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Review

Towards modern understanding of the Achilles tendon properties in human movement research

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ABSTRACT

The Achilles tendon (AT) is the strongest tendon in humans, yet it often suffers from injury. The mechanical properties of the AT afford efficient movement, power amplification and power attenuation during locomotor tasks. The properties and the unique structure of the AT as a common tendon for three muscles have been studied frequently in humans using in vivo methods since 1990′s. As a part of the celebration of 50 years history of the International Society of Biomechanics, this paper reviews the history of the AT research focusing on its mechanical properties in humans. The questions addressed are: What are the most important mechanical properties of the Achilles tendon, how are they studied, what is their significance to human movement, and how do they adapt? We foresee that the ongoing developments in experimental methods and modeling can provide ways to advance knowledge of the complex three-dimensional structure and properties of the Achilles tendon in vivo, and to enable monitoring of the loading and recovery for optimizing individual adaptations.

1. Introduction

The Achilles tendon (AT) is important for efficient locomotion and an injury can immediately impair functional capability with long term consequences (McAuliffe et al., 2019; Hoeffner et al., 2022). Research suggests that AT first appeared in our anatomy ~ 2 million years ago and has been crucial to our survival allowing persistence hunting (Bramble & Lieberman, 2004). The AT allows efficient ambulation by storing and returning a considerable amount of energy as we walk, run or jump (Alexander and Bennet-Clark, 1977; Roberts, 2002). Tendons can return 90–95% of the stored strain energy during elastic recoil making them remarkably efficient. In addition, compliant tendons allow a decoupling of the muscle fascicle behavior from the muscle tendon complex which assists with power amplification during jumping and acceleration tasks, and with power attenuation during landing tasks (Roberts and Azizi, 2010). As tendons elongate when the muscles contract, they can modify muscle function by influencing muscle length and velocity (Herbert and Crosbie, 1997; Lichtwark and Wilson, 2006). For example, by decreasing muscle strain tendons can modify the operating range and thereby the force producing capacity of a muscle (Lieber et al., 1992). Furthermore, by decreasing muscle shortening velocity tendons can reduce the muscle's need for ATP (Ryschon et al., 1997). All of this is possible due to its remarkable structural and material properties which contribute to the efficiency of movement.

The AT is a common tendon for soleus and gastrocnemius muscles (Fig. 1). Although the twisted structure of the AT has been described nearly a century ago in beaver (Bojsen-Møller and Magnusson, 2015), the human cadaver studies in 2000′s (Edama et al., 2015; Szaro et al., 2009), reporting several AT structure types, have accelerated the understanding and research of possible individual-specific properties that may be relevant for performance, injury-risk and rehabilitation. The biomechanical properties of tendons have been reported in classic studies by illustrating force–elongation and stress–strain relationships yielding information about tendon stiffness and Young's modulus. Ultimate strength of tendons provides understanding of injuries and is typically assessed by elongating the tendon to rupture. Consequently, ultimate strength cannot be assessed in humans in vivo.

In this review, we focus on the most important and frequently assessed properties of the human Achilles tendons (Fig. 2). **Strain** is the measure of the longitudinal deformation due to the application of longitudinal stress, and important for tendon adaptation. **Stress** is the ratio of force to the area over which the force is applied. **Stiffness** is a

Abbreviation: AT, Achilles tendon.

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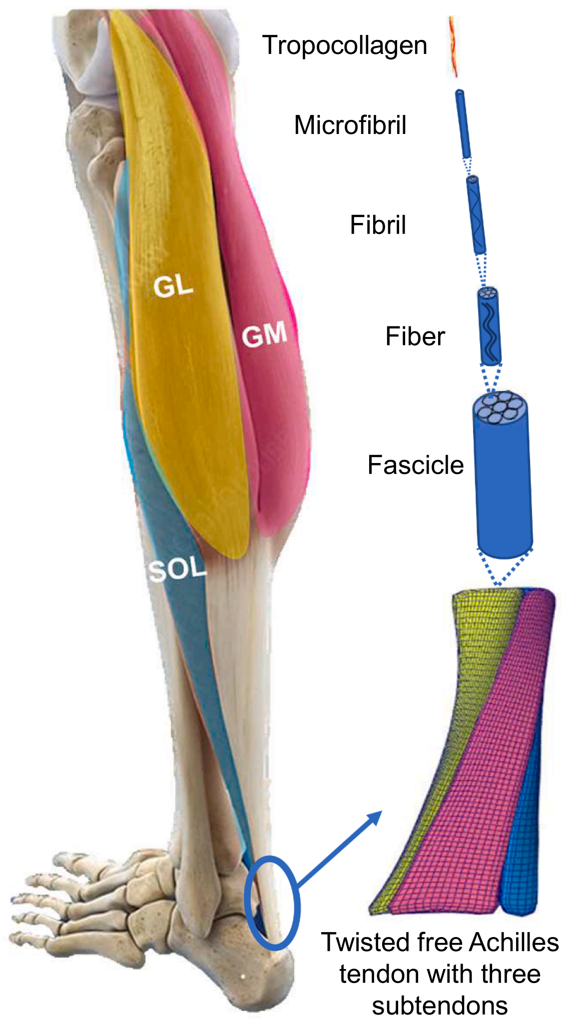

Fig. 1. Achilles tendon is a common tendon for soleus (SOL), medial (GM) and lateral gastrocnemius (GL) muscles. Each muscle has its own subtendon which rotate about each other mediolaterally when traveling distally. Tendons have a distinct hierarchy which has been depicted in the figure according to Handsfield et al., 2016.

measure of the resistance to deformation and it is relevant e.g. for storage of elastic energy. **Young's modulus** reflects material properties independent of size of the tendon. We also review the property of **hysteresis**, which tells about how much of the elastic strain energy is lost during tendon stretch–shortening cycle. Tendons are viscoelastic and in addition to hysteresis have also other time-dependent properties of strain rate, creep and stress relaxation (Butler et al., 1978).

With this review, we walk you through the 50-year history of Achilles tendon research; how AT properties have been studied and what is the current state-of-the art, and place biomechanical properties of the AT in the context of human movement and adaptation.

2. Evolution of knowledge on the Achilles tendon

Why did the properties of tendons start to interest researchers of human movement in the first place? In the 1960′s, Cavagna and colleagues (Cavagna, 1969; Cavagna et al., 1964) studied kinetic and potential energy fluctuation in human movements. They found that during running, efficiency was much higher than during walking or cycling which indicated that there must be an elastic recoil mechanism. At that time, Cavagna et al. concluded that the elastic energy must be stored in the muscles. In the same era, Goslow et al. (1973) showed in cats that the AT reduced the amount of shortening needed from soleus muscle fibers during a step, averting the focus to tendon for elastic recoil. The subsequent animal work by Alexander (Alexander, 1974; Alexander and Vernon, 1975) showed that stretching and recoil of tendons played an important role in reducing energy cost. Few years later Alexander and Bennet-Clark (Alexander and Bennet-Clark, 1977) calculated that the tendon have ~ 10 times the capacity of a muscle to store elastic energy. The importance of the AT for movement energetics was established.

From a clinical perspective, there was a need to study the AT to understand its trauma, treatment and rehabilitative measures. In fact, research on "rupture" and "treatment" have dominated the publications on the AT since 1970 (Fig. 3A-E). Still today, researchers are seeking optimal treatment options to rupture (Fackler et al., 2022) and tendinopathy (Silbernagel et al., 2022) that are the most common problems related to the AT.

The properties of tissue dictate the framework of function. The knowledge of tendon properties 50 years ago was based on in-vitro experiments of ligaments and tendons from cadavers and animals at different structural levels ranging from collagen molecules to fibrils to fibers and whole tendon (Kastelic et al., 1978) (Fig. 1). The basic mechanical properties of tendon, based on experiments with rat tail tendon, were reported already in 1950′s with keen interest on the wavy crimp structure and its straightening upon loading (Rigby et al., 1959). Since collagens (mostly type I) are abundant in tendons providing them tensile strength, much research has been done on the properties of collagens (Fig. 3F-J). The collagens, produced by tendon cells (fibroblasts, tenocytes), lie in a cocktail of proteoglycans, glycosaminoglycans, structural glycoproteins and other smaller molecules (Kannus, 2000). The importance of the non-collagenous matrix has been pointed out in recent studies investigating the interfascicular matrix in the equine energy storing tendon (Thorpe et al., 2012). This matrix allows for sliding between fascicles, enabling the large extensions that occur in AT during movements. In addition, the interfascicular matrix can withstand cyclic loading, and is more elastic in energy storing tendons (Thorpe et al., 2012). This composition gives the tendon its unique properties.

Human in vivo tendon properties of stiffness and Young's modulus were first assessed for tibialis anterior by Maganaris and Paul in 1999, and shortly after researchers focused more on the properties of plantarflexor muscles and the AT (Maganaris and Paul, 2002; Magnusson et al., 2001). In the AT, the tendons of soleus, medial and lateral gastrocnemius muscles are intertwined, thus the AT contains three subtendons with different lengths (Crouzier et al., 2022; Khair et al., 2022a)(Fig. 1). The twisted subtendon structure is known from human cadaver studies (Edama et al., 2015; Pękala et al., 2017; Szaro et al., 2020; van Gils et al., 1996) and recently, the mechanical properties of the subtendons have been investigated. In 2021, Ekiert et al. (Ekiert et al., 2021) reported in the human cadaver AT, that the soleus subtendon had a smaller tensile modulus and greater hysteresis than medial gastrocnemius subtendon, the values of lateral gastrocnemius lying in between. *In vivo*, the human AT shows differential displacements with the anterior tendon displacing more than posterior tendon during voluntary muscle contractions (Chernak Slane and Thelen, 2014) but currently, the movements cannot be unequivocally attributed to specific subtendons (Khair et al., 2022a). However, observations on internal tendon shear have allowed understanding that nonuniform movement is a sign of a healthy tendon, which is decreased in injury (Couppé et al., 2020; Fröberg et al., 2017; Khair et al., 2022b) and in aging (Clark and Franz, 2021; Slane and Thelen, 2015).

3. Towards a modern understanding of AT properties

Assessment of tendon properties requires a measure of tendon length and tendon force. Regarding tendon length, the early human studies in vivo considered the length of the entire muscle–tendon unit based on joint angles (Grieve et al., 1978) before a distinction between muscle and tendon - or tendinous tissue - could be made. Direct assessment of human muscle fascicles using ultrasonography led to the development of a model where the muscle–tendon unit contained a short muscle fiber that was typically represented in a pennate orientation to the line of action coupled with an in-series elastic element (Fukunaga et al., 2001, 1997). Such a model considers erroneously that the tendon and aponeurosis would be in series which has fundamental consequences for estimations of tissue loading, and mechanics and energetics (Epstein et al., 2006), and the need to separate the length of tendon and aponeurosis was recognized.

B-mode ultrasonography was introduced to tendon length and elongation assessments for human movement studies by the group of Fukunaga (Fukashiro et al., 1995; Fukunaga et al., 1996a, 1996b). Many ultrasonography studies, where a movement of a feature corresponding to fascicle insertion to aponeurosis was tracked, have reported tendinous tissue displacements encompassing not only the pure AT, but also aponeurosis tissue (Arampatzis et al., 2007; Ishikawa et al., 2005; Rosager et al., 2002) (Fig. 2G). As noted above, it is important to distinguish aponeurosis from the tendon for accurate assessment of tendon properties, as was done already in some early reports (Finni et al., 2003; Fukunaga et al., 2001; Magnusson et al., 2003; Muramatsu et al., 2001). Fine-tuning of the methodological details of tendon length assessment is still ongoing with a recent study showing that adding only 1–3 cm of aponeurosis above the exact location of the muscle–tendon junction increases the displacement and strain of the AT (Finni et al., 2022).

Over the years, there have been several ways to assess AT length and its change using ultrasonography (Finni et al., 2013; Seynnes et al., 2015). Accuracy of length and elongation assessments improved with correction methods accounting for joint rotation that causes calcaneal displacement (Fukunaga et al., 2001; Magnusson et al., 2001) or directly assessing both the origin and insertion of the tendon in isometric (Muramatsu et al., 2001) and dynamic conditions (Lichtwark and Wilson, 2005). Later, it was considered that the line of action of the AT is not fully straight, and during plantarflexion there is an increase in the curvature due to constraints at the ankle joint (Hodgson et al., 2006). While linear assumption of the tendon is frequently used (Gerus et al., 2011; Zellers et al., 2017), accounting for the curvature yields about 1.2% greater strains (Stosic and Finni, 2011) and ~ 5% smaller moment arm thereby influencing AT force and other derived properties during dynamic tasks (Tecchio et al., 2022).

In recent years the use of three-dimensional (3D) freehand ultrasonography has become more common especially for estimating the length and length changes of the free AT (Barber et al. 2009). The method has been shown to be reliable in healthy participants (Merza et al., 2021) and solves some of the problems with the two-dimensional (2D) tracking such as out-of-plane movements, tracking of only one point and the restriction to a small movement as they need to stay within the image frame. However, this method requires static position and is not applicable in locomotion.

Assessment of the AT force typically relies on dynamometer or force plate assessments to determine the plantar flexor moment (torque) and from there, tendon forces are calculated using moment arm information. The rare human experiments measuring directly in vivo tendon forces using transducers inserted in the AT were performed by the group of Komi (Arndt et al., 1998; Finni et al., 1998; Gregor et al., 1987; Komi, 1996) and described AT forces during various human movements. In a few cases, properties of strain (Finni et al., 2002), stress (Komi et al., 1992; Finni et al., 1998) and hysteresis (Finni, 2006) were reported from these in vivo AT force measurements.

During isolated single joint movements, the plantar flexor torque is typically measured using a dynamometer measuring the torque directly,

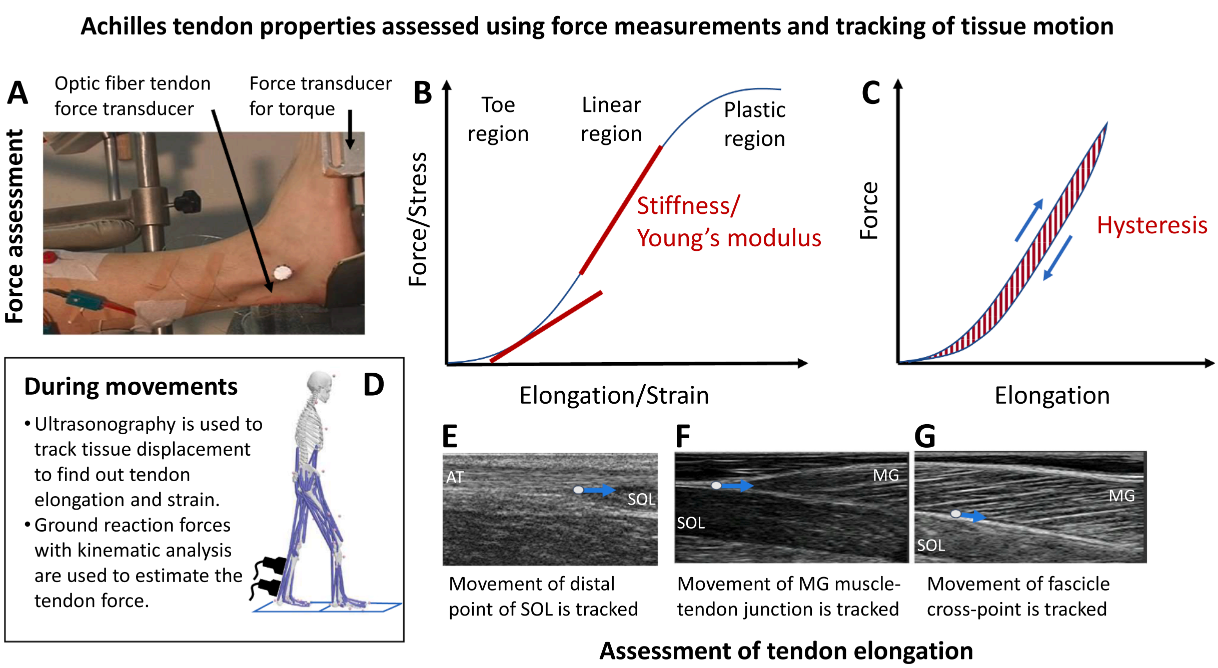

Fig. 2. Typical methods used to assess Achilles tendon properties in isometric condition (A-C, E-G) and during dynamic movements (D). (A) Forces are typically assessed from ankle torque measurements but some studies have used in vivo force transducers. Tendon elongation is typically assessed from ultrasound videos from where the myotendinous junction of SOL (E) or medial gastrocnemius (F) are tracked in order to calculate the changes in AT length during contraction. (B) The force–elongation or the stress–strain curves of tendon contain toe, linear and plastic regions. The slope of the force–elongation curve yields stiffness that varies with force level. When force is divided by the tendon cross-sectional and tendon elongation normalized to initial length of the tendon, the slope of the stress–strain curve yields Young's modulus. There are several ways to assess tendon elongation and they should include measurement of displacement of calcaneal insertion and displacement of the muscle-tendon junction of interest. Most often medial gastrocnemius subtendon length has been measured. If the fascicle cross-point along the aponeurosis is tracked as in (G), the measure does not reflect true tendon property anymore since the aponeurosis has different and variable properties. Hysteresis is the area under the loading and unloading curves from a force–elongation assessment (C). D) During dynamic movements, motion analysis assisted ultrasonography is typically used to assess tendon elongation and strain, and force plate measurements to estimate AT force. Please see text for details of force and tendon length assessments.

Fig. 3. Word cloud compiled of titles of research articles that have been retrieved from PubMed using search term [**Achilles tendon**] (A-E, 600 words shown) and [**Achilles tendon propert***] (F-J, 300 words shown) in different decades. For A-E, titles of the articles were cleared from special characters and the words: achilles, tendon, “tendo achillis”, transl. and author’s. The following words were combined into terms before creating the clouds: “anterior cruciate ligament”, “flexor hallucis longus”, “magnetic resonance”, “randomised controlled trial”, “comparative study”, “experimental study”, “pilot study”, “cross-sectional study”, “preliminary study”. For F-J, titles of the articles were cleared from special characters and the words: achilles, tendon, properties, mechanical, biomechanical.

or a force plate requiring motion capture and an inverse dynamics approach. During an isometric maximal voluntary contraction, some plantarflexion is almost unavoidable which causes a misalignment between the ankle rotation axis and the axis of the dynamometer. This can cause an overestimation of the real plantar flexor torque of approximately 6–10% (Arampatzis et al., 2005a). Furthermore, ankle joint rotation alters the AT and foot moment arms which has direct influence on AT force calculations. In addition, co-contraction of the antagonist muscle could potentially contribute to an underestimation of AT force for about 6–8% (Mademli et al., 2004) (Fig. 4).

When estimating AT force from dynamometer or force plate assessments, defining AT moment arm length is essential in order to calculate tendon force. Methods of AT moment arm estimation include tendon excursion method which assumes that the tendon is inextensible (An et al., 1984; Maganaris et al., 1998), imaged based estimation of the center of rotation (Maganaris et al., 1998) and anatomical landmarks (Arampatzis et al., 2005a; Scholz et al., 2008a) sometimes combined with ultrasound (hybrid methods) (Manal et al., 2013). Some studies have corrected for the perpendicular distance from the skin to the tendon using ultrasound (Kongsgaard et al., 2011). The 2D image-based center of rotation methods contain the limitation that the ankle joint rotation might not only be happening in the sagittal plane and secondly, bulging of the muscle causes the muscle–tendon unit not to act in a straight line (Scholz et al., 2008b).

The changes in AT moment arm due to changes in ankle joint angle can be accounted by regression equations (Grood and Suntay, 1983) and musculoskeletal modeling (Delp et al., 2007), which are able to provide dynamic moment arms. In contrast, many investigations used constant moment arms based on population-based averages which can under or overestimate AT force.

Another important consideration when solving AT forces is the role of synergistic muscles. While the triceps surae has the largest moment arm and the largest physiological cross-sectional area of all plantar flexors, also flexor hallucis longus, flexor digitorum longus, peroneal muscles, tibialis posterior and plantaris contribute (Fukunaga et al., 1996a, 1996b). In addition to the relative physiological cross-sectional area, the individual muscle contributions have been estimated using normalized EMG activity (Crouzier et al., 2020), selective stimulation of calf muscles (Bojsen-Møller et al., 2010; Finni et al., 2001) or muscle glucose uptake (Masood et al., 2016). Moreover, antagonist activity has been considered early on (Magnusson et al., 2001) but their activity level in isometric condition remains often negligible (Peltonen et al., 2010).

When investigating AT force in more complex movements, several methodologies have been used such as fiber optics (Finni et al., 1998), ultrasound tracking of the muscle tendon junction in combination with tendon stiffness (Lichtwark & Wilson, 2006; Kharazi et al., 2021) or a combination of motion analysis and biomechanical modelling (Baxter et al., 2021). During walking, the reported peak AT forces have varied from 1.8 − 2.1 body weights (BW) based on optic fiber force transducer (Finni et al. 1998) to 2.5 BW (Lichtwark & Wilson, 2006) and 2.7 BW (Kharazi et al., 2021), when using AT stiffness in combination with tracking medial gastrocnemius muscle–tendon junction, to 3.3 BW using inverse dynamics and a constant moment arm (Baxter et al., 2021). Furthermore, using neuromusculoskeletal modeling AT peak force of 1.9 BW has been reported (Devaprakash et al., 2022) while 3.9 BW was reached based on reaction forces, kinematic data and a contact-coupled finite element model (Giddings et al., 2000). Thus, there are differences in the range of forces depending on the methodological choices and continuing efforts are needed to evaluate the validity of the approaches.

Currently, state-of-the art tendon force assessments during dynamic movements include a combination of torque or ground reaction force assessments combined with modeling (Lai et al., 2014). This combination allows distinguishing between the gastrocnemii and the soleus muscle force during dynamic activities (Delp et al., 2007). Several optimization techniques are used to determine the contribution of the different muscles to the joint torque in dynamic movement such as static optimization, dynamic optimization, EMG-informed and EMG-driven techniques. As non-invasive direct measurement of these muscle forces remains impossible, validation of these techniques continues to be a challenge. Recently developed non-invasive shear wave method to assess tendon forces during human movement (Martin et al., 2018)

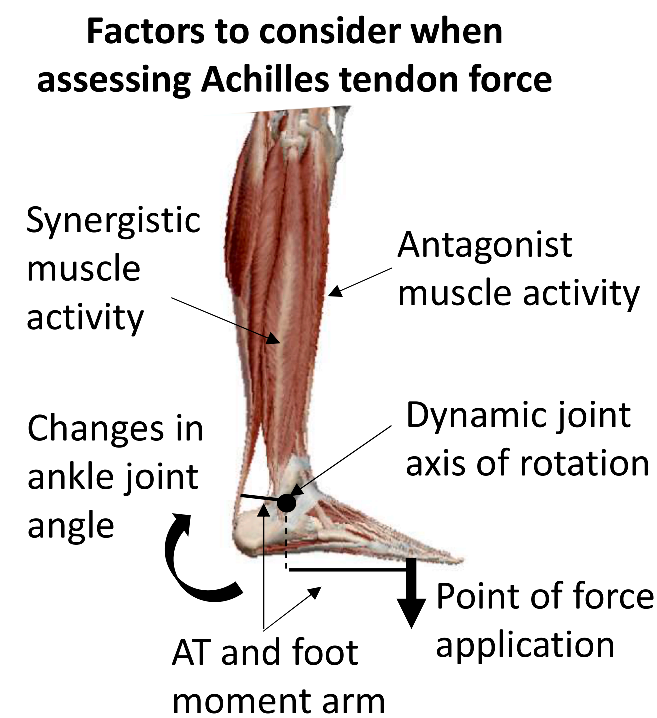

Fig. 4. Achilles tendon force assessments are influenced by several factors. Measurement of the AT and foot moment arm lengths require determination of the point of force application under the ball of the foot, the ankle joint axis of rotation that moves during ankle joint movements, and identification of perpendicular distance from AT to the axis of rotation. Changes in ankle joint angle influences the moment arms not only in dynamic movements, but often also in isometric contractions if the fixation to the dynamometer is not rigid enough. Activation of muscles other than the triceps surae can change the point of force application; the activation of smaller synergistic muscles increasing and antagonist muscle activity decreasing the force. These factors can cause errors in AT force up to 10% if they are not carefully considered during the assessments.

shows promise and, perhaps in the future, may be used to validate other estimation methods.

4. Strain as a trigger for tendon adaptations

Tendon strain is the trigger for tendon adaptations (Magnusson et al., 2010) and important for storing and returning energy. It is therefore crucial to get better insights on how the tendon strains during dynamic activities. Several techniques are available for strain assessments, ranging from tracking the musculotendinous junctions manually or with speckle-based techniques (Magnusson et al., 2003; Werkhausen et al., 2018), to ultrasound-assisted 3D motion capture (Barber et al., 2009) to finite element modeling (Shim et al., 2018). Some invasive approaches have also been used in strain measurements. Magnusson et al. (Magnusson et al., 2003) inserted a needle into the tendon and tracked its displacement to get the free tendon strain. In another study, small tantalum beads – visualized with X-rays – were inserted into both ends of the tendon in a surgical procedure to validate ultrasound-based speckle-tracking of tendon tissue movement (Beyer et al., 2018).

An important methodological aspect is the joint angle at which the tendon resting length is determined, since the strain is defined as the length in a given condition relative to the resting length, divided by the resting length ($\varepsilon = \frac{l-lo}{lo}$). Tendon is considered to be at rest below so-called slack length which is defined as the length at which the tendon starts to elongate when loaded. This slack length and the corresponding joint angle can be assessed by observing displacement of the musculotendinous junction when the ankle joint is passively rotated (Aeles et al., 2017a) or with elastography (Hug et al., 2013). Differences in slack length reflect the length of the toe region, which may also be estimated by extrapolating the linear region of the force–elongation curve to x-axis as done by Shin et al. (Shin et al., 2008a). Some studies use a specific ankle angle such as 90 degrees flexion as the reference or initial length used in strain calculations. However, at this joint angle the AT is already under tension (Aeles et al., 2017b) and the amount of tension might be very different between individuals affecting strain values. Consideration of tendon slack length takes these inter-individual differences into account.

During walking AT strains have been reported to vary between 4.0% and 4.6% (Kharazi et al., 2021; Lichtwark & Wilson 2006). Recently, free AT strains have been estimated based on neuromusculoskeletal modeling. Devaprakash et al. (Devaprakash et al., 2022) estimated peak strains of the whole free tendon of trained runners to range from 7% during walking to nearly 14% during running at 5 m s^{-1}. The latter value is close to failure strain of 15% in vitro (Schechtman and Bader, 1997). The nearly two-fold difference in these strain values may be related to methods of calculation but also the fact that the latter represents the strain in the free tendon and the previous (Kharazi et al., 2021; Lichtwark & Wilson 2006) are based on tracking of the muscle–tendon junction of the medial gastrocnemius relative to the calcaneus insertion, therefore representing medial gastrocnemius subtendon. As discussed below, the subtendons appear to have different properties.

The soleus subtendon (i.e. free tendon) strain has been reported to be smaller than gastrocnemius subtendon strains. In submaximal isometric contractions, free tendon/soleus subtendon strains have been reported to reach values of 3.2% at 30%MVC (Obst et al., 2016), 4.7% at 40% MVC (Finni et al., 2003), ~4% (Lichtwark et al., 2013) – 5.2% at 50% MVC (Farris et al., 2013), 6.4–6.6% at 70%MVC (Obst et al., 2016, 2014) and 8% at 100%MVC (Magnusson et al., 2003), while medial gastrocnemius strains 1.3% at 30%MVC (Obst et al., 2016), ~2.5% at 50%MVC (Lichtwark et al., 2013), 2.6% at 70%MVC (Obst et al., 2016) and 4.7% (Arampatzis et al., 2005b) - ~5% at 100%MVC (Muramatsu et al., 2001). These observations concur with an animal study (Finni et al., 2018) supporting cadaver studies showing that soleus subtendon is more compliant than gastrocnemius also in humans (Ekiert et al., 2021).

Finite element (FE) modeling with a 3D reconstruction of the free AT can be used to compute local 3D tendon strains. These tendon models provide insight into the role of tendon geometry, material properties and tendon twist on the tendon strains. The first FE model of the free AT (Shim et al., 2014) characterized the influence of geometry and material properties and demonstrated that changes in 3D tendon geometry contributed more to local stresses in the tendon than the material properties (Hansen et al., 2017). Recently Funaro et al. showed the influence of tendon twist and rehabilitation exercises on AT strains (Funaro et al., 2022). Results of the simulation demonstrated that the progression in rehabilitation exercises based on the average tendon strain was the same for the three types of twist. The location of the peak strain does vary, and the least twisted tendon has the highest strains. Average strain values during one-legged heel drop exercises were approximately 6% and peak strains were located in the medial gastrocnemius subtendon. Although these models allow investigating the role of isolated contributing factors on tendon strain, they are still simplified models of the complexity of the human body and validation of these models is very difficult due to limitations in experimental methods to assess subtendon strains.

Above, we have discussed tensile strains but the AT experiences also transverse strains. The distally thick AT forms a broad tendon sheet proximally that is influenced by adjacent muscle contractions (Finni et al., 2003). The width of the tendon sheet changes with contraction (Barber et al., 2009) and transverse strain at the level of gastrocnemius myotendinous junction can reach 5% at 50%MVC reflecting widening of the aponeurosis which is attached to a bulging muscle (Farris et al., 2013). Furthermore, while most often a single value for strain is measured, it represents a global strain but it is important to note that there can be heterogeneous strains within the tendon (Chernak Slane and Thelen, 2014; DeFrate et al., 2006; Finni et al., 2003; Svensson et al., 2021).

5. Stress for strength

Tendon stress is determined by dividing the tendon force by the cross-sectional area of the tendon ($\sigma = \frac{F}{A}$). As the AT has an asymmetrical structure with changing geometry going from proximal to distal, the location where the cross-sectional area is measured can influence the magnitude of tendon stress. Typically, researchers aim for the smallest area, identifying the midportion of the free tendon (Lindemann et al., 2020), while other studies have used an average area (Bohm et al., 2014) or a specific distance from the calcaneus (Magnusson et al., 2001; Stenroth et al., 2012)).

In natural movements also transversal and rotational forces, contusions and compression may exist but they are more difficult to assess and here we focus on the assessments in the longitudinal direction, i.e. tensile stress. Human cadaver studies have reported ultimate tensile stress to be 80 MPa at which the tendon breaks (Wren et al., 2003). This is a somewhat lower value than in specimens tested in fresh state or from young donors (Butler et al. 1978) and is likely an underestimation due to problems in clamping the Achilles tendon in cadaver specimens. Using in vivo force transducers, the AT stress has been reported to reach 59 MPa during walking and 111 MPa during running (Komi et al., 1992). Comparison of these values may reflect the low safety margin that the AT has and be one potential explanation for its susceptibility for ruptures.

The highest peak stress during walking of 59 MPa was measured with a buckle force-transducer while 43 MPa was assessed using tendon tapping device (Keuler et al., 2019), 24 MPa using modeling (Devaprakash et al., 2022) and 21 MPa using optic fiber force transducer (Finni et al., 1998). The large variability may be related to methodological differences in assessing AT force or to a smaller extend to methods to measure the cross-sectional area.

6. Stiffness for storing elastic energy and effective force transmission

Stiffness is calculated from the linear portion of the force–elongation curve (Fig. 2). When considering the full curve, starting from the resting length, stiffness increases monotonically with initial stiffness being very low in the so-called toe region. Because tissue stiffness is inversely proportional to its length (Butler et al., 1978), long tendons tend to be more compliant, influencing the speed of force transmission. Higher AT stiffness is associated with greater rate of torque development in both children and adults - the influence being greater in the early rise of force in adults while the greatest effect was on the later force rise in children (Waugh et al., 2013). On the other hand, compliant AT is associated with better utilization of pre-stretch in jumps (Kubo et al., 2007) with a sweet spot allowing maximal efficiency during walking and running (Lichtwark and Wilson, 2008).

A large variation in AT stiffness values has been reported (184 N mm^{-1} to 2622 N mm^{-1}) (see Ekiert et al., 2021). This reported variability could be due to differences in methodology and regarding which part of the tendon (or aponeurosis) was tracked, and the population examined. Using a model, Lichtwark and Wilson (2008) estimated that AT with stiffness of about 150 N mm^{-1} optimizes efficiency of walking while running requires a stiffer tendon of about 250 N mm^{-1}. Individual factors such as muscle volume, muscle fascicle length and length of the toe-region modify the optimal stiffness.

When values of stiffness are reported in the literature, they mostly consider only the linear portion of the force elongation curve, beyond the toe region. The force–elongation curve has been measured using separate assessments with different levels of force or using synchronized measures between force and length which allows to select the linear part of the force–length relationship of the tendon. Using the synchronized data, researchers select the region of the force–length curve which can vary a lot between studies (10–80% (Dick et al., 2016; Maganaris and Paul, 2002; Peltonen et al., 2013); 50–60% (Theis et al., 2012); 50–100% (Bohm et al., 2014; Kubo et al., 2007); 90–100% (Magnusson et al., 2001). In injured condition, also tangent at 50%MVC was used to avoid the influence from synergistic muscles (Khair et al., 2022b). In addition to muscle synergism, stiffness values can be influenced by preconditioning of the tendon (Maganaris, 2003), the rate of force development, electromechanical delay (Morse et al., 2005) and strain rate (Theis et al., 2012). In addition, assessments at different plantar flexion angles provide stiffness values at different regions of the force–length relationship (Fig. 2). Furthermore, all limitations previously mentioned for the calculation of force and tendon elongation should be considered.

In addition to extracting tendon stiffness from the conventional measures of tendon force and length, ultrasound imaging method called shear wave elastography has gained popularity in stiffness assessments. Using acoustic radiation force induced by ultrasound beams to perturb the tissue, the method is non-invasive without external compression or vibration (Bercoff et al., 2004). While the method is at its best for isotropic tissues, it can be used to assess muscle (Bernabei et al., 2020) and more recently also tendon stiffness. The first paper to use this technique for tendons was purely descriptive (Arda et al., 2011). After several further investigators refining the technique, shear wave elastography was used to measure elastic properties of the ruptured Achilles tendon (Frankewycz et al., 2018) but also to improve the knowledge of the material properties of the tendon such as slack length (Hug et al., 2013). However, more methodological studies with shear wave elastography are warranted. While reliability measures have been reported, a recent review calls for more thorough establishment of reliability when assessing elasticity of tendons using elastography (Schneebeli et al., 2021). More importantly, validation reports are scarce. A validation study using pig patellar tendons showed high correlations between shear modulus and traction modulus within each specimen when measured with supersonic shear imaging (Zhang & Fu, 2013). However, each specimen had an individual slope referring that shear modulus values cannot be compared directly between individuals or at a group level, the correlation is much lower. In humans, construct validity has been examined by assuming association between force and stiffness of AT. Using continuous shear wave imaging the validity was evaluated to be sufficient (Corrigan et al., 2019).

7. Young's modulus - properties independent of shape

Using the linear portion of the stress–strain curves the material properties of the Achilles have been determined using a combination of dynamic ultrasound and torque measures. Young's modulus allows insights into the influence of material properties independent from changes in cross-sectional area. Majority of the studies report tendon morphological, material as well as mechanical properties. Young's modulus ($E = \frac{\sigma}{\varepsilon}$), based on the strain of the medial gastrocnemius displacement in male human subjects, was 1200 MPa (Maganaris and Paul, 2002) while Magnusson et al. (2003) found a somewhat lower values (788 MPa) for the free tendon (Magnusson et al., 2003). In addition, large variation in the local strains on the surface of AT have been reported in specimens resulting in variability in Young's modulus between 217 and 897 MPa (DeFrate et al., 2006).

8. Hysteresis produces heat

Hysteresis describes the percentage of elastic strain energy lost due to viscosity during a stretch–shortening cycle (Fig. 2C). In a perfectly elastic material, there would not be hysteresis; an example of such a case could be a forever bouncing elastic ball that does not lose energy in any rebound. Low hysteresis in the AT is advantageous; it allows most of the stored elastic energy to be reused during propulsion of locomotion. Hysteresis in various tendons in vitro ranges from 5 to 10% (Bennett et al., 1986; Pollock and Shadwick, 1994) and it is to be assumed that similar values would be found in vivo. However, when researchers started to assess hysteresis of the human AT by combining dynamometer and ultrasonographic techniques, they reported notably greater values such as 17% (Farris et al., 2011; Kubo et al., 2006), 22% (Kubo et al., 2022) or 26% (Lichtwark and Wilson, 2005).

More notable was the high interindividual variation within these studies where the reported hysteresis could range from 2 to 45% (Farris et al., 2011). High hysteresis generates heat raising temperature and, if exercise is sustained long enough, it may ultimately lead to heat damage and degeneration of the tendon (Wilson and Goodship, 1994). Therefore, it is likely that the high hysteresis values are measurement artifacts rather than of physiological origin (Finni et al., 2013). The large variability and extremely high values of in vivo hysteresis may be related to uncertainties when assessing tendon force as described above (Fig. 4). Other factors contributing to possible errors in hysteresis measurements that have been discussed are lack of preconditioning, inaccuracies in length measurement, challenges in motor control in the unloading phase of the test leading to non-symmetrical loading–unloading phases and data synchronization issues (Finni et al., 2013). Thus, due to the high number of possible sources of variability, future studies should pay careful attention to assessment of hysteresis in the human AT (Lichtwark and Cresswell, 2013; Nordez et al., 2013).

9. Adaptation of AT properties in relation to human movement

Already in the 1970′s it was recognized that tendons can be influenced by immobilization, acute exercise, chronic physical activity, age-related effects, medication, and trauma (Butler et al., 1978). Mechanical load (stress and primarily strain), converted into cellular responses causes alterations in tendon structure and gene expression leading to adaptations (Khan and Scott, 2009). The mechanisms of adaptation in intact human tendons started to unravel with measurements of peritendinous blood flow and tendon metabolism using microdialysis (Langberg et al., 1999). The AT is supplied with small blood vessels throughout its cross-section with lowest vascular density at mid-length along the tendon (Zantop et al., 2003), but the life-long turnover of the mid core of AT tissue is shown to be limited (Heinemeier et al., 2013). It is now known that the AT is metabolically active with collagen synthesis and degradation enzymes both increasing with mechanical loading reflecting a delegate balance between positive adaptation and potential for overloading without sufficient recovery (Kjær, 2004). There are numerous reviews on tendon adaptation (Lazarczuk et al., 2022; Maganaris et al., 2017; Magnusson & Kjaer 2019) and in the following brief sections we keep the focus on the adaptability of AT mechanical properties.

Aging tendon properties

During maturation, tendon stiffness and Young's modulus increase, which was shown already in the early 1970′s in rat tail tendon (Diamant et al., 1972). It is logical to think that when the body mass and muscle's force producing capacity increases during maturation, it creates need also for bigger and stronger tendons. Indeed, in human gastrocnemius tendon, stiffness has positive association with body mass, and Young's modulus associates with peak stress (Waugh et al., 2012). Although participants of the study by Waugh et al. ranged from 5 years to adults, the age itself did not explain these associations. Therefore, it is no surprise, that stiffness and Young's modulus associate with muscle strength across wide range of ages (Stenroth et al., 2012) and sex (Muraoka et al., 2005).

Studies comparing older individuals to young adults have frequently reported lower AT stiffness and Young's modulus (Csapo et al., 2014; Delabastita et al., 2018; Onambele et al., 2006; Stenroth et al., 2016, 2012; Lindemann et al., 2020). However, there may not be differences in properties if the muscle strength is similar between young and old (Stenroth et al., 2012). On the other hand, it has been suggested that in older adults – who do have altered connective tissue properties (Couppé et al., 2014) – increased tendon cross-sectional area can compensate for the lower tendon material properties (Stenroth et al., 2012). The age-related changes in the AT properties have functional consequences to gait (Krupenevich et al., 2022; Stenroth et al., 2017), mobility (Stenroth et al., 2015) and balance (Onambele et al., 2006).

Physical activity and inactivity influence tendon properties

An appropriate physical training stimulates tendon fibroblasts to produce collagens resulting in increased cross-sectional area and tensile strength (Wang, 2006; Wang et al., 2018). Majority of the studies investigating the effect of physical activity and inactivity on the AT properties have used stiffness or Young's modulus of the tendon as a primary outcome and only a few included hysteresis.

A recent systematic review and *meta*-analysis performed by Lazarczuk (Lazarczuk et al., 2022) concluded that mechanical loading was associated with a large increase in Young's modulus, a moderate increase in tendon stiffness, and a small increase in tendon cross-sectional area. Even if hormonal milieu is altered, such as examined in female twins discordant for the use of hormonal replacement therapy, the AT cross-sectional area seems to be tightly genetically controlled and only a sufficient amount of physical activity can bring about morphological differences (Finni et al., 2009)).

In general, all contraction modes of resistance training induce a significant increase in tendon stiffness and Young's modulus while exercise protocols that also include aerobic training do show an effect on tendon properties (Lazarczuk et al., 2022). High strain resistance training induces the largest increases in tendon stiffness compared to low strain protocols (Arampatzis et al., 2010). Returning to normal physical activities after a resistance training rapidly decrease the AT stiffness back to the control values (Kubo et al., 2012). Reeves et al. showed that resistance exercise can decrease hysteresis thereby improving potential for elastic recoil (Reeves et al., 2005).

Different unloading protocols such as limb suspension (Shin et al., 2008b) and bedrest (Reeves et al., 2005) demonstrate a decrease in the AT mechanical properties when unloaded. Shin et al. found a decrease in the Young's modulus of 17% while the transition point (as a measure of the toe region) increased by 55%. Ninety days of bedrest decreased Young's modulus by 57% and stiffness by 58%. This effect was diminished to 37% and 38% respectively when the subjects were allowed to perform some resistance exercises every third day. Consequently, physical activity is vitally important for the health and function of tendons.

Injury and recovery

Much of the research on AT has been driven by the practical need to understand mechanisms of injury and rehabilitation. While AT rupture emerges in titles of journal articles at all examined decades, tendinopathy, which is a common complaint (de Jonge et al., 2011) is visible from 2000′s onwards mostly due to variability in preceding terminology (Fig. 3). (Crouzier et al., 2020; Dias et al., 2019; Finni et al., 2006; Heikkinen et al., 2017; Kannus and Jozsa, 1991; Masood et al., 2014; Zhao et al., 2009). The ruptured tendon, regardless of the treatment method, shows an increased thickness and is typically 6–14% longer than contralateral uninjured tendon influencing strains experienced by the tendon. Tendon elongation causes concurrent adaptations in the muscle tissue (Heikkinen et al., 2017; Khair et al., 2022b) with persisting functional deficits (Hoeffner et al., 2022) and much research is ongoing seeking optimal rehabilitation schemes.

In general, stiffness and Young's modulus are lower in the tendinopathic limb (Arya and Kulig, 2010; Helland et al., 2013) and the ruptured limb (Geremia et al., 2015) although not all studies show differences (Khair et al., 2022b). In this respect, it is important to note not only the methodology used to assess the mechanical parameters but also the type of treatment and rehabilitation, and time course of recovery when comparing the studies. Furthermore, synergistic muscles compensate for the deficiency in plantarflexion after AT rupture (Finni et al., 2006; Heikkinen et al., 2017) and tendinopathy may change the relative contribution of the triceps surae muscles (Crouzier et al., 2020; Masood et al., 2014). These studies highlight the importance of considering altered muscle activation patterns when adaptation of mechanical properties due to pathology are examined (Fig. 4).

Time course of recovery of biomechanical properties from rupture have been examined in few studies using tantalum beads within the AT to measure changes in local tendon length. These studies showed that the greatest elongations of tendon resting length occurred after initial rehabilitation between 6 and 26 weeks after injury (Eliasson et al., 2018). Functional recovery, assessed using heel-rise test at 18 or 52 weeks, associated positively with Young's modulus assessed at 7 weeks (Schepull et al., 2012) or with the AT cross-sectional area assessed at 19 weeks (Rendek et al., 2022), respectively. Thus, biomechanical parameters at early rehabilitation phases may be relevant predictors of good recovery (Funaro et al., 2022; Pękala et al., 2017; Shim et al., 2018; van Gils et al., 1996).

10. Avenues for future research

The complex structure of the AT is currently being examined in humans in vivo using different approaches utilizing MRI or ultrasonography combined with electrical stimulation (Cone et al., 2022; Khair et al., 2022a), and together with modeling, efforts can provide insight into the functional significance of the twisted, individually differing structure of the AT (Funaro et al., 2022; Obrezkov et al., 2022). Interaction of the subtendons with their corresponding muscles warrants for future studies since the muscles have distinct anatomy, physiology, and possibly differential role in AT pathologies. Means to monitor optimal adaptation of tendon would enhance training and rehabilitation practices. For example, monitoring of in vivo strains in subtendons can help to understand functional consequences of loading. Efforts are needed to find biomarkers or parameters that can be reliably assessed to confirm optimal loading and recovery.

It is presently understood that the aponeurosis and tendon, and the three subtendons of Achilles are to be considered and assessed separately since their mechanical properties and behavior are different. However, they cannot be considered as isolated structures but are bound by a three-dimensional connective network which influences tissue behavior and provides future challenges for modeling, demonstrating the need of investigating the AT at the different hierarchical levels and in interaction with adjacent connective and contractile tissues. In the future, we may see attempts to estimate not only the overall forces in the AT, but force distributions and strain rates across the subtendons. The cutting-edge developments and integration of experimental methodologies and modeling should allow future research to consider viscoelasticity, slack length and individual variability in structure and material properties. These advances can provide novel hypothesis and pave the way for designing individual-specific training and rehabilitation avenues.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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