Bojsen-Møller, J., Magnusson, S. P. (2015). Heterogeneous loading of the human Achilles tendon in vivo. *Exercise and sport sciences reviews, 43*, 190-197.

TITLE PAGE:

TITLE: HETEROGENEOUS LOADING OF THE HUMAN ACHILLES TENDON *IN VIVO*

SHORT TITLE: UNEVEN LOADING OF THE ACHILLES TENDON

AUTHORS: Jens Bojsen-Møller[1] & S. Peter Magnusson[2]

[1]Dept of Physical Performance, Norwegian School of Sport Sciences, Oslo, Norway

[2]Institute of Sports Medicine Copenhagen & Musculoskeletal Rehabilitation Research Unit, Bispebjerg Hospital, University of Copenhagen, Denmark

CORRESPONDING AUTHOR:

Jens Bojsen-Møller

Norwegian School of Sport Sciences

Sognsveien 220

0860 Oslo

Norway

Phone +45 26854059

jens.bojsen.moller@nih.no

The authors report no conflicts of interest.

ABSTRACT PAGE

ABSTRACT: (max 60 words)

The free Achilles tendon is considered a homogenous structure that transmits muscular force in a linear manner. However, the tendon undergoes longitudinal rotation and is separated in mechanically independent segments with distinct mechanical and material tissue properties. The present review examines the hypothesis that the human Achilles tendon is asymmetrically loaded, and undergoes heterogeneous deformation during movement.

SUMMARY: (max 20 words)

The present review examines the hypothesis that the Achilles tendon is asymmetrically loaded, and undergoes heterogeneous deformation during human movement.

KEY WORDS:

Achilles tendon, tendon function, tendon rotation, tendon injury

If more than 4 figs (max 7) up to appr 39.000 char. incl. spaces

Currently: 38.444

1. INTRODUCTION

The Achilles tendon transmits contractile force from the main plantarflexor muscles; the soleus, medial and lateral gastrocnemius. Force is transmitted from the contractile tissue through an intricate system of aponeuroses onto the Achilles tendon, and the calcaneus bone. This entire muscle-tendon unit is termed the triceps surae. The free Achilles tendon (i.e. the tendon distal to soleus insertion) is one of the largest tendons in the human body and it is subjected to remarkably large loads during human locomotion, in sports activities and activities of daily life. In fact, loads of up to 11 kN cm^{-2} or 12 times bodyweight have been reported during jumping and running respectively (13, 23). The tendon contributes significantly to movement economy by storing and releasing energy during loading and unloading, and moreover, the triceps surae muscle-tendon unit enables energy dissipation when required for example during high force landings (1, 15, 21).

The Achilles tendon is a frequent site of injury, and the most common condition is chronic pain (tendinopathy). Moreover, unlike other human tendons, rupture of the Achilles tendon is rather frequent (6, 24). Achilles tendon rupture is considered to be related to a low 'safety factor', which suggests that the tendon operates closer to the yielding or rupture point than most other human tendons during high load activities. This low safety factor is likely the result of the trade-off in design between the ability of the tendon to store and release energy, and the stiffness and strength of the structure (21).

Tendons and their serially coupled aponeuroses have traditionally been considered homogenous structures that convey force from the contracting muscles to bone in a linear manner, however technological advances have in recent years enabled more detailed investigation of the tendinous tissues and their functional interplay with associated muscles *in vivo*. Recent studies suggest that the structure and function of the force transmitting tissues in general is more intricate than previously thought. Specifically, the Achilles tendon seems to undergo longitudinal rotation and to consist of mechanically independent sub-portions. Moreover, regional differences in mechanical and material tendon properties may be present. (3, 4, 7, 10, 28, 34).

The present review examines the hypothesis that the Achilles tendon is asymmetrically loaded, and undergoes heterogeneous deformation during human movement. Moreover, the consequence of such behaviour for function and dysfunction is discussed.

2. ANATOMICAL DESIGN OF THE ACHILLES TENDON

The force bearing tissues of the triceps surae consists of separate aponeuroses that merge into the free Achilles tendon distal to the insertion of the soleus muscle. The Achilles tendon has been the subject of study for over a century; when examining a variety of mammal tendons, F.G. Parson (1894) described a longitudinal torsion or rotation of the Achilles tendons (Fig. 1)(32). Further, Parson noted that portions of the Achilles tendon seemed to be independent, and upon 'untwisting' of one canine Achilles tendon, the single tendon subunits became 'unseparated' and 'lay parallel to one another'(32).

Insert figure 1. appr. here

More recently, it has also been reported in humans that the force bearing tissues of the Achilles tendon are mechanically separated well into the free tendon such that tissue bundles that originate from each of the three muscle compartments can be distinguished close to the tendon insertion on the calcaneal bone (8, 10, 34).

Longitudinal Achilles tendon rotation has been re-examined in later studies and it seems that the fascicles or collagen tissue bundles that originate from each muscle compartment undergoes *internal* rotation from proximal to distal such that the Achilles tendon of the right leg undergo counter-clockwise rotation (seen from a cranial viewpoint) from proximal to distal, while the tendon of the left leg undergoes clockwise rotation (Fig. 2) (8, 10, 32, 34). The degree of rotation is difficult to quantify, and there is large interindividual variation, however numbers between 10 and 150° have been reported (10). One very recent study examined 110 cadaver legs and found proximal-to-distal tendon rotation in all. Depending on degree of rotation, the specimens were classified in three groups: In the 'least-rotation' group the soleus inserted antero-medially and the gastrocnemii inserted postero-laterally, which occurred in 50% of the tendons. In the 'moderate rotation' group the soleus inserted medially and the lateral gastrocnemius inserted antero-laterally, and this occurred in

43% of tendons. In the ‘extreme rotation’ group the soleus inserted postero-medially and the lateral gastrocnemius inserted anteriorly, while the medial gastrocnemius inserted postero-laterally and this occurred in 7% of tendons. There were no differences observed between sexes or between the left and right side (10).

Insert Figure 2 appr here

Tendon rotation is thus present in the triceps surae, but the function of the tendon rotation remains unknown. Some authors have suggested that a rotated tendon acquires rope-like properties (7, 32), and one feature of twisted ropes is to enhance the ability to strain and store energy. An alternative explanation was recently suggested in a modelling study on masseter muscles in fish, in which muscle and tendon rotation occurs (9). The study demonstrated that in broad muscles that operate at a distance from the joint axis of rotation, and where the insertional tendon attaches over a wide area of bone, variation might occur in the muscle fibers abilities to exert force simply due to differences in fiber length through the joint range of motion (9). In such muscle-tendon units, suboptimal force production may occur due to a subset of fibers that are operating outside the plateau of the length-tension curve. A rotated tendon, or a design where the muscle fibers rotate or cross each other, was shown to equalize force-length properties for muscle fibers of the broad muscle, thereby optimizing contractile ability. The human triceps surae is in fact a broad ‘muscle’ that operates at a significant distance from the joint compared to most other dorsi and plantarflexors of the lower leg. Moreover, the Achilles tendon does display a quite broad insertional or enthesis area on the calcaneus as seen in the transverse plane, which again is different from that of most other muscles crossing the ankle joint. Other human muscle-tendon units that display rotation are those of the pectoralis major and the latissimus dorsi, which both are wide muscles with a large region of origin and somewhat large area of insertion. Nonetheless, it remains unknown if tendon rotation in humans has in fact the consequences for muscle force exertion that are seen in the masseter muscles of the spotted ratfish (9).

3. EVIDENCE OF ASYMMETRICAL ACHILLES TENDON LOADING

From a functional perspective the Achilles tendon is associated with three separately activated muscles that govern the loading of the tendon, and studies suggest that the tendon consists of mechanically separate tendon portions that each relate to the single muscle compartments (8, 34). In cadaver preparations it has been demonstrated that separate loading of the single triceps surae muscles leads to heterogeneous loading of the Achilles tendon (3). More recently, the triceps surae of cadaver preparations were examined and when the joint angle of the subtalar joint was manipulated the calcaneal in- or eversion influenced the strain profile of the Achilles tendon (25). In a human *in vivo* model Magnusson et al. (2003) examined differences in mechanical properties of the tendon and associated aponeuroses, and to enable identifiable tendon fixed points (by ultrasonography) thin needles were inserted transversely into the Achilles tendon and hereafter subjects performed maximal plantarflexor contractions (28). When the needles were retracted some were permanently distorted (Fig. 3), which seems to be direct evidence of non-uniform Achilles tendon deformation *in vivo*.

Insert Figure 3 and 4 approximately here

Additional investigations have been conducted *in vivo* and one study examined muscle displacement in the triceps surae muscles during different joint configurations of the leg (7). These results indicated the occurrence of uneven Achilles tendon loading and suggested that knee joint position and thus length of the gastrocnemius muscles plays a role in tendon loading (Fig. 5) (7). More recently, uneven deformation of the free Achilles tendon was seen with ultrasonography-based speckle tracking, and greater displacement (~20%) was observed in the deep layer of the tendon compared to superficial aspects during passive dorsiflexion (2) (Fig. 5). A comparable study examined passive and eccentric loading of the free Achilles tendon during different knee joint configurations by use of ultrasound elastography (33). Here, the middle and deep (anterior) portions of the Achilles tendon underwent greater displacement (~ 5-9 mm during an ankle joint excursion of 30°) compared to the posterior area of the tendon (~ 4-6 mm of displacement) (33) (Fig. 5). An additional study by the same research group examined antero-posterior Achilles tendon displacement during walking, and a similar pattern of uneven tendon deformation was observed where greater displacement was seen in the ventral part of the tendon (12). Together, these studies are examples of techniques such as robot vision tracking and elastography that may be promising tools for assessing biomechanical tendon function. However, it should be kept in mind that substantial inter-individual variation exists in Achilles tendon design and/or rotation (8, 10, 34), which makes it difficult to ascribe the observed displacement of tendon regions to single muscle compartments of the triceps surae. To increase the biomechanical understanding of tendon function, future studies need to determine, on an individual basis, which parts of the tendon are associated with each of the separate muscles, and hereafter, load and/or contraction induced tendon deformation can be investigated in greater detail.

Insert figure 5 appr here.

4. MECHANISMS FOR ASYMMETRICAL LOADING

Given the multifaceted structure of the triceps surae muscle-tendon unit there are several potential mechanisms for asymmetrical loading and strain of the Achilles tendon:

Muscle-Tendon Unit Design

The physiological cross-sectional area of the three triceps surae muscles, which is proportional to force generating capacity, have previously been examined, and the lateral gastrocnemius is by far the smallest muscle with ~7% of the total triceps surae physiological cross-sectional area. The medial gastrocnemius represents ~20%, and the soleus has ~73% of the total physiological cross-sectional area (14). With respect to muscle volume the soleus is reported to contain ~55% of the total triceps surae volume while, the medial and lateral gastrocnemius represent ~30 and 15% respectively (14, 22). Thus, the three muscle compartments are quite different with respect to maximal force capability, and it should also be kept in mind that since the gastrocnemii are two-joint muscles, knee joint position will also influence their force-generating capacity. Deformation or strain of the tendinous structures during loading relates to tendon stress (load / tendon cross-sectional area), and a greater tendon area will increase stiffness and thus reduce strain for a given load. It is possible that the cross-sectional areas of the separate Achilles tendon compartments (that are distinctly associated with each muscle compartment (10)) corresponds to the contractile abilities of each muscle compartment (i.e. similar 'muscle-tendon cross-sectional area ratio' between the compartments), which would result in uniform tendon loading and deformation at maximal exertion. But if a difference exists in muscle-tendon area ratio between the three subunits, or if muscle compartments are unevenly activated in relative terms (% max), these are potential candidates for heterogeneous Achilles tendon deformation. The ratio between the physiological muscle cross-sectional area of the three single muscles and the associated cross-sectional area of their respective tendon subunit remains to be investigated, and such information will have great relevance for future understanding the Achilles tendon function and loading profile.

Neural Activation

In addition to anatomical design, neural activation may also influence the load distribution in the Achilles tendon since the three muscles of the triceps surae are activated independently by the nervous system. Plantarflexor activation has been examined during different contractile tasks with surface electromyography (EMG), and it seems clear that neural activation differs between muscles depending on contraction type and/or joint configuration (31, 35). Recently, the activation of the triceps surae muscles was examined combining EMG and positron emission tomography. In line with previous work where contractions were performed with an extended knee joint, the muscles appeared to be heterogeneously activated, such that the medial gastrocnemius showed higher intensity compared to the soleus and medial gastrocnemius (30). One recent study examined muscle activation and its distribution within the triceps surae by use of T2 magnetic resonance imaging during plantarflexor efforts with the knee joint extended. With this technique activated intermuscular regions could elegantly be visualized, and interestingly, a greater (relative) volume (~50%) of the medial gastrocnemius was activated, while the relative activated volume of the soleus and the lateral gastrocnemius was ~35% (22). Moreover, longitudinal differences were observed in activated muscle volume within the medial gastrocnemius (neuromuscular compartmentalization), which suggests that the nervous system by precise activation can carefully control the exact force output or joint moment to accommodate the contractile task. Taken together, neural activation of the triceps surae muscles is intricate, and it is plausible that joint configuration and uneven activation of the single muscle compartments may induce heterogeneous Achilles tendon deformation.

Material And Structural Tissue Properties

The stiffness of the structure is not only governed by tendon cross-sectional area, but also the *material properties* of the tissue. Although there may be differences in material properties between tendons of one individual, the force bearing tissue within one muscle-tendon unit has generally been considered similar with respect to tissue morphology. Nonetheless, differences in material properties have been observed within different regions of the same human tendon. It has been shown that modulus, peak and yield stress differ in the anterior compared to the posterior portions of the human patellar tendon (16, 17). Similar data are until now not available for the human Achilles tendon, but longitudinal variation in strain of the serially coupled aponeurosis and tendon has been observed during loading (11). It has furthermore been shown that the stiffness of the aponeurosis (maximal strain < 2%) exceeded that of the free tendon *in vivo* (maximal strain app 8%) (28, 29). Difference in strain between tendons and aponeuroses may result from the mechanical effect of contractile tissue that inserts upon the aponeurosis (26) and/or to differences in neural activation within the muscle volume, such that during specific tasks only parts of the muscle is activated, which in turn modulates the loading of the force bearing tissue (22, 35). Moreover aponeurosis properties may be modulated by loading in the transverse plane that increases stiffness in the perpendicular plane (the longitudinal direction) via medio-lateral deformation, according to Poisson's ratio. In fact, both animal and human studies have demonstrated such biaxial strain during active loading that in turn influenced mechanical properties in the longitudinal direction (5, 20). If the separate aponeuroses change properties in an uneven manner during contraction this may in turn result in reduced coalescing of the contractile forces and potentially contribute to uneven loading of the more distal tendon. The magnitude of these effects during daily loading, and the influence on the function of the muscle-tendon unit remains to be understood, but it seems likely that the in vivo mechanical and material properties may influence functional capacities such as ability to store and release energy, to transmit force accurately or to act as a mechanical damper.

5. ACHILLES TENDON DESIGN AND HETEROGENOUS LOADING. FUNCTION AND DYSFUNCTION

Why Tendon Rotation?

As mentioned previously, tendon rotation may reflect a design that enables muscle fibers that are situated far apart in the associated muscles to operate at more similar lengths during the full joint range of motion (9), but whether such a mechanism pertains to the Achilles tendon is not yet known. Another hypothesis is that the rotation facilitates the ability to store and release energy during loading and unloading respectively. Ropes are engineered in different ways such that twisted ropes are designed for situations where high strains and storage of mechanical energy are required, while ropes with parallel fibers are utilized when minimal strain is required. This analogy may seem reasonable for human tendon design since some tendons are more involved in position control and effective force transmission, such as for example tendons of the hand or forearm, while the Achilles tendon (in addition to the transmission of force) is highly involved in energy storage and release during locomotion. Previous studies have in fact argued for the existence of a trade-off between position control and energy storage and release for tendon design (7). Finally, tendon rotation could serve to regulate intratendinous pressure during the extremely high stresses and strains that are imposed particularly on the Achilles tendon: In a coherent or linear structure internal pressure is reduced more under tensile stress compared to a rotated structure. Albeit highly speculative, modulation of intratendinous pressure may play a role for maintaining vessel and nerve function, and potential fluid diffusion that in turn may relate to the health and function of the tissue.

The exact role of Achilles tendon rotation remains unknown, but if future imaging technologies can enable quantification of tendon rotation *in vivo* this would be a powerful model to examine the role of rotation on e.g. movement performance, economy of movement and/or injury, given the large inter-individual variation (10).

Why Heterogeneous Deformation?

Functionally, the triceps surae muscle-tendon unit is mainly considered to be responsible for plantarflexion, but since the subtalar joint axis passes laterally to the calcaneal insertion of the tendon, the triceps surae is also a strong invertor of the foot. If the three triceps surae muscles are connected functionally to separate tendon compartments, such a design would enable greater control of ankle and subtalar joint moments since each muscle can function as a separate actuator. For example, given the tendon rotation described above, the soleus muscle inserts on the medial side of the Achilles tendon and therefore at a greater distance to the inversion-eversion joint axis. This means that hypothetically, the soleus can selectively contribute to inversion to a greater extent than the gastrocnemius muscles. Concurrently, the medial gastrocnemius, which by far has the largest cross-sectional area of the gastrocnemius muscles, inserts posterio-laterally in the Achilles tendon, which could be a mechanism to optimize plantarflexion or even eversion moment about the ankle joint. Extending this line of thought, it should be kept in mind that the gastrocnemius muscles are two-joint muscles that span both the ankle (and subtalar) and knee joint. Therefore, knee joint position during e.g. human gait may in fact influence the length and thus contractile abilities of the gastrocnemius muscles: For example, during the latter part of the stance phase during running, the ankle joint moves into plantarflexion while the knee joint is extending, which means that mechanical energy may be transferred from knee joint extensors into plantarflexion (15). At the same time, if the medial gastrocnemius transmits force via a separate tendon portion within the Achilles tendon, the knee joint extension may optimize the length of the gastrocnemius muscle with respect to creating maximal plantarflexion moment. Further, if the two gastrocnemius muscles inserts into the posterior-lateral part of the Achilles tendon insertion zone, the effect on plantarflexion or even eversion moment that occurs in the final part of the stance phase may be even further optimized simply by anatomical design. It is clear that such mechanisms remain speculative and warrant confirmation.

Tendon Injury And Rehabilitation

Although one of the strongest tendons in the body, repetitive loading of the Achilles tendon often leads to overuse injuries, including tendinopathy. Tendinopathy is characterized by pain, tenderness upon palpation, local swelling and impaired performance (6, 24). Tendinopathy is a considerable problem in both elite and recreational athletes. In fact, in runners the incidence of tendon injuries has been estimated to 22% with a lifetime cumulative incidence of as high as 52% (24, 27). Moreover, the symptoms and reduction in performance may be quite protracted and last for years. The exact injury mechanism remains elusive, but understanding how tendon tissue is mechanically loaded might be a key to understanding the pathogenesis, and thus provide the basis for injury prevention. As mentioned above, it is possible that the free Achilles tendon is subjected to heterogeneous loading because i) the Achilles tendon is coupled to three distinct muscles with separate neural innervation, ii) the three separate muscles include one and two-joint muscles and are therefore influenced by both ankle and knee joint position, and iii) the Achilles tendon insertion is relatively wide and is therefore mechanically influenced by subtalar inversion and eversion. Taken together, changes in tendon loading may result from unfavourable neural activation or from a suboptimal position of the subtalar joint. But also acute changes such as fatigue induced adaptation in neural activation or even locomotion on unusual or slanted surfaces may influence tendon loading. Significant interindividual variation has been observed with respect to Achilles tendon rotation (8, 10), but if similar variation exists with respect to the mechanical separation of the Achilles tendon subportions, and further, whether tendon rotation or mechanical heterogeneity is related to injury, remains to be examined.

Different treatment strategies have been described in the literature, but *loading* interventions have become an accepted form of treatment for tendinopathies (6) and the promising outcome may in fact relate to mechanical loading and tissue deformation. To fully 'engage' all three muscles and thus the entire free Achilles tendon any rehabilitation strategy would need to include exercises with some degree of knee flexion and full knee extension while performing resisted ankle motion throughout the joint range of motion. This approach would engage all the tendon tissue, but also perhaps create some intratendinous shear, and it remains to be established if such loading and/or shear is in fact advantageous in a rehabilitation perspective. Tendon fascicles are separate functional units of tendons, and nerves and vessels are located in the intrafascicular space that may ‘see’ the shear (18). As previously mentioned, it has been shown that calcaneus position may yield intratendinous strain differences by up to 15% (Fig. 6), and therefore it may also be important to consider rear foot positioning during the resisted plantarflexion exercises (25). It appears that calcaneal eversion yielded greater strain of the medial portion of the Achilles tendon, while the opposite held true for calcaneal inversion, and therefore changes in foot wear to control or modify the range of motion of the subtalar joint during gait may potentially also be implemented in rehabilitation.

Insert fig 6 appr here

As such loading regimes yield good clinical results, and although especially eccentric loading has received some attention, there remains little support for the advantage of isolated eccentric training (6). Currently available studies rarely used comparable load magnitudes when comparing eccentric training to other loading regimes but muscles can produce greater maximal force eccentrically than concentrically and this is rarely exploited during rehabilitation exercises. Moreover, animal work shows that concentric or eccentric contraction to the same force level does not differentially influence the expression of collagen at the cellular level, and even if the eccentric contraction force exceeds that of the concentric contraction, the collagen expression remains the same (19). It remains outside the scope of this review, but collectively these findings demonstrate that cellular and tendon tissue responses seem independent of contraction mode, and thus questions whether contraction mode is of importance during rehabilitation of tendon injury.

6. CONCLUSION AND PERSPECTIVES

The present review examined the hypothesis that the Achilles tendon is asymmetrically loaded, and undergoes heterogeneous deformation during human movement. The Achilles tendon seems to consist of distinct portions each associated to the three muscle compartments, and furthermore the tendon portions undergo rotation about the longitudinal axis. Heterogeneous tendon deformation may be associated with issues related to anatomical design, by different material or structural properties in the force bearing tissues, and/or by uneven neural activation of muscles. The consequence of heterogeneous deformation for tendon performance, function and injury is not currently known. Future studies should investigate neural activation of the triceps surae muscle compartments in different tasks, enable measurement of tendon rotation in vivo, determine anatomical design features such as muscle-tendon cross-sectional area ratio of the single muscles. Moreover, specific tendon loading should be examined in a detailed manner during different contractile tasks. Hereby, the role of heterogeneous Achilles tendon loading with respect to tendon function, force transfer and energy storage and release may be understood in greater detail. The biomechanical role of Achilles tendon function should be examined with the goal of understanding performance in various contractile tasks. Finally, the role of tendon mechanics in dysfunction and injury should be investigated such that mechanism of injury can be exposed, and thereby enable development of more optimal rehabilitation and/or injury prevention strategies.

FIGURE LEGENDS

Figure 1. *Achilles tendon rotation has previously been observed in humans and lower mammals, but this feature has received limited attention in general, and any consequence for tendon function or dysfunction related to rotation remains unknown. The present illustration is from the Achilles tendon of a beaver reported more than a century ago. (From F. G. Parsons, 1894, with permission).*

Figure 2. *Posterior view of the right triceps surae muscle tendon unit and the Achilles tendon insertion on the calcaneal bone. Arrows demonstrate that tendon fascicle bundles that originate from the medial gastrocnemius insert on the postero-lateral side of the calcaneus, while fascicle bundles from the lateral gastrocnemius insert on the lateral-anterior aspect of the tendon. Hence, the right tendon undergoes counter-clockwise rotation going from proximal to distal, while the tendon of the left leg (not shown) undergoes clockwise rotation. Oval cartoons depict cross sections of the right free Achilles tendon at a proximal site (upper image) and just above the calcaneal insertion (lower image).*

Figure 3. *Syringe needles were inserted transversely through the Achilles tendon during maximal plantarflexion efforts. Upon retraction the steel needles were permanently distorted, which demonstrates the occurrence of heterogeneous Achilles tendon deformation.*

Figure 4. Conceptual figure*. Joint configuration or uneven activation of separate muscles that insert on a common tendon may induce asymmetrical tendon loading, and differences in intratendinous stress (SOL: soleus, GM: gastrocnemius, AT: Achilles tendon).*

Figure 5: Evidence of heterogeneous tendon deformation.
Panel 1*: Shear displacement between the medial gastrocnemius and the soleus during isometric contractions with extended and flexed knee joint. Displacement was obtained with ultrasonography, and shear was determined by subtracting the displacement of the soleus from that of the medial gastrocnemius throughout ramp contractions. With the knee joint in*

extension, displacement of the gastrocnemius exceeded that of the soleus, while the opposite occurred in the flexed-knee position (From Bojsen-Møller et al. 2004 with permission)
Panel 2: *Average (n=9) displacements of superficial and deep Achilles tendon portions measured with ultrasound elastography. Passive (Pass) and eccentric (Ecc) loading tasks were performed and greater tissue displacements (Negative direction corresponds with distal) were observed when the knee was extended (Ex) as compared to flexed (Fl). From these data it seems clear that the tendon undergoes heterogeneous deformation. (From Slane et al. 2014 with permission).* ***Panel 3:*** *Images illustrating the ultrasonography based speckle-tracking technique where displacement of single regions of interest within the tendon can be measured during contractions or passive joint motion.* ***Image a****: Sagittal scan ultrasound image of the Achilles tendon (AT) with coloured regions of interest positioned in the superficial (top), central and deep (bottom) layers of the Achilles tendon.* ***Image b and c****: During passive movement (dorsiflexion DF and plantarflexion PF) differences in displacement between the deep, mid and superficial aspect of the tendon are visualized. (From Arndt et al. 2012, with permission)*

Figure 6: **Subtalar joint position influences Achilles tendon loading**. The left 3 figures illustrate the triceps surae muscle tendon unit seen from a posterior view. Left drawing illustrates tendon strains with a neutral calcaneus position, middle drawing with the subtalar joint in inversion, and right drawing with calcaneal eversion. Full lines represent tissues on the posterior (superficial) aspect of the tendon; dashed lines represent anterior tendon portions. The length of the arrows approximates strain magnitude. Inversion of the subtalar joint (middle) induces greater strain in the lateral aspect of the tendon, while eversion (right) induces increased strain in the medial aspect of the Achilles tendon. Medio-lateral strain differences induced by poor positioning of the subtalar joint during e.g. running, may potentially lead to injury, while manipulating the calcaneus position by insole, footwear or training may potentially present a rehabilitating effect. (SO: soleus, GM: medial gastrocnemius, GL lateral gastrocnemius). (From Lersch et al. 2012, with permission).

References

1. Alexander RM. Energy-saving mechanisms in walking and running. *The Journal of experimental biology*. 1991;160:55-69.

2. Arndt A, Bengtsson AS, Peolsson M, Thorstensson A, Movin T. Non-uniform displacement within the Achilles tendon during passive ankle joint motion. *Knee surgery, sports traumatology, arthroscopy : official journal of the ESSKA*. 2012;20(9):1868-74.

3. Arndt A, Bruggemann GP, Koebke J, Segesser B. Asymmetrical loading of the human triceps surae: I. Mediolateral force differences in the Achilles tendon. *Foot & ankle international*. 1999;20(7):444-9.

4. Arndt A, Bruggemann GP, Koebke J, Segesser B. Asymmetrical loading of the human triceps surae: II. Differences in calcaneal moments. *Foot & ankle international*. 1999;20(7):450-5.

5. Azizi E, Roberts TJ. Biaxial strain and variable stiffness in aponeuroses. *The Journal of physiology*. 2009;587(Pt 17):4309-18.

6. Beyer R, Kongsgaard M, Hougs Kjaer B, Ohlenschlaeger T, Kjaer M, Magnusson SP. Heavy Slow Resistance Versus Eccentric Training as Treatment for Achilles Tendinopathy: A Randomized Controlled Trial. *The American journal of sports medicine*. 2015.

7. Bojsen-Moller J, Hansen P, Aagaard P, Svantesson U, Kjaer M, Magnusson SP. Differential displacement of the human soleus and medial gastrocnemius aponeuroses during isometric plantar flexor contractions in vivo. *Journal of applied physiology*. 2004;97(5):1908-14.

8. Cummins EJ, Anson BJ, et al. The structure of the calcaneal tendon (of Achilles) in relation to orthopedic surgery, with additional observations on the plantaris muscle. *Surgery, gynecology & obstetrics*. 1946;83:107-16.

9. Dean MN, Azizi E, Summers AP. Uniform strain in broad muscles: active and passive effects of the twisted tendon of the spotted ratfish Hydrolagus colliei. *The Journal of experimental biology*. 2007;210(Pt 19):3395-406.

10. Edama M, Kubo M, Onishi H et al. The twisted structure of the human Achilles tendon. *Scandinavian journal of medicine & science in sports*. 2014.

11. Finni T, Hodgson JA, Lai AM, Edgerton VR, Sinha S. Nonuniform strain of human soleus aponeurosis-tendon complex during submaximal voluntary contractions in vivo. *Journal of applied physiology*. 2003;95(2):829-37.

12. Franz JR, Slane LC, Rasske K, Thelen DG. Non-uniform in vivo deformations of the human Achilles tendon during walking. *Gait & posture*. 2015;41(1):192-7.

13. Fukashiro S, Komi PV, Jarvinen M, Miyashita M. In vivo Achilles tendon loading during jumping in humans. *European journal of applied physiology and occupational physiology*. 1995;71(5):453-8.

14. Fukunaga T, Roy RR, Shellock FG, Hodgson JA, Edgerton VR. Specific tension of human plantar flexors and dorsiflexors. *Journal of applied physiology*. 1996;80(1):158-65.

15. Gregoire L, Veeger HE, Huijing PA, van Ingen Schenau GJ. Role of mono- and biarticular muscles in explosive movements. *International journal of sports medicine*. 1984;5(6):301-5.

16. Hansen P, Haraldsson BT, Aagaard P et al. Lower strength of the human posterior patellar tendon seems unrelated to mature collagen cross-linking and fibril morphology. *Journal of applied physiology*. 2010;108(1):47-52.

17. Haraldsson BT, Aagaard P, Krogsgaard M, Alkjaer T, Kjaer M, Magnusson SP. Region-specific mechanical properties of the human patella tendon. *Journal of applied physiology*. 2005;98(3):1006-12.

18. Haraldsson BT, Aagaard P, Qvortrup K et al. Lateral force transmission between human tendon fascicles. *Matrix biology : journal of the International Society for Matrix Biology*. 2008;27(2):86-95.

19. Heinemeier KM, Olesen JL, Haddad F et al. Expression of collagen and related growth factors in rat tendon and skeletal muscle in response to specific contraction types. *The Journal of physiology*. 2007;582(Pt 3):1303-16.

20. Iwanuma S, Akagi R, Kurihara T et al. Longitudinal and transverse deformation of human Achilles tendon induced by isometric plantar flexion at different intensities. *Journal of applied physiology*. 2011;110(6):1615-21.

21. Ker RF. The design of soft collagenous load-bearing tissues. *The Journal of experimental biology*. 1999;202(Pt 23):3315-24.

22. Kinugasa R, Kawakami Y, Fukunaga T. Muscle activation and its distribution within human triceps surae muscles. *Journal of applied physiology*. 2005;99(3):1149-56.

23. Komi PV, Fukashiro S, Jarvinen M. Biomechanical loading of Achilles tendon during normal locomotion. *Clinics in sports medicine*. 1992;11(3):521-31.

24. Kujala UM, Sarna S, Kaprio J. Cumulative incidence of achilles tendon rupture and tendinopathy in male former elite athletes. *Clinical journal of sport medicine : official journal of the Canadian Academy of Sport Medicine*. 2005;15(3):133-5.

25. Lersch C, Grotsch A, Segesser B, Koebke J, Bruggemann GP, Potthast W. Influence of calcaneus angle and muscle forces on strain distribution in the human Achilles tendon. *Clinical biomechanics*. 2012;27(9):955-61.

26. Lieber RL, Leonard ME, Brown-Maupin CG. Effects of muscle contraction on the load-strain properties of frog aponeurosis and tendon. *Cells, tissues, organs*. 2000;166(1):48-54.

27. Lopes AD, Hespanhol Junior LC, Yeung SS, Costa LO. What are the main running-related musculoskeletal injuries? A Systematic Review. *Sports medicine*. 2012;42(10):891-905.

28. Magnusson SP, Hansen P, Aagaard P et al. Differential strain patterns of the human gastrocnemius aponeurosis and free tendon, in vivo. *Acta physiologica Scandinavica*. 2003;177(2):185-95.

29. Magnusson SP, Narici MV, Maganaris CN, Kjaer M. Human tendon behaviour and adaptation, in vivo. *The Journal of physiology*. 2008;586(1):71-81.

30. Masood T, Bojsen-Moller J, Kalliokoski KK et al. Differential contributions of ankle plantarflexors during submaximal isometric muscle action: a PET and EMG study. *Journal of electromyography and kinesiology : official journal of the International Society of Electrophysiological Kinesiology*. 2014;24(3):367-74.

31. Moritani T, Oddsson L, Thorstensson A. Differences in modulation of the gastrocnemius and soleus H-reflexes during hopping in man. *Acta physiologica Scandinavica*. 1990;138(4):575-6.

32. Parsons FG. On the Morphology of the Tendo-Achillis. *Journal of anatomy and physiology*. 1894;28(Pt 4):414-8.

33. Slane LC, Thelen DG. Non-uniform displacements within the Achilles tendon observed during passive and eccentric loading. *Journal of biomechanics*. 2014;47(12):2831-5.

34. Szaro P, Witkowski G, Smigielski R, Krajewski P, Ciszek B. Fascicles of the adult human Achilles tendon - an anatomical study. *Annals of anatomy = Anatomischer Anzeiger : official organ of the Anatomische Gesellschaft*. 2009;191(6):586-93.

35. Tamaki H, Kitada K, Akamine T, Sakou T, Kurata H. Electromyogram patterns during plantarflexions at various angular velocities and knee angles in human triceps surae muscles. *European journal of applied physiology and occupational physiology*. 1997;75(1):1-6.

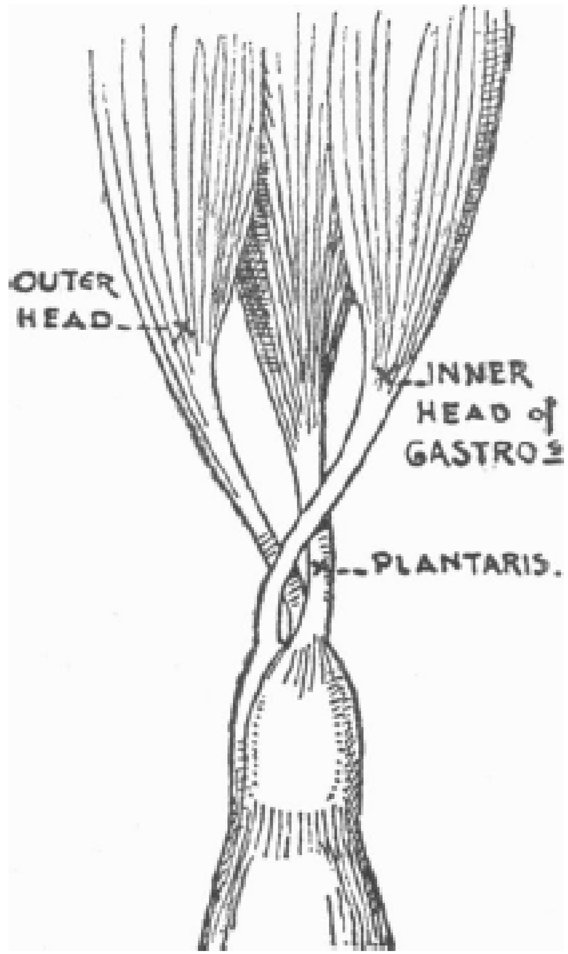


Fig. 1.—Tendo-Achillis of Beaver (*Castor canadensis*).

Figure 1

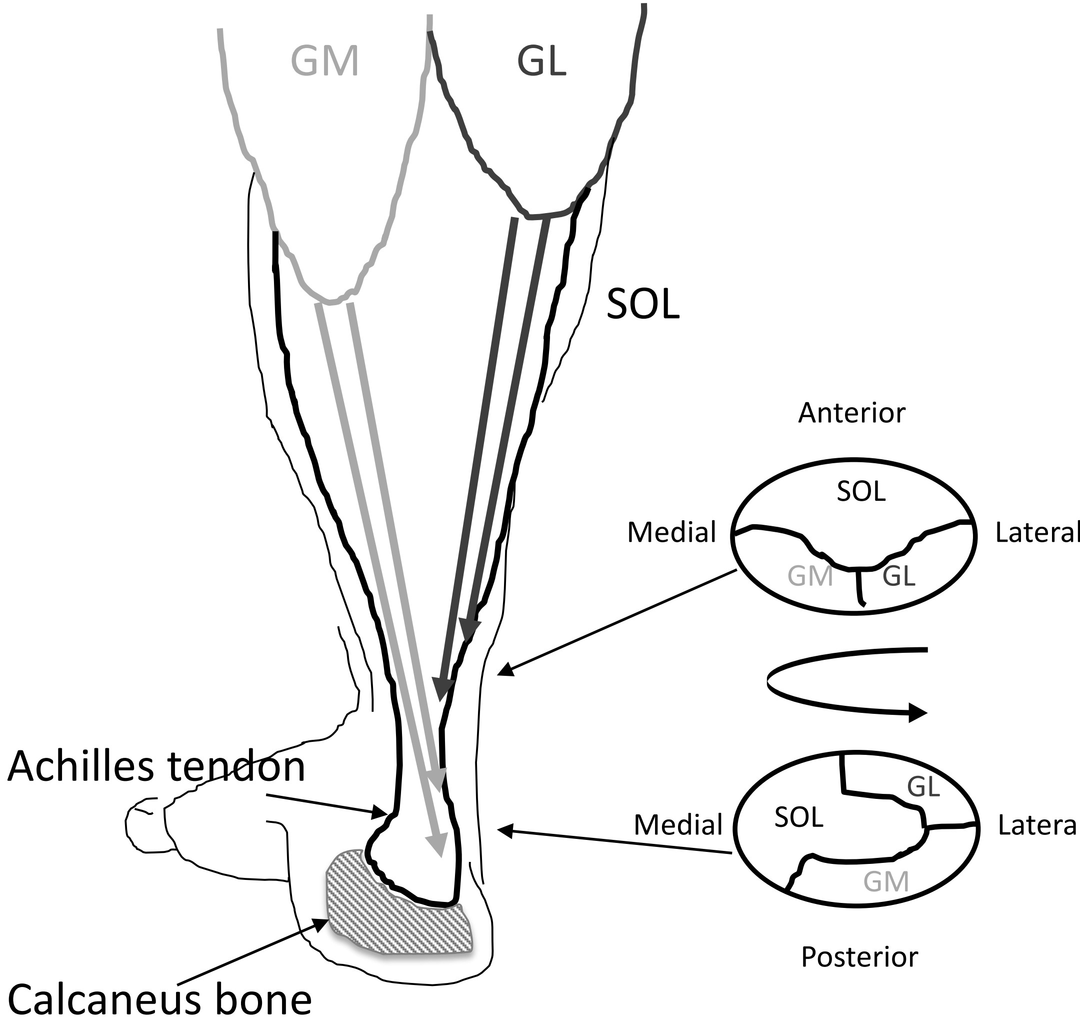

GM
GL
SOL
Anterior
SOL
Medial
Lateral
GM
GL
GL
SOL
Medial
Lateral
GM
Posterior
Achilles tendon
Calcaneus bone

Figure 2

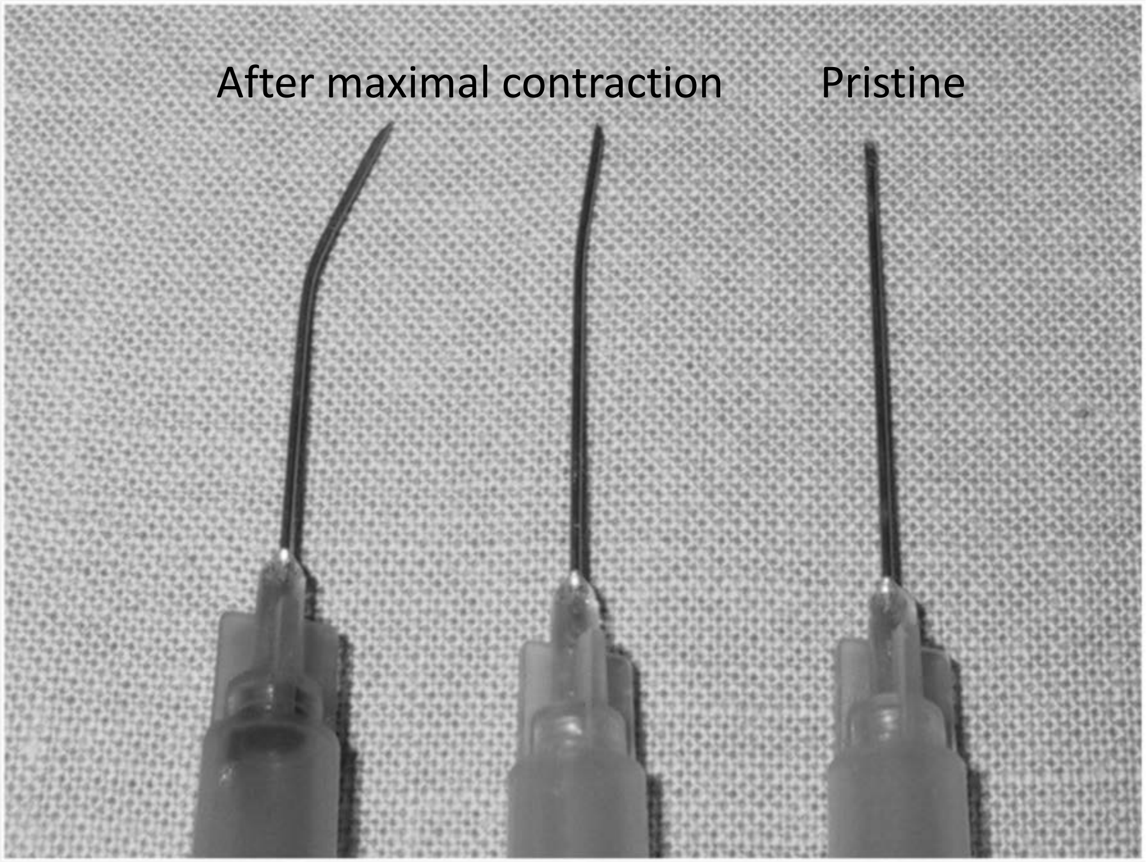


Figure 3

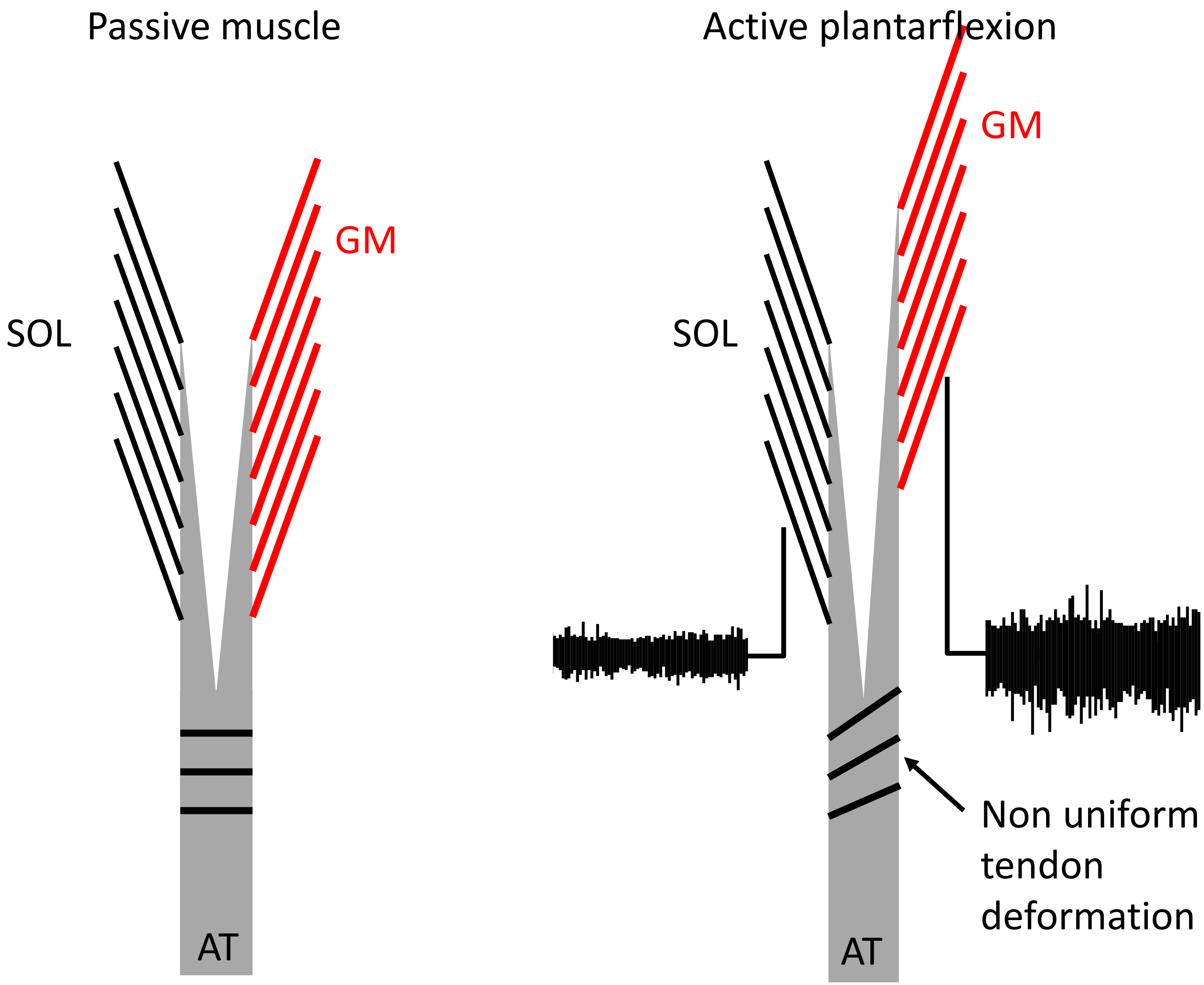
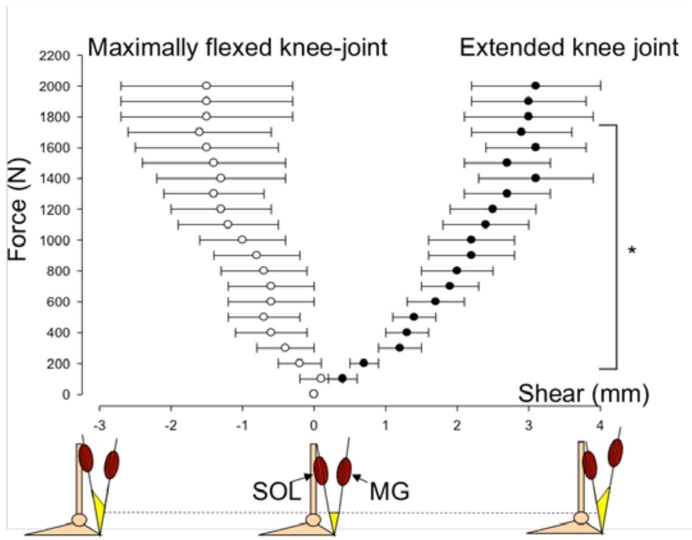


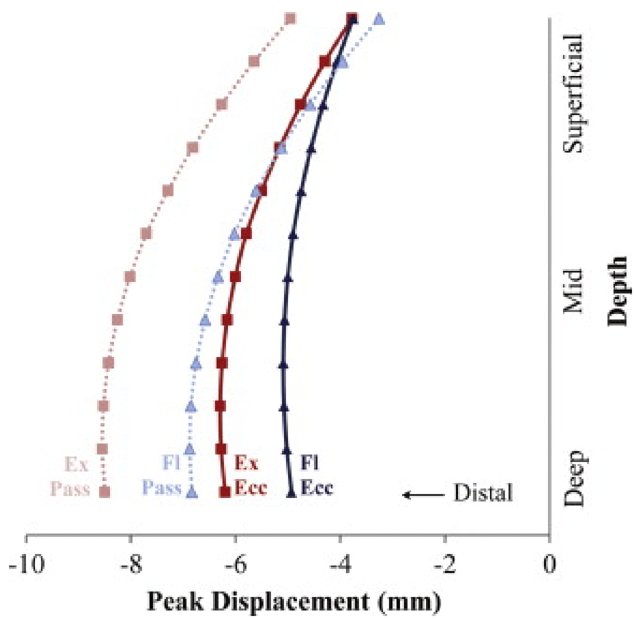
Figure 4 – conceptual figure

1.



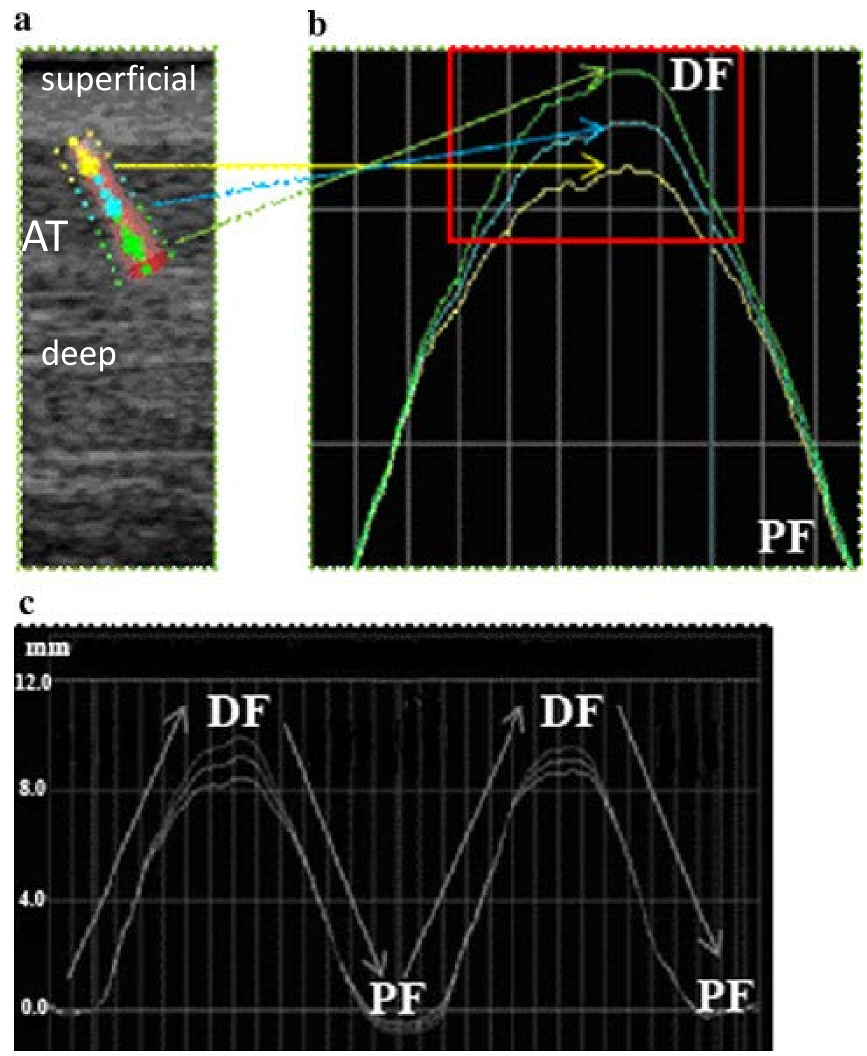
Maximally flexed knee-joint
Extended knee joint
Force (N)
2200
2000
1800
1600
1400
1200
1000
800
600
400
200
0
*
Shear (mm)
-3
-2
-1
0
1
2
3
4
SOL
MG

2.



Ex
Pass
Fl
Pass
Ex
Ecc
Fl
Ecc
Distal
Superficial
Mid
Deep
Depth
-10
-8
-6
-4
-2
0
Peak Displacement (mm)

3.



a
b
superficial
AT
deep
DF
PF
c
mm
12.0
8.0
4.0
0.0
DF
DF
PF
PF

Figure 5

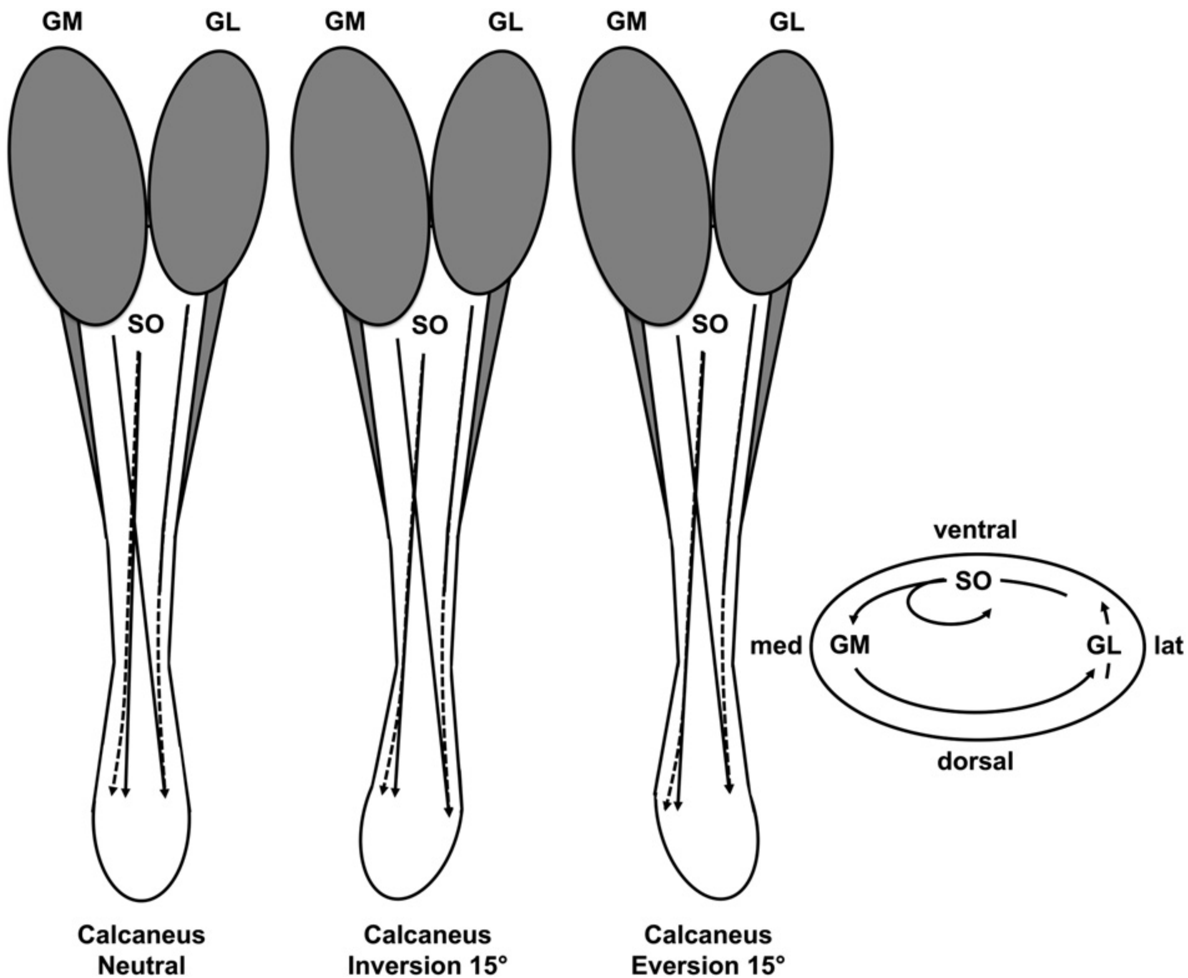

GM
GL
GM
GL
GM
GL
SO
SO
SO
Calcaneus
Neutral
Calcaneus
Inversion 15°
Calcaneus
Eversion 15°
ventral
SO
med
GM
GL
lat
dorsal

Figure 6