Tendons have previously been regarded inert structures that mainly transmit forces from muscle to bone. However, with technological/methodological gains in recent decades, the ability to examine \textit{in vivo} tendon function has improved significantly, and moreover, it has become clear that tendinous tissues, like most other tissues, undergo adaptation in consequence of changes in loading. Although mechanical function and load adaptation is not entirely understood, a large body of recent literature has contributed to the comprehension of tendon function. The present paper examines current knowledge on tendon mechanical function during human movement, and tendon response to acute and chronic changes in loading.

\textbf{KEYWORDS:} tendon, aponeurosis, ultrasonography, mechanical properties

\textit{Mechanical properties:} The slope of the load-deformation relation describes stiffness of force-loaded \textit{structures}. Further, ‘Young’s modulus’ is derived as the slope of the stress-strain relation that in turn yields information of \textit{material} properties. Tendon tissues are viscoelastic, and consequently the load-deformation or stress-strain plots are not linear but display a so-called ‘toe region’ where deformation pr. load is greater at low loads compared to higher loads.

\textit{Measurement of tendon mechanical properties:} Earlier studies have used cadaver material to examine mechanical properties of the force bearing tissues (Lieber et al. 1991, Scott and Loeb, 1995, Butler et al. 1984, Wren et al. 2001, Haraldsson et al. 2005). Recently, mechanical properties of tendon have been assessed at microscopical levels by use of atomic force microscopy (Svensson et al 2012). The advantage with \textit{in vitro} experiments is the direct assessment of variables, but the \textit{in vitro} tissue placement does not resemble the \textit{in vivo} setting, and therefore examination of intact tissues are warranted. Methodological and technical advances in ultrasonography (US) have enabled measurement of human tendon mechanical properties during \textit{in vivo} loading by measuring tendon displacement during muscle contraction. (Fukashiro et al 1995, Ito et al 1998; Maganaris et al 1999; Magnusson et al 2001, 2003; Kubo et al 2002; Seynnes et al 2009). Initially slow isometric contractions were applied, but with increasing time resolution also tendon function during dynamic high force contractions have been examined (Ishikawa et al. 2007). The technique has been improved and refined, and when conducted carefully it seems that valid measurements can be obtained, although it should be noted that no gold standard exists. Additional imaging techniques have been applied, and by use of cine phase contrast MRI tendinous and/or muscle tissues have been tracked in 3D during voluntary (repetitive, submaximal) contraction efforts (Finni et al. 2003).

\textit{Tendon mechanical structure:} The two human tendons that are subject to most \textit{in vivo} investigations are the Achilles and the patellar tendon. Both tendons are involved in, and undergo heavy loading during human locomotion. Nonetheless these tendons display distinct differences with respect to structure and anatomical design: The patella tendon originates and inserts on bone, while the Achilles tendon originates from three separately innervated muscles. The patella tendon has a large CSA relative to its length compared to the Achilles tendon; finally, the patella tendon has design of parallel fascicle bundles, while the Achilles tendon seems to display a fascicle rotation (Cummins et al. 1946, Szaro et al 2009). The functional significance rotation is not known, but is has been suggested to contribute to energy
storage properties, which in fact is an important feature of especially the Achilles tendon. With respect to cross sectional area (CSA) both tendons show increased CSA going from proximal to distal (Kongsgaard et al 2005, 2007, Seynnes 2009). Differences in CSA influences per definition tendon stress, which in turn may play a role for injury, and frequent injury sites in both tendons are those of lesser CSA. With respect to loading during forceful movements the Achilles tendon operates at higher loads relative to its strength, which likely contributes to the high frequency of rupture compared to that of the patella tendon.

**Force transfer:** Tendons and aponeuroses have traditionally been considered homogenous force bearing structures. Recent evidence however has pointed out that in vivo function may be more complex. Firstly, the mechanical properties of the aponeurosis differ from that of the free tendon despite serial connection and similar tissue properties. This observed difference may be a result of the experimental setting (cadaver vs. *in vivo*), such that stiffness of the *in vivo* aponeurosis exceeds that of the free tendon (Magnusson et al. 2003), while opposite for the cadaver preparation. The active contracting muscle fibers that in the *in vivo* setting anchor on the aponeurosis has been suggested to influence in vivo properties (Magnusson et al. 2008). Also, differences in material properties have been observed within different regions of the human patellar tendon such that fascicles of the anterior aspect of the tendon displayed greater modulus compared to fascicles on the posterior side (Haraldsson et al. 2005). Moreover, cadaver studies have confirmed that separate loading of separate triceps surae muscles lead to heterogeneous loading of the Achilles tendon (Arndt et al. 1999), and a recent study demonstrated that also joint configuration i.e. calcaneal in- or eversion influenced the strain profile of the tendon (Lersch et al. 2012). In vivo studies have indicated uneven Achilles tendon loading in different joint configurations (Bojsen-Møller et al. 2004), and a study where needles were inserted transversely through the tendon during maximal plantarflexor contractions yielded direct evidence of non uniform tendon deformation since needles were permanently distorted upon retraction (Magnusson et al. 2003). Non uniform soleus tendon-aponeurosis deformation, has further been observed in vivo by use of cine phase MRI during plantarflexor efforts (Finni et al. 2003). Taken together, these studies provide evidence of intratendinous shear stress that in turn may play a role for tendon function and dysfunction. Finally, recent studies have provided evidence that contractile force can be transmitted laterally within a limb where muscles and tendons are situated in close proximity. In animal models intermuscular force transmission has been shown to occur between muscle synergists and even antagonists, (Huijing et al 2007, 2008), and in an *in vivo* human study somewhat similar findings were seen (Bojsen-Møller et al. 2010). The functional significance of lateral force transmission although the functional significance is yet to be understood (Maas and Sandercock 2008, Herbert et al. 2008).

**Material and morphological adaptations to training:** Despite limited vascularity and low occurrence of fibroblasts, tendon tissues have been shown to be metabolically responsive to loading (Langberg et al 1999; Hannukainen et al 2005; Bojsen-Møller et al 2006; Heinemeier & Kjaer 2011). The response however seems less than that of muscle tissue, and a recent study suggests that turnover is in fact extremely lethargic in certain areas of the Achilles tendon (Heinemeier et al 2013). The common belief is that newly synthesized collagen is deposited into the fibrillar structure, making tendons stiffer and stronger and, eventually, increasing their cross-sectional area (CSA). Nonetheless, the precise consequence of the tendon metabolic response to increased loading for changes at the functional level remains elusive. Changes in mechanical properties have been found almost systematically after training, although different methodological approaches likely mask the exact dose-response relationship of such changes. Recent studies indicate that increases in tendon stiffness range from 15% to 71% after a few weeks of resistance training (Kubo et al 2001; Kongsgaard et al 2007; Arampatzis et al 2007;
Seynnes et al 2009). Conversely, the effects of resistance training on the capacity to retain elastic energy, do not seem clearly established (Kubo et al 2003; Reeves et al 2003). An increase in modulus has in fact been observed in training studies (Seynnes et al 2009; Arampatzis et al 2010). However, unlike reports from animal studies (Birch et al. 1999) and cross-sectional observations in athletes (Rosager et al. 2002), changes in tendon CSA following resistance training were not demonstrated until recently (Kongsgaard et al 2007; Arampatzis et al 2007). Hence, strength training and activities involving impacts seem to induce increases in tendon stiffness, tensile modulus and CSA, while the time course and relative magnitude of these changes differ considerably between studies and the exact mechanisms underpinning tendon adaptation are largely unknown. Stresses (Couppé et al 2008) and strains (Arampatzis et al 2007) higher than those experienced in daily activities are prerequisites, but other factors such as overall loading volume also seem to influence tendinous adaptations to training (Seynnes et al 2007).

**Influence of disuse (and ageing):** In line with these postulated mechanisms, a decrease in muscular activity and force generating capacity has been shown to result in the deterioration of tendon properties (DeBoer et al 2007; Couppé et al 2012). Yet, the long-term decline in muscle size and function associated with ageing and disuse do not seem to affect tendon mechanics consistently (24). In fact, age-related changes in tendon composition (i.e. decreased collagen content vs. increased collagen cross-links) may contribute to maintain tendon mechanical properties. Furthermore, the tendon capacity to adapt to resistive exercise seems preserved in older individuals (16).

**Conclusion:** Recent investigations have indicated that the in vivo function of the tendon-aponeurosis unit is complex, and that mechanical properties of force bearing tissues may well be influenced by the interface between contractile and force transmitting tissues. Moreover, force transmission within aponeuroses and tendons may occur in a heterogenous manner governed by muscle activation and joint configuration. Tendons respond metabolically to loading, and given sufficient stimulus over time also mechanical and material properties may change, while conversely unloading and disuse has the opposite effect.

**REFERENCES**

Couppé et al. 2012, Clinical Biomechanics (Bristol, Avon)