated to reduce ankle ROM (2, 52). This finding might be indicative of a mechanical force transmission across the posterior myofascial chain, which is further substantiated by data from Cruz-Montecinos et al. (20). In a sitting position and with the knees extended, their participants performed an anterior tilt of the pelvis. Simultaneous ultrasound tracking of the *M. gastrocnemius* deep fascia revealed its cranial displacement in the cranial direction. In a follow-up experiment, similar observations were recorded during cervical flexion (19).

Some recent trials aimed to examine the relevance of mechanical force transmission on adjacent body structures using classical treatments in applied practice. Based on the idea of nonlocal exercise effects mediated by myofascial chains, isometric stretching of the calf and hamstring muscles was dem-

Table 1. Cadaveric studies investigating myofascial force transmission across components of myofascial chains, according to Krause et al. (43)

Chain	Transition	Reference	n	Results
Straight posterior chain	Plantar fascia (PF)–Achilles tendon (AT)	(14a)	8	Force transmission in all cases, stronger mechanical interaction at increasing metatarsophalangeal dorsiflexion, 100 N applied to AT caused 116–256 N tension in PF, whereas 500 N caused tensile forces of 314–511 N in the PF.
		(21a)	7	Strong association of forces applied to the AT and measured force in PF ($r = 0.76$); during simulations of walking, nearly one-half of the AT forces can be detected in the PF.
	<i>M. gastrocnemius</i> –hamstrings			No data from cadaveric studies available. Cruz-Montecinos (19) demonstrated displacement of the deep fascia of the <i>M. gastrocnemius</i> upon pelvic tilting, which might be indicative of a mechanical strain transmission.
	<i>M. biceps femoris</i> (BF)–sacrospinous ligament (SL)	(86a)	6	Force transfer between 7 and 69%; high interindividual variation and systematic differences in dependence of SL fixation to the ischial tuberosity.
(88)		10	Traction applied to BF caused local displacement of the deep lamina of the lumbar fascia, but no quantified assessment of forces was performed.	
Diagonal posterior chain	<i>M. latissimus dorsi</i> (LD)–contralateral <i>M. gluteus maximus</i> (GM)	(5a)	8	SL tension greatest upon traction applied to GM and BF (if fused); SL and BF connected in only 50%; no quantified assessment of forces was performed.
		(88)	10	Pulling the LD and GM caused bilateral displacement of the lumbar fascia, which varied considerably among specimens; force application of 10 N to LD or GM (in the direction of the attaching muscles fascicles) led to a tensile force of 4.9/0.8 N in the posterior layer of the lumbar fascia (level of L3). Slight motion of the superficial lamina of the lumbar fascia after tractioning of the cranial LD fibers; homolateral and (slight) contralateral displacement of the lumbar fascia at L4–S2 upon tractioning the caudal fibers of LD; traction applied to GM yielded more pronounced contralateral displacement of LD when compared with the homolateral LD.
	<i>M. gluteus maximus</i> – <i>M. vastus lateralis</i>			No studies.
	Diagonal anterior chain	<i>M. adductor longus</i> (AL)–contralateral <i>M. rectus abdominis</i> (RA)	(55a)	10
				No studies.
	<i>M. rectus abdominis</i> – <i>M. pectoralis major</i>			No studies.

n, sample size.

onstrated to increase cervical spine flexibility (90, 92). Grieve et al. (26) examined potential nonlocal exercise effects following a tool-assisted self-massage of the foot and observed an increased sit-and-reach distance (a measure of hamstring extensibility) following treatment. Their findings were replicated in a larger trial with 169 participants (38).

Practical implications. Within physiological conditions, interventions based on myofascial chains might help to maximize effectiveness. Although this has not been studied, it is possible that combined local (e.g., cervical spine) and nonlocal (e.g., dorsal lower limb) stretching is more effective than local exercise alone. In musculoskeletal disorders, remote treatments may be reasonable if a local application is contraindicated. Patients afflicted with neck pain often display a restricted cervical ROM. As manual therapeutic manipulations involve the risk of serious adverse events (11), interventions at distant localizations represent a viable alternative. Furthermore, the role of myofascial force transmission across myofascial chains might be of relevance in chronic pain conditions that result from cumulative tissue overloading. It can be hypothesized that local pathological alterations of mechanical tissue properties are projected to neighboring and remote regions, causing nonlocal symptoms. Such remote manifestations have been described for several health problems.

Chronic low back-pain patients tend to exhibit increased stiffness and reduced flexibility in the hamstring muscles (22, 50, 79), which are connected to the lower back within the posterior myofascial chain. In subjects with sacroiliac joint

dysfunction, abnormal electromyographic activity has been observed in the latissimus dorsi and the contralateral gluteus maximus during walking (53). A similar pattern becomes evident in back-pain patients during hip extension in a prone position (41). The hyperactivity of the two muscles, connected in the diagonal posterior chain, might represent an attempt to create stability by tensing the posterior layer of the thoracolumbar fascia, which has a major role in force closure and force transfer between the upper and lower limb (88).

Plantar fasciitis (fasciosis) is another pathology possibly displaying nonlocal abnormalities in components of myofascial chains. With the *M. gastrocnemius* and the hamstring muscles, two parts of the posterior chain display pathologically increased tissue stiffness (44, 59). According to a literature analysis (25), the stretching of the calf muscles might be an effective method of treatment.

Finally, imbalanced and hypertonic adductor and rectus abdominis muscles have been suspected to be a cause of groin pain, which frequently affects soccer players (40). Both muscles are morphologically connected in the frontal diagonal chain. However, no studies examining the therapeutic value of interventions targeting this continuity are available.

Limitations and future perspectives. Mechanical force transmission across myofascial chain components has clearly been evidenced in cadaver experiments. Two aspects limit the transferability of these findings to living conditions. First, the majority of the trials used embalmed cadavers for biomechanical testing. Fixation in formalin increases crosslinking in col-

lagenous tissues and alters the concentration of HA (1, 15, 45). Both processes are suspected to alter the mechanical properties of human connective tissues. Second, data obtained in cadaveric research obviously do not reflect the contribution of the central nervous system. Consequently, due to the presence of muscle activity in the living body, force values collected in such experiments might represent an under- or overestimation.

Unlike cadaveric studies, existing *in vivo* trials (25, 90, 92), on the topic of myofascial force transmission, used functional outcomes, such as ROM. Although this translational approach provides valuable findings for clinical practice, it represents a black box with reference to the genesis of the effects. Without a direct measurement of mechanical force or its surrogates, only indirect assumptions can be made, and remote exercise effects cannot be confidently ascribed to a mechanical force transmission across myofascial chains. The most important alternative explanation of nonlocal treatment effects consists of supraspinal reactions, such as a systemic reduction of stretch tolerance. Future research should hence combine functional assessments and simultaneous imaging, thereby attempting to clarify the respective causal contributions of both dimensions. Additionally, mechanical tissue properties, such as tissue stiffness and elastic storage capacity, measured at local areas of application and adjacent myofascial chain components, might help to substantiate the findings.

Besides delineating the relative contribution of myofascial force transmission to nonlocal exercise effects and examining its principles under *in vivo* conditions, the identification of factors explaining the variance in transmission capacity warrants further investigation. Depending on its localization, the connective tissue investing the muscles displays considerable morphological and structural differences. Fascia tends to be thinner in the upper limb (e.g., antibrachial fascia, 755 μm) (76) than in the lower limb (e.g., fascia lata, 926–944 μm) (76). The same applies to the anterior region of arms and legs compared with the posterior side. Furthermore, the composition of the extracellular matrix exhibits substantial differences: whereas the portion of elastin fibers is rather high in the pectoral fascia, almost exclusively, collagenous fibers can be found within the fascia lata (71). High fascia thickness and collagen content might represent a facilitator in myofascial force transmission, whereas lower thickness and less collagen could reduce tensile strength. If so, the relevance of myofascial force transmission would be higher on the posterior body side and in the lower limb.

In addition to varying according to its localization, the structure and form of the connective tissue are subject to change throughout a lifespan. Aging connective tissue displays increased crosslinking and a reduced collagen content (17). Moreover, the amount of fibers connecting the Achilles tendon and the plantar aponeurosis diminishes with increasing age (68, 73). It is unclear if this phenomenon exclusively occurs at the ankle joint. Both age-related reorganization and reduced morphological continuity can negatively impact myofascial force transmission. In a clinical trial (38), the remote effects following a self-massage treatment of the plantar foot were slightly age dependent (decreasing throughout the lifespan), which corroborates these thoughts. Another factor possibly influencing myofascial force transmission is the amount of physical activity. Inactivity, immobilization, and systematic loading of the connective tissue have been demonstrated to elicit morpho-

logical and/or structural adaptations (12, 18, 36, 84). However, in the study of Kalo et al. (38), no influence of physical activity could be detected.

CONCLUSION

In light of the issues discussed above, the classical perception of the skeletal muscles as independent actuators requires a thorough revision. The active components of the movement system represent only one part of a body-wide tensional network that is characterized by direct mechanical interactions between muscles and their synergists, antagonists, and other adjacent muscles. More holistic approaches that take into account the influences from respective fascial components may enhance performance and effectively tackle musculoskeletal disorders in both athletes and patients.

ACKNOWLEDGMENTS

The authors thank Uluç Pamuk, who provided assistance in preparing some of the figures shown in this paper.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

J.W., R.S., and C.A.Y. prepared figures; J.W., R.S., C.A.Y., and W.B. drafted manuscript; J.W., R.S., C.A.Y., and W.B. edited and revised manuscript; J.W., R.S., C.A.Y., and W.B. approved final version of manuscript.

REFERENCES

1. Abe M, Takahashi M, Horiuchi K, Nagano A. The changes in crosslink contents in tissues after formalin fixation. *Anal Biochem* 318: 118–123, 2003. doi:10.1016/S0003-2697(03)00194-5.
2. Andrade RJ, Lacourpaille L, Freitas SR, McNair PJ, Nordez A. Effects of hip and head position on ankle range of motion, ankle passive torque, and passive gastrocnemius tension. *Scand J Med Sci Sports* 26: 41–47, 2016. doi:10.1111/sms.12406.
3. Ateş F, Temelli Y, Yucesoy CA. Human spastic gracilis muscle isometric forces measured intraoperatively as a function of knee angle show no abnormal muscular mechanics. *Clin Biomech (Bristol, Avon)* 28: 48–54, 2013. doi:10.1016/j.clinbiomech.2012.08.012.
4. Ateş F, Temelli Y, Yucesoy CA. Intraoperative experiments show relevance of inter-antagonistic mechanical interaction for spastic muscle's contribution to joint movement disorder. *Clin Biomech (Bristol, Avon)* 29: 943–949, 2014. doi:10.1016/j.clinbiomech.2014.06.010.
5. Ateş F, Yucesoy CA. Effects of botulinum toxin type A on non-injected bi-articular muscle include a narrower length range of force exertion and increased passive force. *Muscle Nerve* 49: 866–878, 2014. doi:10.1002/mus.23993.
- 5a. Barker PJ, Briggs CA, Bogeski G. Tensile transmission across the lumbar fasciae in unembalmed cadavers: effects of tension to various muscular attachments. *Spine* 29: 129–138, 2004.
6. Benetazzo L, Bizzego A, De Caro R, Frigo G, Guidolin D, Stecco C. 3D reconstruction of the crural and thoracolumbar fasciae. *Surg Radiol Anat* 33: 855–862, 2011. doi:10.1007/s00276-010-0757-7.
7. Bernabei M, van Dieën JH, Baan GC, Maas H. Significant mechanical interactions at physiological lengths and relative positions of rat plantar flexors. *J Appl Physiol (1985)* 118: 427–436, 2015. doi:10.1152/jappphysiol.00703.2014.
8. Berthier C, Blaineau S. Supramolecular organization of the subsarcolemmal cytoskeleton of adult skeletal muscle fibers. A review. *Biol Cell* 89: 413–434, 1997. doi:10.1016/S0248-4900(97)89313-6.
9. Bhattacharya V, Barooah PS, Nag TC, Chaudhuri GR, Bhattacharya S. Detail microscopic analysis of deep fascia of lower limb and its surgical implication. *Indian J Plast Surg* 43: 135–140, 2010. doi:10.4103/0970-0358.73424.
10. Bhowmick S, Singh A, Flavell RA, Clark RB, O'Rourke J, Cone RE. The sympathetic nervous system modulates CD4(+)FoxP3(+) regula-

- tory T cells via a TGF-beta-dependent mechanism. *J Leukoc Biol* 86: 1275–1283, 2009. doi:10.1189/jlb.0209107.
11. **Biller J, Sacco RL, Albuquerque FC, Demaerschalk BM, Fayad P, Long PH, Noorollah LD, Panagos PD, Schievink WI, Schwartz NE, Shuaib A, Thaler DE, Tirschwell DL; American Heart Association Stroke Council.** Cervical arterial dissections and association with cervical manipulative therapy: a statement for healthcare professionals from the american heart association/american stroke association. *Stroke* 45: 3155–3174, 2014. [Erratum. *Stroke* 45 (10): 3155–3174, 2014.] doi:10.1161/STR.000000000000016.
 12. **Bohm S, Mersmann F, Arampatzis A.** Human tendon adaptation in response to mechanical loading: a systematic review and meta-analysis of exercise intervention studies on healthy adults. *Sports Med Open* 1: 7, 2015. doi:10.1186/s40798-015-0009-9.
 13. **Bojsen-Møller J, Schwartz S, Kalliokoski KK, Finni T, Magnusson SP.** Intermuscular force transmission between human plantarflexor muscles in vivo. *J Appl Physiol* (1985) 109: 1608–1618, 2010. doi:10.1152/jappphysiol.01381.2009.
 14. **Butler DL, Grood ES, Noyes FR, Zernicke RF, Brackett K.** Effects of structure and strain measurement technique on the material properties of young human tendons and fascia. *J Biomech* 17: 579–596, 1984. doi:10.1016/0021-9290(84)90090-3.
 - 14a. **Carlson RE, Fleming LL, Hutton WC.** The biomechanical relationship between the tendoachilles, plantar fascia and metatarsophalangeal joint dorsiflexion angle. *Foot Ankle Int* 21:18–25, 2000.
 15. **Chapman JA, Tzaphlidou M, Meek KM, Kadler KE.** The collagen fibril—a model system for studying the staining and fixation of a protein. *Electron Microsc Rev* 3: 143–182, 1990. doi:10.1016/0892-0354(90)90018-N.
 16. **Chimich D, Shrive N, Frank C, Marchuk L, Bray R.** Water content alters viscoelastic behaviour of the normal adolescent rabbit medial collateral ligament. *J Biomech* 25: 831–837, 1992. doi:10.1016/0021-9290(92)90223-N.
 17. **Couppé C, Hansen P, Kongsgaard M, Kovanen V, Suetta C, Aagaard P, Kjaer M, Magnusson SP.** Mechanical properties and collagen cross-linking of the patellar tendon in old and young men. *J Appl Physiol* (1985) 107: 880–886, 2009. doi:10.1152/jappphysiol.00291.2009.
 18. **Couppé C, Suetta C, Kongsgaard M, Justesen L, Hvid LG, Aagaard P, Kjaer M, Magnusson SP.** The effects of immobilization on the mechanical properties of the patellar tendon in younger and older men. *Clin Biomech (Bristol, Avon)* 27: 949–954, 2012. doi:10.1016/j.clinbiomech.2012.06.003.
 19. **Cruz-Montecinos C, Cerda M, Sanzana-Cuche R, Martín-Martín J, Cuesta-Vargas A.** Ultrasound assessment of fascial connectivity in the lower limb during maximal cervical flexion: technical aspects and practical application of automatic tracking. *BMC Sports Sci Med Rehabil* 8: 18, 2016. doi:10.1186/s13102-016-0043-z.
 20. **Cruz-Montecinos C, González Blanche A, López Sánchez D, Cerda M, Sanzana-Cuche R, Cuesta-Vargas A.** In vivo relationship between pelvis motion and deep fascia displacement of the medial gastrocnemius: anatomical and functional implications. *J Anat* 227: 665–672, 2015. doi:10.1111/joa.12370.
 21. **Eng CM, Pancheri FQ, Lieberman DE, Biewener AA, Dorfmann L.** Directional differences in the biaxial material properties of fascia lata and the implications for fascia function. *Ann Biomed Eng* 42: 1224–1237, 2014. doi:10.1007/s10439-014-0999-3.
 - 21a. **Erdemir A, Hamel AJ, Fauth AR, Piazza SJ, Sharkey NA.** Dynamic loading of the plantar aponeurosis. *J Bone Joint Surg Am* 86:546–552, 2004.
 22. **Feldman DE, Shrier I, Rossignol M, Abenhaim L.** Risk factors for the development of low back pain in adolescence. *Am J Epidemiol* 154: 30–36, 2001. doi:10.1093/aje/154.1.30.
 23. **Findley T, Chaudhry H, Dhar S.** Transmission of muscle force to fascia during exercise. *J Bodyw Mov Ther* 19: 119–123, 2015. doi:10.1016/j.jbmt.2014.08.010.
 24. **Follonier Castella L, Gabbiani G, McCulloch CA, Hinz B.** Regulation of myofibroblast activities: calcium pulls some strings behind the scene. *Exp Cell Res* 316: 2390–2401, 2010. doi:10.1016/j.yexcr.2010.04.033.
 25. **Garrett TR, Neibert PJ.** The effectiveness of a gastrocnemius-soleus stretching program as a therapeutic treatment of plantar fasciitis. *J Sport Rehabil* 22: 308–312, 2013. doi:10.1123/jsr.22.4.308.
 26. **Grieve R, Goodwin F, Alfaki M, Bourton AJ, Jeffries C, Scott H.** The immediate effect of bilateral self myofascial release on the plantar surface of the feet on hamstring and lumbar spine flexibility: a pilot randomised controlled trial. *J Bodyw Mov Ther* 19: 544–552, 2015. doi:10.1016/j.jbmt.2014.12.004.
 27. **Haut TL, Haut RC.** The state of tissue hydration determines the strain-rate-sensitive stiffness of human patellar tendon. *J Biomech* 30: 79–81, 1997. doi:10.1016/S0021-9290(96)00108-X.
 28. **Herbert RD, Hoang PD, Gandevia SC.** Are muscles mechanically independent? *J Appl Physiol* (1985) 104: 1549–1550, 2008. doi:10.1152/jappphysiol.90511.2008.
 29. **Hinz B.** The myofibroblast: paradigm for a mechanically active cell. *J Biomech* 43: 146–155, 2010. doi:10.1016/j.jbiomech.2009.09.020.
 30. **Hoppe K, Schleip R, Lehmann-Horn F, Jäger H, Klingler W.** Contractile elements in muscular fascial tissue—implications for in-vitro contracture testing for malignant hyperthermia. *Anaesthesia* 69: 1002–1008, 2014. doi:10.1111/anae.12752.
 31. **Huijing PA.** Epimuscular myofascial force transmission: a historical review and implications for new research. International Society of Biomechanics Muybridge Award Lecture, Taipei, 2007. *J Biomech* 42: 9–21, 2009. doi:10.1016/j.jbiomech.2008.09.027.
 32. **Huijing PA, Baan GC.** Extramuscular myofascial force transmission within the rat anterior tibial compartment: proximo-distal differences in muscle force. *Acta Physiol Scand* 173: 297–311, 2001. doi:10.1046/j.1365-201X.2001.00911.x.
 33. **Huijing PA, van de Langenberg RW, Meesters JJ, Baan GC.** Extramuscular myofascial force transmission also occurs between synergistic muscles and antagonistic muscles. *J Electromyogr Kinesiol* 17: 680–689, 2007. doi:10.1016/j.jelekin.2007.02.005.
 34. **Huijing PA, Yaman A, Ozturk C, Yucesoy CA.** Effects of knee joint angle on global and local strains within human triceps surae muscle: MRI analysis indicating in vivo myofascial force transmission between synergistic muscles. *Surg Radiol Anat* 33: 869–879, 2011. doi:10.1007/s00276-011-0863-1.
 35. **Huxley HE.** The mechanism of muscular contraction. *Science* 164: 1356–1365, 1969. doi:10.1126/science.164.3886.1356.
 36. **Järvinen TA, Józsa L, Kannus P, Järvinen TL, Järvinen M.** Organization and distribution of intramuscular connective tissue in normal and immobilized skeletal muscles. An immunohistochemical, polarization and scanning electron microscopic study. *J Muscle Res Cell Motil* 23: 245–254, 2002. doi:10.1023/A:1020904518336.
 37. **Junker JP, Kratz C, Tollbäck A, Kratz G.** Mechanical tension stimulates the transdifferentiation of fibroblasts into myofibroblasts in human burn scars. *Burns* 34: 942–946, 2008. doi:10.1016/j.burns.2008.01.010.
 38. **Kalo K, Wilke J, Vogt L, Banzer W.** Age-dependency of non-local exercise effects following self-myofascial release of the plantar foot. CONNECT 2017. Baden-Württemberg, Germany: Ulm University, 2017.
 39. **Karakuzu A, Pamuk U, Ozturk C, Acar B, Yucesoy CA.** Magnetic resonance and diffusion tensor imaging analyses indicate heterogeneous strains along human medial gastrocnemius fascicles caused by submaximal plantar-flexion activity. *J Biomech* 57: 69–78, 2017. doi:10.1016/j.jbiomech.2017.03.028.
 40. **Karlsson MK, Dahan R, Magnusson H, Nyquist F, Rosengren BE.** Soccer and gender effect of groin pain. *Dtsch Z Sportmed* 65: 38–42, 2014. <https://pdfs.semanticscholar.org/9122/9b734f4121535c4772e936783dba14518999.pdf>
 41. **Kim JW, Kang MH, Oh JS.** Patients with low back pain demonstrate increased activity of the posterior oblique sling muscle during prone hip extension. *PM R* 6: 400–405, 2014. doi:10.1016/j.pmrj.2013.12.006.
 42. **Kirilova M, Stoytchev S, Pashkouleva D, Kavardzhikov V.** Experimental study of the mechanical properties of human abdominal fascia. *Med Eng Phys* 33: 1–6, 2011. doi:10.1016/j.medengphy.2010.07.017.
 43. **Krause F, Wilke J, Vogt L, Banzer W.** Intermuscular force transmission along myofascial chains: a systematic review. *J Anat* 228: 910–918, 2016. doi:10.1111/joa.12464.
 44. **Labovitz JM, Yu J, Kim C.** The role of hamstring tightness in plantar fasciitis. *Foot Ankle Spec* 4: 141–144, 2011. doi:10.1177/1938640010397341.
 45. **Lin W, Shuster S, Maibach HI, Stern R.** Patterns of hyaluronan staining are modified by fixation techniques. *J Histochem Cytochem* 45: 1157–1163, 1997. doi:10.1177/002215549704500813.
 46. **Maas H, Baan GC, Huijing PA.** Intermuscular interaction via myofascial force transmission: effects of tibialis anterior and extensor hallucis longus length on force transmission from rat extensor digitorum longus muscle. *J Biomech* 34: 927–940, 2001. doi:10.1016/S0021-9290(01)00055-0.

- 46a. **Maas H, Baan GC, Huijing PA.** Muscle force is determined also by muscle relative position: isolated effects. *J Biomech* 37: 99–110, 2004.
47. **Maas H, Baan GC, Huijing PA, Yucesoy CA, Koopman BH, Grootenboer HJ.** The relative position of EDL muscle affects the length of sarcomeres within muscle fibers: experimental results and finite-element modeling. *J Biomech Eng* 125: 745–753, 2003. doi:10.1115/1.1615619.
48. **Maas H, Sandercock TG.** Are skeletal muscles independent actuators? Force transmission from soleus muscle in the cat. *J Appl Physiol* (1985) 104: 1557–1567, 2008. doi:10.1152/jappphysiol.01208.2007.
49. **Malaiya R, McNee AE, Fry NR, Eve LC, Gough M, Shortland AP.** The morphology of the medial gastrocnemius in typically developing children and children with spastic hemiplegic cerebral palsy. *J Electromyogr Kinesiol* 17: 657–663, 2007. doi:10.1016/j.jelekin.2007.02.009.
50. **Marshall PW, Mannion J, Murphy BA.** Extensibility of the hamstrings is best explained by mechanical components of muscle contraction, not behavioral measures in individuals with chronic low back pain. *PM R* 1: 709–718, 2009. doi:10.1016/j.pmrj.2009.04.009.
51. **Mathewson MA, Ward SR, Chambers HG, Lieber RL.** High resolution muscle measurements provide insights into equinus contractures in patients with cerebral palsy. *J Orthop Res* 33: 33–39, 2015. doi:10.1002/jor.22728.
52. **Mitchell B, Bressel E, McNair PJ, Bressel ME.** Effect of pelvic, hip, and knee position on ankle joint range of motion. *Phys Ther Sport* 9: 202–208, 2008. doi:10.1016/j.ptsp.2008.08.002.
53. **Mooney V, Pozos R, Vleeming A, Gulick J, Swenski D.** Exercise treatment for sacroiliac pain. *Orthopedics* 24: 29–32, 2001.
- 53a. **Myers TW.** *Anatomy Trains: Myofascial Meridians for Manual & Movement Therapists.* Oxford: Elsevier, 2009.
54. **Myers TW.** The ‘anatomy trains’. *J Bodyw Mov Ther* 1: 91–101, 1997. doi:10.1016/S1360-8592(97)80010-1.
55. **Ng CP, Hinz B, Swartz MA.** Interstitial fluid flow induces myofibroblast differentiation and collagen alignment in vitro. *J Cell Sci* 118: 4731–4739, 2005. doi:10.1242/jcs.02605.
- 55a. **Norton-Old KJ, Schache AJ, Barker PJ, Clark RA, Harrison SM, Briggs CA.** Anatomical and mechanical relationship between the proximal attachment of adductor longus and the distal rectus sheath. *Clin Anat* 26: 522–530, 2013.
56. **Ottani V, Raspanti M, Ruggeri A.** Collagen structure and functional implications. *Micron* 32: 251–260, 2001. doi:10.1016/S0968-4328(00)00042-1.
57. **Pamuk U, Karakuzu A, Ozturk C, Acar B, Yucesoy CA.** Combined magnetic resonance and diffusion tensor imaging analyses provide a powerful tool for in vivo assessment of deformation along human muscle fibers. *J Mech Behav Biomed Mater* 63: 207–219, 2016. doi:10.1016/j.jmbm.2016.06.031.
58. **Pamuk U, Yucesoy CA.** MRI analyses show that kinesio taping affects much more than just the targeted superficial tissues and causes heterogeneous deformations within the whole limb. *J Biomech* 48: 4262–4270, 2015. doi:10.1016/j.jbiomech.2015.10.036.
59. **Patel A, DiGiovanni B.** Association between plantar fasciitis and isolated contracture of the gastrocnemius. *Foot Ankle Int* 32: 5–8, 2011. doi:10.3113/FAL.2011.0005.
60. **Pavan PG, Stecco A, Stern R, Stecco C.** Painful connections: densification versus fibrosis of fascia. *Curr Pain Headache Rep* 18: 441, 2014. doi:10.1007/s11916-014-0441-4.
61. **Piehl-Aulin K, Laurent C, Engström-Laurent A, Hellström S, Henriksson J.** Hyaluronan in human skeletal muscle of lower extremity: concentration, distribution, and effect of exercise [eng]. *J Appl Physiol* (1985) 71: 2493–2498, 1991.
62. **Reed RK, Lidén A, Rubin K.** Edema and fluid dynamics in connective tissue remodelling. *J Mol Cell Cardiol* 48: 518–523, 2010. doi:10.1016/j.jmcc.2009.06.023.
63. **Sandercock TG, Maas H.** Force summation between muscles: are muscles independent actuators? *Med Sci Sports Exerc* 41: 184–190, 2009. doi:10.1249/MSS.0b013e318183c0c3.
64. **Schleip R, Duerselen L, Vleeming A, Naylor IL, Lehmann-Horn F, Zorn A, Jaeger H, Klingler W.** Strain hardening of fascia: static stretching of dense fibrous connective tissues can induce a temporary stiffness increase accompanied by enhanced matrix hydration. *J Bodyw Mov Ther* 16: 94–100, 2012. doi:10.1016/j.jbmt.2011.09.003.
65. **Schleip R, Klingler W, Lehmann-Horn F.** Active fascial contractility: fascia may be able to contract in a smooth muscle-like manner and thereby influence musculoskeletal dynamics. *Med Hypotheses* 65: 273–277, 2005. doi:10.1016/j.mehy.2005.03.005.
66. **Schleip R, Klingler W, Lehmann-Horn F.** Fascia is able to contract in a smooth muscle-like manner and thereby influence musculoskeletal mechanics. *J Biomech* 39: S488, 2006.
67. **Snow SW, Bohne WH, DiCarlo E, Chang VK.** Anatomy of the Achilles tendon and plantar fascia in relation to the calcaneus in various age groups. *Foot Ankle Int* 16: 418–421, 1995. doi:10.1177/107110079501600707.
68. **Squier CA.** The effect of stretching on formation of myofibroblasts in mouse skin. *Cell Tissue Res* 220: 325–335, 1981. doi:10.1007/BF00210512.
69. **Staubesand J, Li Y.** Begriff und Substrat der Faziensklerose bei chronisch-venöser Insuffizienz. *Phlebologie* 26: 72–79, 1997.
70. **Stecco A, Macchi V, Masiero S, Porzionato A, Tiengo C, Stecco C, Delmas V, De Caro R.** Pectoral and femoral fasciae: common aspects and regional specializations. *Surg Radiol Anat* 31: 35–42, 2009. doi:10.1007/s00276-008-0395-5.
71. **Stecco A, Macchi V, Stecco C, Porzionato A, Ann Day J, Delmas V, De Caro R.** Anatomical study of myofascial continuity in the anterior region of the upper limb. *J Bodyw Mov Ther* 13: 53–62, 2009. doi:10.1016/j.jbmt.2007.04.009.
72. **Stecco C, Corradin M, Macchi V, Morra A, Porzionato A, Biz C, De Caro R.** Plantar fascia anatomy and its relationship with Achilles tendon and paratenon. *J Anat* 223: 665–676, 2013. doi:10.1111/joa.12111.
73. **Stecco C, Gagey O, Macchi V, Porzionato A, De Caro R, Aldegheri R, Delmas V.** Tendinous muscular insertions onto the deep fascia of the upper limb. First part: anatomical study. *Morphologie* 91: 29–37, 2007. doi:10.1016/j.morpho.2007.05.001.
74. **Stecco C, Pavan P, Pachera P, De Caro R, Natali A.** Investigation of the mechanical properties of the human crural fascia and their possible clinical implications. *Surg Radiol Anat* 36: 25–32, 2014. doi:10.1007/s00276-013-1152-y.
75. **Stecco C, Porzionato A, Lancerotto L, Stecco A, Macchi V, Day JA, De Caro R.** Histological study of the deep fasciae of the limbs. *J Bodyw Mov Ther* 12: 225–230, 2008. doi:10.1016/j.jbmt.2008.04.041.
76. **Stecco C, Porzionato A, Macchi V, Stecco A, Vigato E, Parenti A, Delmas V, Aldegheri R, De Caro R.** The expansions of the pectoral girdle muscles onto the brachial fascia: morphological aspects and spatial disposition. *Cells Tissues Organs* 188: 320–329, 2008. doi:10.1159/000121433.
77. **Stecco C, Stern R, Porzionato A, Macchi V, Masiero S, Stecco A, De Caro R.** Hyaluronan within fascia in the etiology of myofascial pain. *Surg Radiol Anat* 33: 891–896, 2011. doi:10.1007/s00276-011-0876-9.
78. **Tafazzoli F, Lamontagne M.** Mechanical behaviour of hamstring muscles in low-back pain patients and control subjects. *Clin Biomech (Bristol, Avon)* 11: 16–24, 1996. doi:10.1016/0268-0033(95)00038-0.
79. **Thornton GM, Shrive NG, Frank CB.** Altering ligament water content affects ligament pre-stress and creep behaviour. *J Orthop Res* 19: 845–851, 2001. doi:10.1016/S0736-0266(01)00005-5.
80. **Tian M, Herbert RD, Hoang P, Gandevia SC, Bilston LE.** Myofascial force transmission between the human soleus and gastrocnemius muscles during passive knee motion. *J Appl Physiol* (1985) 113: 517–523, 2012. doi:10.1152/jappphysiol.00111.2012.
81. **Tijs C, van Dieën JH, Maas H.** No functionally relevant mechanical effects of epimuscular myofascial connections between rat ankle plantar flexors. *J Exp Biol* 218: 2935–2941, 2015. doi:10.1242/jeb.122747.
82. **Tittel K.** *Beschreibende und funktionelle Anatomie des Menschen.* Stuttgart: G. Fischer, 1987.
83. **Tomasek JJ, Gabbiani G, Hinz B, Chaponnier C, Brown RA.** Myofibroblasts and mechano-regulation of connective tissue remodelling [ENG]. *Nat Rev Mol Cell Biol* 3: 349–363, 2002. doi:10.1038/nrm809.
84. **Tuncay I, Kucuker H, Uzun I, Karalezli N.** The fascial band from semitendinosus to gastrocnemius: the critical point of hamstring harvesting: an anatomical study of 23 cadavers. *Acta Orthop* 78: 361–363, 2007. doi:10.1080/17453670710013933.
85. **van der Wal J.** The architecture of the connective tissue in the musculoskeletal system—an often overlooked functional parameter as to proprioception in the locomotor apparatus. *Int J Ther Massage Bodywork* 2: 9–23, 2009.
- 86a. **Van Wingerden JP, Vleeming A, Snijders CJ, Stoockart R.** A functional-anatomical approach to the spine-pelvis mechanism: interaction between the biceps femoris muscle and the sacrotuberous ligament. *Eur Spine J* 2: 140–144, 1993.
87. **Varela F, Frenk S.** The organ of form: towards a theory of biological shape. *J Soc Biol Struct* 10: 73–83, 1987. doi:10.1016/0140-1750(87)90035-2.

88. **Vleeming A, Pool-Goudzwaard AL, Stoeckart R, van Wingerden JP, Snijders CJ.** The posterior layer of the thoracolumbar fascia. Its function in load transfer from spine to legs. *Spine* 20: 753–758, 1995. doi:10.1097/00007632-199504000-00001.
- 88a. **Vleeming A, Van Wingerden JP, Snijders CJ, Stoeckart R, Stijnen T.** Load application to the sacrotuberous ligament; influences on sacroiliac joint mechanics. *Clin Biomech* 4: 204–209, 1989.
89. **Wilke J, Krause F, Vogt L, Banzer W.** What is evidence-based about myofascial chains: a systematic review. *Arch Phys Med Rehabil* 97: 454–461, 2016. doi:10.1016/j.apmr.2015.07.023.
90. **Wilke J, Niederer D, Vogt L, Banzer W.** Remote effects of lower limb stretching: preliminary evidence for myofascial connectivity? *J Sports Sci* 34: 2145–2148, 2016. doi:10.1080/02640414.2016.1179776.
91. **Wilke J, Schleip R, Klingler W, Stecco C.** The lumbodorsal fascia as a potential source of low back pain: a narrative review. *BioMed Res Int* 2017: 5349620, 2017. doi:10.1155/2017/5349620.
92. **Wilke J, Vogt L, Niederer D, Banzer W.** Is remote stretching based on myofascial chains as effective as local exercise? A randomised-controlled trial. *J Sports Sci* 35: 2021–2027, 2017.
93. **Willems ME, Huijijng PA.** Heterogeneity of mean sarcomere length in different fibres: effects on length range of active force production in rat muscle. *Eur J Appl Physiol Occup Physiol* 68: 489–496, 1994. doi:10.1007/BF00599518.
94. **Wirhed R.** *Sportanatomie und Bewegungslehre.* Stuttgart, New York: Schattauer, 2001.
95. **Wrobel LK, Fray TR, Molloy JE, Adams JJ, Armitage MP, Sparrow JC.** Contractility of single human dermal myofibroblasts and fibroblasts. *Cell Motil Cytoskeleton* 52: 82–90, 2002. doi:10.1002/cm.10034.
96. **Yahia LH, Pigeon P, DesRosiers EA.** Viscoelastic properties of the human lumbodorsal fascia. *J Biomed Eng* 15: 425–429, 1993. doi:10.1016/0141-5425(93)90081-9.
97. **Yaman A, Ozturk C, Huijijng PA, Yucesoy CA.** Magnetic resonance imaging assessment of mechanical interactions between human lower leg muscles in vivo. *J Biomech Eng* 135: 91003, 2013. doi:10.1115/1.4024573.
98. **Yucesoy CA.** Epimuscular myofascial force transmission implies novel principles for muscular mechanics. *Exerc Sport Sci Rev* 38: 128–134, 2010. doi:10.1097/JES.0b013e3181e372ef.
99. **Yucesoy CA, Baan G, Huijijng PA.** Epimuscular myofascial force transmission occurs in the rat between the deep flexor muscles and their antagonistic muscles. *J Electromyogr Kinesiol* 20: 118–126, 2010. doi:10.1016/j.jelekin.2008.09.012.
100. **Yucesoy CA, Baan GC, Koopman BH, Grootenboer HJ, Huijijng PA.** Pre-strained epimuscular connections cause muscular myofascial force transmission to affect properties of synergistic EHL and EDL muscles of the rat. *J Biomech Eng* 127: 819–828, 2005. doi:10.1115/1.1992523.
101. **Yucesoy CA, Huijijng PA.** Specifically tailored use of the finite element method to study muscular mechanics within the context of fascial integrity: the linked fiber-matrix mesh model. *Int J Mult Comp Eng* 10: 155–170, 2012. doi:10.1615/IntJMultCompEng.2011002356.
102. **Yucesoy CA, Huijijng PA.** Substantial effects of epimuscular myofascial force transmission on muscular mechanics have major implications on spastic muscle and remedial surgery. *J Electromyogr Kinesiol* 17: 664–679, 2007. doi:10.1016/j.jelekin.2007.02.008.
103. **Yucesoy CA, Koopman BH, Baan GC, Grootenboer HJ, Huijijng PA.** Effects of inter- and extramuscular myofascial force transmission on adjacent synergistic muscles: assessment by experiments and finite-element modeling. *J Biomech* 36: 1797–1811, 2003. doi:10.1016/S0021-9290(03)00230-6.
104. **Yucesoy CA, Turkoğlu AN, Umur S, Ateş F.** Intact muscle compartment exposed to botulinum toxin type A shows compromised intermuscular mechanical interaction. *Muscle Nerve* 51: 106–116, 2015. doi:10.1002/mus.24275.