The role of hind limb tendons in gibbon locomotion: springs or strings?

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Summary

Tendon properties have an important effect on the mechanical behaviour of muscles, with compliant tendons allowing near isometric muscle contraction and facilitating elastic energy storage and recoil. Stiff tendons, on the other hand, facilitate rapid force transfer and precise positional control. In humans, the long Achilles tendon contributes to the mechanical efficiency of running via elastic energy storage and recovery, and its presence has been linked to the evolution of habitual bipedalism. Gibbons also possess relatively long hind limb tendons, however, their role is as yet unknown. Based on their large dimensions, and inferring from the situation in humans, we hypothesize that the tendons in the gibbon hind limb will facilitate elastic energy storage and recoil during hind limb powered locomotion.

To investigate this, we determined the material properties of the gibbon Achilles and patellar tendon *in vitro* and linked this with available kinematic and kinetic data to evaluate their role in leaping and bipedalism. Tensile tests were conducted on tendon samples using a material testing machine and the load-displacement data were used to calculate stiffness, Young's modulus and hysteresis. In addition, the average stress-in-life and energy absorption capacity of both tendons was estimated.

We found a functional difference between the gibbon Achilles and patellar tendon, with the Achilles tendon being more suitable for elastic energy storage and release. The patellar tendon, on the other hand, has a relatively high hysteresis, making it less suitable to act as elastic spring. This suggests that the gibbon Achilles tendon might fulfil a similar function as in humans, contributing to reducing the locomotor cost of bipedalism by acting as elastic spring, while the high stiffness of the patellar tendon might favour fast force transfer upon recoil and, possibly, enhance leaping performance.

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Introduction

Tendons as elastic energy stores

Tendons link muscle to bone and have an important function in force transfer from contracting muscle fibres to bone - or, in the case of bi-articular muscles, force transmission from one joint to another - resulting in joint motion. In addition, it has been shown that tendons also have an important role in reducing the cost of locomotion by: (1) reducing the amount and rate of shortening of muscle fibres, allowing near isometric force production and contraction in their optimal fibre length range (Biewener and Roberts, 2000; Lichtwark et al., 2007a-b; Lichtwark and Barclay, 2010); (2) acting as elastic springs, storing and releasing elastic strain energy during locomotion (Alexander, 2002). Such an energy-saving function has been demonstrated for different tendons in a wide range of species, such as the hind limb tendons in hopping kangaroos and wallabies (Dawson and Taylor, 1973; Alexander and Vernon, 1975; Biewener et al., 1995; Ker et al., 2000) and the Achilles tendon in humans (Lichtwark et al., 2007a-b).

Not all tendons are, however, suitable to act as 'elastic springs'. The amount of strain energy that can be stored in a tendon depends on the elongation of the tendon. In turn, this depends both on the tendon force and the dimensions and material properties of the tendon, in particular its volume and compliance or stiffness. To enable energy-saving in locomotion via stretch and recoil of tendons, tendons should have a compliance that allows a certain degree of elongation when subjected to forces acting during normal ambulation, ca. 4% strain in human walking (Ishikawa et al., 2005; Lichtwark et al., 2007a-b) and 3-6% strain in horse walking (Dimery et al., 1986). If tendons are too stiff relative to the occurring forces, the capacity to store energy as elastic energy in the tendon will be limited, whereas tendons that are too compliant might hamper motor and positional control and the increase risk of injury.

While tendon stiffness is dependent on tendon dimensions, the Young's modulus, i.e., the ratio of stress over strain, is not affected by specific dimensions of the tendon (Peltonen et al., 2010; Peltonen et al., 2012). The Young's modulus has been documented for various mammalian tendons and amounts to roughly 1.2 GPa (Pollock and Shadwick, 1994); though reported values range from 0.4 up to 1.7 GPa (Ker et al., 1988; Zajac, 1989; Pollock et al., 1994). Whether this wide range of reported values is due to differences between species, tendons (i.e. functional demand) or measurement techniques remains unclear (Matson et al., 2012).

Another important property of a tendon is its hysteresis, i.e. the amount of energy lost as heat upon recoil. The lower the hysteresis, the higher the efficiency of the tendon. Hysteresis rates vary widely, with values ranging from 3-38% in mammalian tendons (Ker, 1981; Pollock and Shadwick, 1994; Maganaris et al., 2000) and reported values of 19-26% for the human Achilles tendon (Maganaris et al., 2002; Lichtwark and Wilson, 2005).

In addition, a characteristic that is often disregarded – because it is difficult to measure - is the resonant frequency of the tendon, i.e. the frequency at which a maximum amplitude is achieved with a minimum input force. While resonant frequencies are to be avoided in man-made constructions, achieving resonance is actually desirable in animal locomotion as it minimizes locomotor cost (Farley et al., 1993; Ahlborn et al., 2006).

Because the tendon is one part of the functional muscle tendon unit (MTU), tendon properties should always be viewed in relation to the properties of the muscle(s) to which the tendon is attached, namely its force-generating capacity and the muscle fibre length. The stress imparted to the tendon is proportional to the ratio of the physiological cross-sectional area of the muscle (PCSA) - which is a measure of the force-generating capacity of the muscle - to the cross-sectional area of the tendon (TCSA). The higher this ratio, the more stress will be exerted on the tendon, resulting in a higher tendon strain and energy absorption capacity. Thus a configuration where a long, thin tendon is connected to a large, pennate muscle will favour enhanced elastic energy savings due to the high force-generation potential of the relatively short muscle fibres (Biewener, 1998a), compared to a configuration where this tendon is connected to a slender, parallel-fibred muscle. The moment arm of the muscle (group) also plays a crucial role and, more specifically, the ratio of muscle moment arm to ground force moment arm (the so-called 'effective moment arm' (Biewener, 2005)). A recent study on human running biomechanics (Raichlen et al., 2011; Scholz et al., 2008) has demonstrated that the muscle moment arm even has a stronger influence on the amount of energy stored in the Achilles tendon than its mechanical properties, with shorter muscle moment arms leading to higher tendon stresses and higher amounts of energy stored.

Finally, alongside suitable tendon properties relative to the force-generating capacity of the muscle, appropriate kinematics and locomotor dynamics are required to allow elastic energy storage and release in the tendons. Negative joint power should precede positive joint power to facilitate conversion and storage of potential energy in elastic strain energy in stretched tendons and subsequent tendon recoil, allowing release of the elastic energy (Rubenson et al., 2011). This prerequisite is, for example, fulfilled in the calf muscles during human running, allowing storage and release of elastic energy in the Achilles tendon.

The Achilles tendon in hominoids

Among hominoids (Superfam. Hominoidea), the Achilles tendon is considered a hallmark feature of modern humans related to the evolution of habitual bipedalism. Its dimensions and mechanical properties make it particularly suitable to act as an elastic spring during human walking and, in particular, running (Bramble and Lieberman, 2004). Apart from humans, the lesser apes or gibbons (Fam. Hylobatidae) are the only extant hominoids to possess a relatively long Achilles tendon with a substantial external portion. In contrast, the (nonhuman) great apes only possess a short Achilles tendon which is located inside the triceps surae muscle (Payne et al., 2006). This observation led us previously to speculate that the gibbon Achilles tendon might act as an elastic energy store during hind limb powered locomotion (Vereecke and Aerts, 2008).

Gibbons are highly arboreal primates which rely predominantly on suspensory locomotion, in particular brachiation, to travel across the forest canopy, yet, hind limb powered locomotion - such as leaping, climbing and bipedalism - is also regularly used. Gibbons will leap to cross large gaps in the forest canopy, while bipedal bouts on top of branches or vines are used as a run-up for leaps or between periods of brachiation. Seeing that hind limb powered locomotion (i.e., leaping, climbing, bipedalism) constitutes an important part of the gibbon's locomotor repertoire (up to 40% of travel time (Fleagle, 1976)), it seems reasonable to assume that anatomical adaptations in the hind limb which might reduce the locomotor cost of leaping, climbing and bipedalism will be favoured, as long as this does not negatively affect the efficiency and/or performance of brachiation. This lets us suggest that a relatively long Achilles tendon could have evolved in the hylobatid lineage, independent from the evolution of the Achilles tendon in hominins, as an adaptation to increase overall locomotor efficiency. Long tendons in the hind limb allow the muscle mass of the hind limb to be located more proximally, minimizing distal inertia and, as such, the efficiency of brachiation, while they could simultaneously contribute to reducing the locomotor cost of leaping and bipedalism by acting as elastic springs. Without a direct measure of the energetics of gibbon locomotion it remains difficult to assess this proposition, however, we can evaluate the theoretical possibility for elastic energy storage and release in the hind limb tendons of gibbons by investigating their anatomical and mechanical properties. To evaluate the hypothesis that the relatively long tendons in the gibbon hind limb can act as elastic springs during hind limb powered locomotion we have harvested samples of the Achilles and patellar tendon, both prominent hind limb tendons, in a series of fresh-frozen gibbon cadavers and have determined their material properties

Material & Methods

Specimens and sample preparation

Tendon samples were taken from the left or right hind limb of fresh-frozen gibbon cadavers (patellar tendon: n = 8, Achilles tendon: n = 14). Cadavers were obtained through collaboration with the National Museums of Scotland (Edinburgh, Scotland) and the Royal Zoological Society of Antwerp (Belgium). All animals included in this study were housed in zoos and died under natural circumstances. None of the specimens demonstrated musculoskeletal pathologies (Table 1).

The cadavers were thawed at room temperature and the triceps surae and quadriceps femoris were freed from surrounding tissue. The quadriceps femoris were cut at site of origin (iliac spine and femur shaft) and insertion (tibial tuberosity), while the triceps surae were either cut at both origin (femoral condyles) and insertion (tuber calcanei) (set B) or only at origin and kept attached to the calcaneus (set A). The different preparation of sets A and B was due to a different clamping technique used for these two sets of Achilles tendon, but did not influence the anatomical measurements that were taken.

Following the procedure described in (Vereecke et al., 2005) a series of measurements was taken of each muscle head using a digital scale (Sartorius, Bradford, MA, USA) and digital callipers (Mitutoyo, Japan). Measurements are illustrated on Figure 2 and include: muscle belly mass (m [g]), muscle fascicle length (FL [mm]), pennation angle (PA [degrees]), muscle-tendon unit length (MTU [mm]), external and internal tendon length (ETL, ITL [mm]; all with precision of 0.1 mm and 1 g). External tendon length was defined as the length of the outer tendon portion (i.e. from the most distal muscle fibres to the distal end of the tendon), while internal tendon length refers to the inner aponeurotic portion of the tendon (i.e. from the proximal end of the tendon to the most distal muscle fibres). Tendon length (TL) is defined as the total length of the tendon (i.e., TL= ETL + ITL).

The measurements - as detailed above - were used to calculate the physiological cross-sectional area (PCSA [mm^2]) of the muscle groups, which was estimated as:

$$PCSA = [m \times \cos(PA)]/[\rho \times FL] \qquad (1)$$

where m is muscle belly mass, PA is pennation angle, FL is fibre length and ρ is density of muscle tissue, 1.0597 x 10^{-3} gmm^{-3} (Mendez and Keys, 1960). Note that this is a density value obtained for unfixed rabbit and canine muscle tissue and that the muscle density in gibbons might be slightly different.

For the triceps surae, the PCSA was calculated as the sum of the PCSA of the lateral and medial gastrocnemius and soleus muscles. For the quadriceps femoris, the PCSA was calculated as the sum of the PCSA of the rectus femoris and the three vasti (lateral, medial and intermedius). PCSA is used to estimate maximum force producing capacity (Ward and Lieber, 2005). To allow comparison with humans, PCSA is scaled to body mass to the two-thirds [i.e., PCSA/(body mass)$^{2/3}$].

Next, the external tendon was cut from the muscle belly, to obtain a uniform tendon section without muscle fibres. At the proximal end of the tendon, a section of 1 mm was taken, and length and mass measured carefully (precision: 0.01 mm and 0.1 g) to enable calculation of tendon cross-sectional area (TCSA), which was estimated as:

$$TCSA = m/[\rho \times tendon\ section\ length] \qquad (2)$$

where ρ is the density of unfixed, moist tendon tissue, 1.12 x 10^{-3} gmm^{-3} (Ker, 1981) [see also (Hashemi et al., 2005): 0.67-2.68 x 10^{-3} gmm^{-3}].

The proximal and distal ends of the tendon samples were dried over a distance of 10 mm, while the rest of tendon was kept hydrated (using damp tissue and PVC film). The tendon samples were clamped, at the proximal and distal dry parts, using flat metal, self-tightening plates. In a subset of the Achilles tendon samples in which the distal part was kept attached to the calcaneus (set A), samples were fixed by clamping the proximal dry end (self-tightening clamp) and the calcaneus (custom-made clamp). In each case, the tendon section length corresponds to the actual part being tested and was measured as the distance between the inner borders of both clamps after the tendon sample had been mounted in a materials tester.

The patellar tendons were tested with the patella still imbedded in the tendon. In this way, the full length of the patellar tendon could be tested, a situation which is most representative of the condition *in vivo*. This means, however, that the actual measured tendon includes both the so-called quadriceps tendon (proximal to the patella) and patellar ligament (between patella and tibial tuberosity). Thus, in this paper, the ‘patellar tendon’ is defined as the tendon running from the quadriceps femoris to its insertion on the tibial tuberosity. The choice to test both the proximal and distal part of the tendon, with imbedded patella, was based on the observation that both parts are continuous ontogenetically which is retained in adult morphology by collagen fibres running over the patellar bone (Mérida-Velasco et al., 1997; Franchi et al. 2009; Toumi et al., 2012). Testing the whole complex together was considered the best approximation of the situation *in vivo*. It should be noted that in most studies on the functional anatomy of humans, the 'patellar tendon' (sometimes called patellar ligament) is most commonly defined as the tendon portion between patella and tibial tuberosity. This should be kept in mind when comparing values obtained in this study with other published values.

Test protocol

The material properties of the tendon samples were obtained using an Instron materials testing machine (Instron Corp, Canton, MA, USA), after calibrating the load cell to 0 N with slack tendon. A load-controlled cyclic sine wave test (1kHz sampling rate, recording every cycle) with a starting load of 5 N was used for all tendon samples. For each tendon sample, two to three cyclic tests consisting of 40 cycles were performed, increasing the maximal load in each subsequent test. These cyclic tests were followed by a single ramp test to obtain data under maximal tendon stress. Test protocol conditions were based on previously published studies by Ker and colleagues (Ker, 1981; Ker et al., 2000) investigating material properties of tendons *in vitro* and were adapted to the specificities of the current samples.

Due to the limited sample size of our original data set - related to the limited and unpredictable availability of cadaveric material of gibbons - we chose to increase our data set by adding more samples in the following year. This resulted in a larger dataset, yet comprising two sets of samples tested with slightly different testing conditions. Set A included only Achilles tendon samples, while set B included both Achilles and patellar tendon samples. Tests for set A were done using an Instron model 8500 at 4 Hz and 36°C (University of Leeds, UK). Set B was tested using an Instron model E3000 at 2 Hz and 20°C (The University of Liverpool, UK). The frequencies correspond to the *in vivo* loading frequencies observed during slow to fast bipedalism (contact times range from 0.2 to 0.6 seconds).

Data analysis

Data analysis was done using GNU Octave 3.2.4 software. For each tendon sample, load versus displacement curves were plotted for the cyclic test with the highest maximal load. As some conditioning occurs during the first loading cycles (as is the case in all tendons; (Pollock and Shadwick, 1994; Maganaris, 2003), cycle 20 was selected for calculation of the hysteresis to ensure proper preconditioning of the tendon sample. A second-order polynomial was plotted to the load-displacement data during loading and unloading respectively, and integrated for the maximal recorded load of the tendon sample in that test. The hysteresis, H [%], was calculated as the difference between the integral of the loading and unloading curve, divided by the integral of the loading curve. The hysteresis represents the amount of energy lost as heat during unloading as a percentage of total energy stored in the tendon during loading.

The tendon's material properties (stiffness, stress and strain) were calculated using the load and displacement data recorded during the single ramp test.

Stiffness, S [Nmm^{-1}], was determined as the slope of the linear regression of the load-displacement data during loading above 50% MVC (i.e., maximum volumetric contraction, which was estimated by multiplying the PCSA with a maximal isometric muscle stress of 0.30 Nmm^{-2})(Erskine et al., 2009). Coefficients of determination (r^2) of the included data were between 0.9950 and 0.9998, supporting a good linearity of the load-displacement relationship (above 50% MVC). Average stiffness and standard deviation (s.d.) of the samples were calculated for the Achilles and patellar tendon.

Stress, Ɛ [MPa], and strain, σ [%], were calculated by dividing load by TCSA and tendon elongation by tendon sample length, respectively. In a similar fashion as determining stiffness, the Young’s modulus, E [MPa], was calculated as the slope of the linear regression of the stress-strain data in the linear portion of the loading curve (above 5 MPa or higher). The coefficient of determination (r^2) of the regression equations was between 0.9924 and 0.9997. For each tendon, the highest calculated modulus was reported. In addition, the stress values of each tendon were calculated at 2%, 3%, 4% and 5% strain and plotted as box plots (average ± s.d.) to illustrate the inter-individual variability.

The energy absorption capacity of a tendon, u [J], is the amount of strain energy that can be stored and released in a tendon and can be calculated in a number of ways, either simply as the area under the load-displacement curve during unloading ($u=½*S*\Delta TL^2$) or by the formula provided by (Biewener and Baudinette, 1995):

$$u = \left({}^{1}\!/_{2} \times \left[{}^{\varepsilon l^2}\!/_{E}\right] \times Vt \times \left({}^{[100-H]}\!/_{100}\right)\right) \qquad (3)$$

where Vt is the volume of the tendon, calculated by multiplying TL by TCSA (assuming uniform cross-sectional area), H is hysteresis, E is Young's modulus and $\mathcal{E}l$ is the stress-in-life value of the tendon [MPa]. The stress-in-life value is an estimate of the tendon stress in locomotion, and is calculated as the ratio of PCSA to TCSA, multiplied by the maximal isometric muscle stress, 0.3 Nmm^{-2} [Erskine et al., 2009; range of published values: 0.15-0.53 Nmm^{-2} (Close, 1972; Narici et al., 1992)].

Results are presented as mean ± standard deviation (s.d.). All statistical analyses were performed in GNU Octave or Excel 2007.

Available kinematic and kinetic data from previous studies of bipedal locomotion (Vereecke and Aerts, 2008; Vereecke et al., 2006b) and leaping (Channon et al., 2010a; Channon et al., 2011a, b) in gibbons were used to investigate the role of the Achilles and patellar tendon during locomotion.

Results

Comparative architecture of the quadriceps femoris and triceps surae in gibbons and humans

The triceps surae has a comparable architecture in gibbons and humans, consisting of a pennate medial and lateral gastrocnemius, originating from the medial and lateral femoral condyles, and a short-fibered, pennate soleus, inserting via a shared Achilles tendon to the calcaneal tuberosity. The volumetric division in soleus, medial and lateral gastrocnemius is, however, different in gibbons and humans. In gibbons, either the lateral gastrocnemius (36-46% of triceps PCSA) or soleus (25-40% of triceps PCSA) make up the largest part of the triceps surae, in both volume and PCSA (Channon et al., 2009; Vereecke et al., 2005), while in humans the soleus typically constitutes ~60% of PCSA the triceps surae (Morset al., 2005). The Achilles tendon is well-developed in gibbons, amounting to 40% of the triceps surae MTU length (i.e., ETL/MTU; 74% if both external tendon and inner aponeurotic portion are considered). This relatively long Achilles of gibbons is remarkable, seen its absence or small size in other nonhuman apes (Payne et al., 2006). Among the hominoids, a long Achilles tendon is also observed in humans, with an external tendon length amounting to 64-95% of the MTU length of the triceps surae (Table 2).

The gibbon quadriceps femoris consists of the large muscle bellies of the vastus lateralis and intermedius, and the more slender vastus medialis and rectus femoris, a similar organisation as is found in humans (O’Brien et al., 2010; Blazevich et al., 2006). The muscle fibres of these four heads insert into a common quadriceps tendon which is attached to the patella and continues as the 'patellar tendon' from the apex of the patella to the tibial tuberosity. The length of the patellar tendon amounts to 12% of the quadriceps MTU length in gibbons (i.e. ETL/MTU; or 64% if external tendon and inner aponeurotic portion are considered; Table 2). In humans, the length of the patellar tendon (ETL) amounts to 19-22% of the quadriceps MTU and is thus relatively longer than in gibbons (note that reported values of gibbon and human patellar tendon include length of the patella and of the quadriceps tendon; Table 2).

The triceps surae are relatively more slender in gibbons compared to humans (scaled PCSA of 278 vs. 1098; Table 2, Figure 1), which is expected given the predominantly suspensory lifestyle of gibbons. The same can be said for the quadriceps, which PCSA is also relatively smaller in gibbons compared to humans (scaled PCSA of 548 vs.884-1259; Table 2), yet the quadriceps are twice as large as the triceps surae in gibbons, while these muscle groups have almost equal PCSAs in humans. This might point to a task division between both muscle groups in gibbons, with the quadriceps being more important for production and/or absorption of work in leaping and bipedalism and the triceps surae being more reliant on elastic storage and recoil.

Comparative data on the dimensions of the triceps surae and quadriceps femoris are provided in Table 2, Figure 1 and 2.

Stiffness, Young's modulus and hysteresis

The average stiffness of the gibbon's Achilles tendon was 99.6 Nmm^{-1} (s.d. = 42.7 Nmm^{-1}) and 299.1 Nmm^{-1} (s.d. = 95.6 Nmm^{-1}) for the patellar tendon (Figure 3). The Young's modulus was 701.3 MPa (mean, s.d. = 286.5 MPa) for the Achilles tendon and 300.1 MPa (s.d. = 130.0 MPa) for the patellar tendon (Fig. 3). Hysteresis was lower for the Achilles tendon, 13.5% (s.d. = 3.4%), than for the patellar tendon, 25.5% (s.d. = 4.2%).

The force-elongation curves of the 14 Achilles tendon samples and the 8 patellar tendon samples during loading and unloading are shown in Figure 4A-B. The figures clearly illustrate the visco-elastic nature of tendon, with a nonlinear behaviour under low loads ('toe region'), and a linear behaviour at higher load values (typically above 50% MVC). Stiffness and Young's modulus values are obtained in the linear portion of the force-elongation curves. To illustrate the tendon properties under lower load conditions, which might very well prevail during habitual locomotion, we have also calculated stress values (and s.d.) at 2%, 3%, 4% and 5% strain for both tendons (Figure 5).

Elastic energy absorption capacity and stress-in-life

The energy absorption capacity of the Achilles tendon at 30 MPa, the average stress-in-life of the tendon, is 0.799 J using the formula (3) (Biewener and Baudinette, 1995). Using the same formula and an average stress-in-life of 17 MPa, the estimated energy absorption capacity obtained for the patellar tendon amounts to 1.560 J.

Discussion

Gibbon Achilles and patellar tendon: elastic energy storage vs. force transfer and control?

Comparison of the gibbon Achilles and patellar tendon demonstrates some substantial differences in dimensions and material properties. The gibbon Achilles tendon has a relatively low stiffness and is long and thin, compared to the dimensions of the triceps surae (high ETL/FL and PCSA/TCSA ratios; Table 2). This indicates that it will be subjected to relatively high levels of tendon stress and strain during locomotion, facilitating storage of elastic strain energy. The hysteresis of the Achilles tendon is reasonably low, indicating that upon recoil, 86.5% of the stored energy will be available to contribute to the positive mechanical work that has to be delivered to raise and accelerate the body centre of mass and the limbs. The patellar tendon, on the other hand, has less favourable material properties to facilitate elastic energy storage and release. Its hysteresis is rather high, averaging to 25.5%, meaning that a quarter of the stored strain energy will be lost as heat during recoil. Despite the quadriceps being bulky, powerful muscles, the patellar tendon is a low-stressed tendon with a high safety factor compared to the Achilles tendon due to its relatively large diameter and, hence, low PCSA/TCSA ratio (i.e. 56 *vs.* 100 for the Achilles tendon; Table 2). However, the Young's modulus of the patellar tendon is also significantly lower than that of the Achilles tendon ($E =$ 0.3 GPa *vs.*0.7 GPa; $p = 0.0014$, $t = 3.719$, $df = 20$); this means that even under low stresses, the patellar tendon will be subjected to substantial tendon strain, which might facilitate elastic energy storage in locomotion.

The visco-elastic nature of tendons allows stretch and recoil during locomotion, increasing locomotor efficiency, yet this elasticity or compliance also affects positional control. An interesting parameter hereof is the ratio of external tendon length to muscle fascicle length (ETL/ FL). The higher this ratio, the more influence the tendon properties have on the behaviour of the MTU, while a low ratio indicates a small effect of tendon extension on MTU length suggesting optimization for precise positional control. The ratio for the gibbon Achilles tendon is six times higher than for the patellar tendon (2.4 vs.0.4; Table 2), suggesting a spring-like function for the Achilles tendon while the patellar tendon might be more suitable for rapid force transfer and positional control, despite its low Young modulus. This observation also corresponds to the relatively high measured stiffness for the patellar tendon (300 Nmm^{-1} vs. 100 Nmm^{-1} for the Achilles tendon).

Recent work by Lichtwark and colleagues (Lichtwark and Barclay, 2010) has shown that tendons with a low stiffness improve both power output and efficiency of muscles. In tests using artificial mice tendons, they showed that muscles connected in series to a relatively compliant tendon had a higher mechanical efficiency than with a stiff tendon. Translated to gibbon tendons, this would mean that the gibbon Achilles tendon, with a relative compliance (i.e., RC = 1/S*MVC/FL) of 10%, would achieve a muscle efficiency of ~32%, while the patellar tendon, with a RC of 3%, would have an efficiency of ~26% [by comparison, the RC of 'stiff' rat Achilles tendon is 5%, while the 'compliant' wallaby Achilles tendon has a RC of 35%; (Lichtwark et al., 2005)]. Compliant tendons are particularly important to improve the power output of short-fibred muscles which have a restricted shortening range, such as the triceps surae in gibbons and humans.

Finally, stiffness values of tendons have also been correlated to tendon strength: more compliant tendons (lower stiffness) are weaker, stiffer tendons are stronger (Matson et al., 2012). This would suggest that the gibbon Achilles tendon is more susceptible to injury than the patellar tendon.

In conclusion, the anatomical dimensions and mechanical properties of the gibbon Achilles and patellar tendon suggest that these hind limb tendons fulfil a different role in locomotion. The Achilles tendon seems suitable for elastic energy storage and release, due to its low hysteresis and relatively high compliance and because the tendon is connected in series to the short-fibred, pennate triceps surae (leading to a high ETL/FL ratio of the MTU). Such muscle architecture combined with the material properties of the Achilles tendon likely results in a higher muscle efficiency compared to that achieved by the patellar tendon, which is stiffer, has a higher hysteresis and a lower ETL/FL.

Stress-in-life of hind limb tendons

No direct measures of tendon force, or stress, are available for gibbons, yet the stress-in-life value (i.e., PCSA/TCSA*0.3 MPa) can be used as a rough estimate of tendon stress occurring in locomotion, with high stress values pointing to a spring-like function and a higher fatigue resistance (Ker et al., 2000). For the Achilles tendon we obtained a stress-in-life value of 30 MPa, while the estimated stress in the patellar tendon was 17 MPa, suggesting the Achilles tendon might be more suitable for elastic energy storage (and recoil), as well as being more fatigue resistant. Though these values are based on theoretical calculations, rather than on actual measurements, they roughly correspond to the stress levels obtained in our experiments at 4% Achilles tendon strain (27 MPa; s.d.: 11 MPa) and 5% patellar tendon strain (14 MPa; s.d.: 7 MPa; Figure 5); strain values which are comparable to those observed in human walking and jumping [4-6%;(Kurokawa et al., 2001, 2003; Ishikawa et al., 2005; Lichtwark et al., 2007a-b)].

During normal ambulation, stresses in mammalian tendons have been reported to range from 5 to 25 MPa (Biewener and Roberts, 2000; Svensson et al., 2011), while increasing in fast locomotion and strenuous activities. The tendon stresses of galloping horses amount up to 40-50 MPa (Biewener, 1998b); in humans, stresses of 40 MPa have been reported in the patellar tendon during jumping (Svensson et al., 2011) and up to 111 MPa in the Achilles tendon during running (Ker et al., 1988).

Estimates of tendon stresses are useful, as they allow us to calculate the energy absorption capacity of the tendons during locomotion. Calculations using stress-in-life values of 30 MPa for the Achilles tendon and 17 MPa for the patellar tendon yielded energy absorption capacities of 0.799 J and 1.560 J. When scaled to an average body mass of 6 kg, this gives us 0.13 $Jkg^{-1}$and 0.26 Jkg^{-1}, respectively. Thus, with its relatively low modulus the patellar tendon achieves a higher energy absorption capacity than the Achilles tendon, at lower stress values. In these calculations, tendon volume is calculated as the product of TCSA and total tendon length, assuming a constant diameter of the tendon over its full length. The TCSA has been reported to vary across the length of feline (and human) tendons (Cui et al., 2009), yet a constant TCSA is not an unreasonable assumption to be made in the estimation of energy absorption capacity. The gibbon patellar tendon has a rather constant diameter (with exclusion of the patella) and although the Achilles tendon tapers distally (in mediolateral direction), it also becomes thicker (in anteroposterior direction) leading to a relatively constant cross-sectional area. It should also be noted that tendon length - which is used in our calculations of energy absorption capacity - includes both outer tendon (ETL) and inner aponeurotic part (ITL), because previous studies have shown that stress is dissipated over both parts (Muramatsu et al., 2001; Arampatzis et al., 2007). Most human studies have, however, only included the outer portion of the tendon in their measurements.

Previous studies on gibbon bipedalism (Vereecke et al., 2006a,b) have shown that the amount of external work performed during a bipedal bout averages around 3.5 J or 0.72 $Jkg^{-1}m^{-1}$. This means that, in theory, the Achilles tendon could contribute for 18% and the patellar tendon for 36% of the energy requirements of bipedalism via elastic recoil, provided that tendon stress levels of, respectively, 30 MPa and 17 MPa are reached, and that all requirements for elastic storage and recoil are fulfilled. During leaping, the external work amounts to 3.83 $Jkg^{-1}m^{-1}$ in an average orthograde single-footed leap (Channon et al. 2010a), leading to theoretical energy contributions of 1-7%. Yet, these theoretical calculations do not take into account that tendon stresses might be higher in leaping than in bipedalism. The obtained values should therefore be considered as rough estimates of the contribution of both tendons to the locomotor cost of gibbons via an elastic energy-saving mechanism.

Role of the hind limb tendons in gibbon locomotion

Despite their predominantly suspensory lifestyle, gibbons also regularly engage in hind limb powered locomotion, namely bipedalism, climbing and leaping (up to 40% of their travel time (Fleagle, 1976)). The kinematics and dynamics of bipedalism and leaping of gibbons have been the subject of previous studies, where we showed that gibbons are proficient leapers as well as adept in bipedalism even though showing no clear morphological adaptations to these locomotor modes (Vereecke et al., 2006; Channon et al., 2010a; Channon et al., 2011a). We know that tendons can enhance muscle efficiency by allowing near isometric contraction of the muscles to which they are connected, yet we specifically wondered whether the gibbon hind limb tendons could also contribute to the power generating capacities of muscles via elastic energy storage and recovery.

The material properties of the Achilles tendon seem well suited to fulfil this task, and the dynamics of bipedalism also facilitate storage and recoil of elastic strain energy in the Achilles tendon. Although gibbons rarely run bipedally, i.e. have a flight phase, their bipedal locomotion can be described dynamically by a spring-mass mechanism, with in-phase fluctuation of potential and kinetic energy and lowest position of the centre of mass (COM) during midstance (Figure 6B, top), as is the case for human running (Vereecke et al., 2006). The downward motion of the body centre of mass coincides with negative ankle joint power (Vereecke and Aerts, 2008) and knee flexion and ankle dorsiflexion, stretching the patellar and Achilles tendon, allowing conversion of potential energy to elastic strain energy (Figure 6B, middle). In the final part of stance, knee extension is followed by ankle plantarflexion, unloading the tendons as the ground reaction force drops, and facilitating recoil and release of energy. The released energy can contribute to forward acceleration and propulsion of the COM, as it coincides with an upwards motion of the COM and positive COM and ankle joint work (Figure 6B, bottom). This suggests that the Achilles tendon can have a similar role in gibbon bipedalism as in human running; acting as an elastic spring to increase the locomotor efficiency.

The role of the patellar tendon in gibbon bipedalism is more difficult to evaluate as we have no accurate calculations of knee joint power. We can, however, infer its potential role in gibbon bipedalism by looking at the joint angles and by considering its function in human bipedalism. The knee joint kinematics show a similar double-humped profile in gibbon and human bipedalism, with knee flexion followed by extension in stance and swing (Figure 6B, middle). These knee joint kinematics facilitate stretch and subsequent recoil of the patellar tendon, allowing elastic energy storage and release when coinciding with negative joint work (energy absorption) and positive joint work (energy generation) respectively.
In human locomotion, the knee displays a mainly negative joint work and power profile, which points to a primary function as damper (energy absorption) and in adjusting limb stiffness (Farris and Sawicki, 2011). Energy recovery via recoil of the patellar tendon does not lead to a substantial reduction in energy requirements due to the high efficiency of the mostly eccentric contraction of the quadriceps in human bipedalism. In gibbon bipedalism, the knee remains more flexed throughout stance (Figure 6B, middle) compared to human bipedalism, requiring strong eccentric contraction of the quadriceps to counteract gravity and

the activity of the hamstrings. As observed in humans, elastic energy storage could occur in the patellar tendon during gibbon bipedalism, yet, tendon recoil probably contributes little to the energy requirements.

During leaping, the knee and ankle joint kinematics again facilitate stretch and recoil of the hind limb tendons (Figure 6A, middle). Unlike bipedalism, leaping is an acyclic motion with a continuous upward motion of the COM (Figure 6A, top) and hence predominantly positive COM work. The joints contributing to this mechanical energy production most likely show negative and positive power peaks - allowing storage and recoil of elastic energy - yet this cannot be unequivocally demonstrated due to the lack of separate work and power profiles of the different joints. We presume that loading of the hind limb tendons with energy release upon recoil will occur in leaping, in particular in leaps with an apparent countermovement, contributing to mechanical power generation and enhancing muscle performance. Again, the compliant Achilles tendon is the more likely candidate for elastic energy storage and release, while the quadriceps muscle-tendon unit seems more suitable for power production (considering the large volume of the quadriceps and short muscle moment arm) and transmission of energy from the large hip extensors (Channon et al., 2009; Channon et al., 2010b).

The gibbon hind limb tendons: how do they compare to other mammalian tendons?

The values we obtained for the Young’s modulus of the gibbon hind limb tendons - 0.3 GPa for the patellar tendon and 0.7 GPa for the Achilles tendon - are at the lower end of reported moduli of mammalian tendons [range 0.4-1.7 GPa (Ker et al., 1988; Zajac, 1989; Pollock et al., 1994)], but do fall within the range reported for human Achilles [0.14 to 0.90 GPa (Magnusson et al., 2003; Defrate et al., 2006; Waugh et al., 2012)] and patellar tendons [0.12-0.85 GPa (Hashemi et al., 2005); 0.30-0.85 GPa (Svensson et al. 2011)]. Using ultrasound techniques, much higher moduli were, however, obtained in humans; 2 GPa and higher for the Achilles tendon (Maganaris et al., 2008; Peltonen et al., 2010) and 1-1.5 GPa for the patellar tendon (Magnusson et al., 2008; Hansen et al., 2006). This wide range of reported values illustrates the difficulties in obtaining accurate material properties from tendons, and the differences between *in vitro* and *in vivo* results suggests that test protocol affects the obtained results (Hansen et al., 2006; Hashemi et al., 2005; Maganaris et al., 2008). One of the difficulties in *in vivo* studies seems to be the accurate determination of tendon dimensions (Magnusson et al., 2008; Svensson et al., 2011). In addition, *in vitro* studies work with post-mortem material and often test only part of the free tendon, whereas the aponeurosis is also accounted for in ultrasound studies and vascularisation is intact which might affect material properties (Benjamin et al., 2008). This makes it difficult to compare material properties obtained from different studies, however, data obtained using the same methodologies (e.g. same research groups, equal force range) are largely comparable, as well as data of different tendons obtained in the same study, e.g. tendon properties in the feline (Cui et al., 2009) and turkey hind limb (Matson et al., 2012). These latter studies indicate that there might be differences between tendons of different muscles, suggesting a structural adaptation of tendon in relation to its function. This challenges earlier findings of similar tendon properties across different muscles and species (Bennett et al., 1986; Maganaris and Paul, 2002; Pollock and Shadwick, 1994). Our results on the gibbon Achilles and patellar tendon support the idea of adaptation of tendon structure to a differing functional demand, yet structural differences should be further documented by a histological comparison between the tendons of different muscles.

Methodological considerations

There are some limitations of this study that should be kept in mind when evaluating the data. This study presents unique data and includes as many different individuals as possible, however, the total sample size remains limited. This is an inevitable issue when studying endangered taxa, such as the hylobatids (Cites I list). To maximize sample size, experiments were done in two separate sets (A and B) in consecutive years, as access to specimens was dependent on death by natural causes. All included specimens were captive animals and activity levels of the animals might have been reduced compared to wild gibbons. The specimens were all adult animals, yet cover a wide age range (9-41 years). These factors might affect tendon properties, though the effect of age and exercise has not been demonstrated unequivocally (Hashemi et al., 2005; Benjamin et al., 2008; Couppé et al., 2009). Secondly, care was taken to have proper clamping of the tendon samples, using serrated clamps gripping on dried-out ends, yet some clamping effects cannot be ruled out. During our experiments, the tendon samples were loaded until rupture, after the cyclic tests, and the site of rupture was visually inspected. Samples showing slipping during the single-ramp tests or which ruptured near the clamp (3 out of 25) were discarded from the analysis. Finally, the patellar tendon samples included the patella, which certainly affects measured stiffness and makes comparison with other studies, which have only investigated the patellar ligament, difficult. Testing the whole patellar tendon complex was, however, considered the best approximation of the situation *in vivo*.

Conclusion

This study suggest that, theoretically, the gibbon Achilles tendon might contribute to reducing the locomotor cost of bipedalism and leaping by acting as an elastic spring. The patellar tendon seems a less likely candidate for storage and release of elastic strain energy during hind limb powered locomotion but might be more suitable for rapid force transfer and positional control, despite its low Young modulus. Full body dynamics of gibbon bipedalism and leaping should be addressed in future studies to confirm or refute the energy-saving role of the hind limb tendons in gibbon locomotion.

List of Abbreviations

COM: centre of mass

E: Young’s Modulus

ETL: external tendon length

FL: muscle fascicle length

H: hysteresis

m: muscle belly mass

MA: moment arm

MTU: muscle tendon unit

MVC: maximum volumetric contraction/VMC: maximal isometric muscle force production

PA: pennation angle

PCSA: physiological cross-sectional area

RC: relative compliance

S: stiffness

s.d.: standard deviation

TCSA: tendon cross-sectional area

TL: tendon length

Vt: volume of tendon

Ɛ: stress

Ɛl: stress-in-life

σ: strain

ρ: the density of tendon tissue

u: energy absorption capacity

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References

Ahlborn, B. K., Blake, R. W., and Megill, W. M. (2006). Frequency tuning in animal locomotion. *Zoology*, **109**, 43–53.

Alexander, R. M. (1984). Elastic energy stores in running vertebrates. *Integrative and Comparative Biology*, **24**, 85–94.

Alexander, R. M. (2002). Tendon elasticity and muscle function. *Comparative Biochemistry and Physiology. Part A*, **133**, 1001–1011.

Arampatzis, A., Karamanidis, K., Morey-Klapsing, G., De Monte, G., and Stafilidis, S. (2007). Mechanical properties of the triceps surae tendon and aponeurosis in relation to intensity of sport activity. *Journal of Biomechanics*, **40**, 1946–1952.

Benjamin, M., Kaiser, E., and Milz, S. (2008). Structure-function relationships in tendons: a review. *Journal of Anatomy*, **212**, 211–228.

Bennett, M., Ker, R. F., Imery, N., and Alexander, R. M. (1987). Mechanical properties of various mammalian tendons. *J. Zool. Lond.*, **209**, 537–548.

Bennet, M. B., Ker, R. F., and Alexander, R. M. (1989). Elastic strain energy storage in the feet of running monkeys. *Journal of Zoology*, **217**, 469–475.

Biewener, A. A. (2005). Biomechanical consequences of scaling. *Journal of Experimental Biology*, **208**, 1665–76.

Biewener, A. A. and Blickhan, R. (1988). Kangaroo rat locomotion: design for elastic energy storage or acceleration? *Journal of Experimental biology*, **140**, 243–55.

Biewener, A. A. and Baudinette, R. (1995). In vivo muscle force and elastic energy storage during steady-speed hopping of tammar wallabies (Macropus eugenii). *Journal of Experimental Biology*, **198**, 1829–1841.

Biewener, A. A. (1998a). Muscle function in vivo : a comparison of muscles used for elastic energy savings versus muscles used to generate mechanical power. *American Zoology*, **38**, 703–717.

Biewener, A. A. (1998b). Muscle-tendon stresses and elastic energy storage during locomotion in the horse. *Comparative Biochemistry and Physiology. Part B*, **120**, 73–87.

Biewener, A. A. and Roberts, T. J. (2000). Muscle and tendon contributions to force, work, and elastic energy savings: a comparative perspective. *Exercise and Sport Sciences Reviews*, **28**, 99–107.

Blazevich, A. J., Gill, N. D., and Zhou, S. (2006). Intra- and intermuscular variation in human quadriceps femoris architecture assessed in vivo. *Journal of Anatomy*, **209**, 289–310.

Bramble, D. M. and Lieberman, D. E. (2004). Endurance running and the evolution of Homo. *Nature*, **432**, 345–52.

Channon, A. J., Günther, M. M., Crompton, R. H., and Vereecke, E. E. (2009). Mechanical constraints on the functional morphology of the gibbon hind limb. *Journal of Anatomy*, **215**, 383–400.

Channon, A. J., Crompton, R. H., Günther, M. M., D'Août, K., and Vereecke, E. E. (2010a). The biomechanics of leaping in gibbons. *American Journal of Physical Anthropology*, **143**, 403–416.

Channon, A. J., Crompton, R. H., Günther, M. M., and Vereecke, E. E. (2010b). Muscle moment arms of the gibbon hind limb: implications for hylobatid locomotion. *Journal of Anatomy*, **216**, 446–62.

Channon, A. J., Gunther, M. M., Crompton, R. H., D'Août, K., Preuschoft, H., and Vereecke, E. E. (2011a). The effect of substrate compliance on the biomechanics of gibbon leaps. *Journal of Experimental Biology*, **214**, 687–696.

Channon, A. J., Usherwood, J. R., Crompton, R. H., Günther, M. M., and Vereecke, E. E. (2011b). The extraordinary athletic performance of leaping gibbons. *Biology Letters,* **8,** 1:46-49.

Close, R. I. (1972). Dynamic properties of mammalian skeletal muscles. *Physiol Rev*, **52**, 129–197.

Couppé, C., Hansen, P, Kongsgaard, M., Kovanen, V, Suetta, C., Aagaard, P, Kjaer, M, and Magnusson, S P (2009). Mechanical properties and collagen cross-linking of the patellar tendon in old and young men. *Journal of Applied Physiology*, **107**, 880–6.

Cui, L., Maas, H., Perreault, E. J., and Sandercock, T. G. (2009). In situ estimation of tendon material properties: differences between muscles of the feline hindlimb. *Journal of Biomechanics*, **42**, 679–85.

Dawson, T. J. and Taylor, C. R. (1973). Energetic Cost of Locomotion in Kangaroos. *Nature*, **246**, 313–314.

Defrate, L. E., Van der Ven, A., Boyer, P. J., Gill, T. J., and Li, G. (2006). The measurement of the variation in the surface strains of Achilles tendon grafts using imaging techniques. *Journal of Biomechanics*, **39**, 399–405.

Dimery, N. J., Alexander, R. M., and Ker, R. F. (1986). Elastic extension of leg tendons in the locomotion of horses (*Equus caballus*). *Journal of Zoology*, **210**, 415–425.

Erskine, R. M., Jones, D. A., Maganaris, C. N., and Degens, H. (2009). In vivo specific tension of the human quadriceps femoris muscle. *Eur J Appl Physiol*, **2**, 827–838.

Farley, C. T., Glasheen, J., and Mahon, T. A. M. C. (1993). Running springs: speed and animal size. *Comparative and General Pharmacology*, **86**, 71–86.

Farris, D. J. and Sawicki, G. S. (2011). The mechanics and energetics of human walking and running: a joint level perspective. *J R Soc Interface,* **9,** 66:110-118.

Fleagle, J. G. (1976). Locomotion and posture of the Malayan siamang and implications for hominoid evolution. *Folia Primatol. (Basel)*, **26**, 245–269.

Franchi, M., Quaranta, M., Macciocca, M., Pasquale, V. De, Ottani, V., and Ruggeri, A. (2009). Structure relates to elastic recoil and functional role in quadriceps tendon and patellar ligament. *Micron*, **40**, 370–377.

Hansen, P., Bojsen-Møller, J., Aagaard, P, Kjaer, M., and Magnusson, S. P. (2006). Mechanical properties of the human patellar tendon, in vivo. *Clinical Biomechanics*, **21**, 54–8.

Hashemi, J., Chandrashekar, N., and Slauterbeck, J. (2005). The mechanical properties of the human patellar tendon are correlated to its mass density and are independent of sex. *Clinical Biomechanics*, **20**, 645–52.

Ishikawa, M., Komi, P. V, Grey, M. J., Lepola, V., and Brüggemann, G. (2005). Muscle-tendon interaction and elastic energy usage in human walking. *Journal of Applied Physiology*, **99**, 603–608.

Ker, R. F. (1981). Dynamic tensile properties of the plantaris tendon of sheep (Ovis aries). *Journal of Experimental Biology*, **93**, 283–302.

Ker, R. F., Alexander, R. M., and Bennett, M. B. (1988). Why are mammalian tendons so thick? *Journal of Zoology*, **216**, 309–324.

Ker, R. F., Wang, X. T., and Pike, A. V. (2000). Fatigue quality of mammalian tendons. *Journal of Experimental Biology*, **203**, 1317–27.

Kurokawa, S., Fukunaga, T., and Fukashiro, S. (2001). Behavior of fascicles and tendinous structures of human gastrocnemius during vertical jumping. *Journal of Applied Physiology*, **90**, 1349–1358.

Kurokawa, S., Fukunaga, T., Nagano, A., and Fukashiro, S. (2003). Interaction between fascicles and tendinous structures during counter movement jumping investigated in vivo. *Journal of Applied Physiology*, **95**, 2306–2314.

Lichtwark, G. A. and Wilson, A. M. (2005). Effects of series elasticity and activation conditions on muscle power output and efficiency. *Journal of Experimental Biology*, **208**, 2845–2853.

Lichtwark, G. A., Bougoulias, K., and Wilson, A. M. (2007a). Muscle fascicle and series elastic element length changes along the length of the human gastrocnemius during walking and running. *Journal of Biomechanics*, **40**, 157–164.

Lichtwark, G. A. and Wilson, A. M. (2007b). Is Achilles tendon compliance optimised for maximum muscle efficiency during locomotion ? *Journal of Biomechanics*, **40**, 1768–1775.

Lichtwark, G. A. and Barclay, C. J. (2010). The influence of tendon compliance on muscle power output and efficiency during cyclic contractions. *Journal of Experimental Biology*, **213**, 707–14.

Maganaris, C. N. (2003). Tendon conditioning: artefact or property? *Proc R Soc Lond B*, **270 Suppl**, S39–42.

Maganaris, C. N. and Paul, J. P. (2000). Hysteresis measurements in intact human tendon. *Journal of Biomechanics*, **33**, 1723–7.

Maganaris, C. N. and Paul, J. P. (2002). Tensile properties of the in vivo human gastrocnemius tendon. *Journal of Biomechanics*, **35**, 1639–1646.

Maganaris, C. N., Narici, M. V, and Maffulli, N. (2008). Biomechanics of the Achilles tendon. *Disability and Rehabilitation*, **30**, 1542–7.

Magnusson, S. P., Hansen, P, Aagaard, P, and Brønd, J. (2003). Differential strain patterns of the human gastrocnemius aponeurosis and free tendon , in vivo. *Acta Physiologica Scandinavica*, 185–195.

Magnusson, S. P., Narici, M. V., Maganaris, C. N., and Kjaer, M. (2008). Human tendon behaviour and adaptation, in vivo. *Journal of Physiology*, **586**, 71–81.

Matson, A., Konow, N., Miller, S., Konow, P. P., and Roberts, T. J. (2012). Tendon material properties vary and are interdependent among turkey hindlimb muscles. *The Journal of Experimental Biology*, **215**, 3552–3558.

Mendez, J. and Keys, A. (1960). Density and composition of mammalian muscle. *Metabolism*, **9**, 184–188.

Mérida-Velasco, J. A., Sánchez-Montesinos, I., Espín-Ferra, J., Mérida-Velasco, J. R., Rodríguez-Vázquez, J. F., and Jiménez-Collado, J. (1997). Development of the human knee joint ligaments. *The Anatomical Record*, **248**, 259–68.

Morse, C. I., Thom, J. M., Birch, K. M., and Narici, M. V (2005). Changes in triceps surae muscle architecture with sarcopenia. *Acta Orthopaedica*, **183**, 291–298.

Muramatsu, T., Muraoka, T., Takeshita, D., Kawakami, Y., Hirano, Y., and Fukunaga, T. (2001). Mechanical properties of tendon and aponeurosis of human gastrocnemius muscle in vivo. *Journal of Applied Physiology*, **90**, 1671–1678.

Narici, M. V, Landoni, L., and Minetti, A. E. (1992). Assessment of human knee extensor muscle stress from in vivo physiological cross-sectional area and strength measurements. *Eur J Appl Physiol*, **65**, 438–444.

O'Brien, T. D., Reeves, N. D., Baltzopoulos, V., Jones, D. A., and Maganaris, C. N. (2010). Mechanical properties of the patellar tendon in adults and children. *Journal of Biomechanics*, **43**, 1190–1195.

Payne, R., Crompton, R. H., Isler, K., Savage, R., Vereecke, E. E., Günther, M. M., Thorpe, S. K. S., and D'Août, K. (2006). Morphological analysis of the hindlimb in apes and humans. I. Muscle architecture. *Journal of Anatomy*, **208**, 709–24.

Peltonen, J., Cronin, N. J., Avela, J., and Finni, T. (2010). In vivo mechanical response of human Achilles tendon to a single bout of hopping exercise. *Journal of Experimental Biology*, **213**, 1259–65.

Peltonen, J., Cronin, N. J., Stenroth, L., Finni, T., and Avela, J. (2012). Achilles tendon stiffness is unchanged one hour after a marathon. *Journal of Experimental Biology*, **215**, 3665–71.

Pollock, C. and Shadwick, R. (1994). Relationship between body mass and biomechanical properties of limb tendons in adult mammals. *American Journal of Physiology*, **266**, 1016–1021.

Raichlen, D. A., Armstrong, H., and Lieberman, D. E. (2011). Calcaneus length determines running economy: Implications for endurance running performance in modern humans and Neandertals. *Journal of Human Evolution*, **60**, 299–308.

Rubenson, J., Lloyd, D. G., Heliams, D. B., Besier, T. F., and Fournier, P. A. (2011). Adaptations for economical bipedal running: the effect of limb structure on three-dimensional joint mechanics. *Interface*, **8**, 740–55.

Scholz, M. N., Bobbert, M. F., Van Soest, A. J., Clark, J. R., and Van Heerden, J. (2008). Running biomechanics: shorter heels, better economy. *Journal of Experimental Biology*, **211**, 3266–71.

Svensson, R. B., Hansen, P., Hassenkam, T., Haraldsson, B. T., Aagaard, P., Kovanen, V., Krogsgaard, M., Kjaer, M., and Magnusson, S. P. (2011). Mechanical properties of human patellar tendon at the hierarchical levels of tendon and fibril. *Journal of Applied Physiology*, **112**, 419–26.

Toumi, H., Larguech, G., Filaire, E., Pinti, A., and Lespessailles, E. (2012). Regional variations in human patellar trabecular architecture and the structure of the quadriceps enthesis: a cadaveric study. *Journal of Anatomy*, **220**, 632–7.

Vereecke, E. E., D'Août, K., Payne, R., and Aerts, P. (2005). Functional analysis of the foot and ankle myology of gibbons and bonobos. *Journal of Anatomy*, **206**, 453–76.

Vereecke, E. E., D'Août, K., and Aerts, P. (2006). The dynamics of hylobatid bipedalism: evidence for an energy-saving mechanism? *Journal of Experimental Biology*, **209**, 2829–2838.

Vereecke, E. E. and Aerts, P. (2008). The mechanics of the gibbon foot and its potential for elastic energy storage during bipedalism. *Journal of Experimental Biology*, **211**, 3661–70.

Ward, S. R. and Lieber, R. L. (2005). Density and hydration of fresh and fixed human skeletal muscle. *Journal of Biomechanics*, **38**, 2317–2320.

Waugh, C. M., Blazevich, A. J., Fath, F., and Korff, T. (2012). Age-related changes in mechanical properties of the Achilles tendon. *Journal of Anatomy*, **220**, 144–155.

Zajac, F. E. (1989). Muscle and tendon: properties, models, scaling, and application to biomechanics and motor control. *Critical Reviews in Biomedical Engineering*, **17**, 359–411.

Figures

Figure 1 - Schematic representation of the triceps surae (dark blue: medial and lateral gastrocnemius; light blue: soleus) with the Achilles tendon and the quadriceps (dark red: rectus femoris; light red: vasti) with the patellar tendon in gibbons (left) and humans (right). Drawn to the same scale. [colour figure]

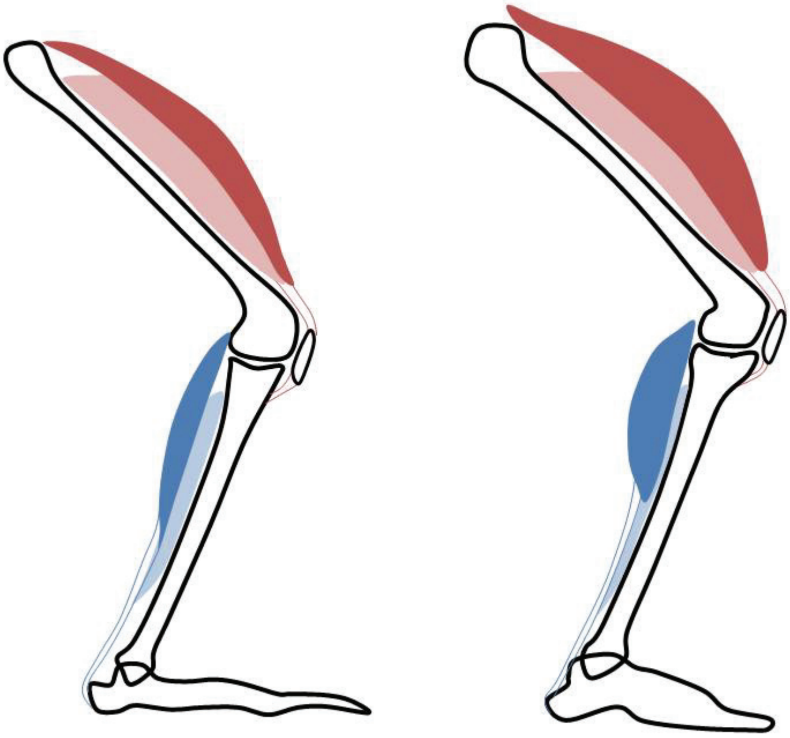
Figure 2 - Anatomical dimensions of the triceps surae and quadriceps femoris of a gibbon. MTU = muscle tendon unit length, TL = total tendon length (not visible for quadriceps femoris); ETL = external tendon length.

Figure 3 - Stiffness and Young's modulus of the Achilles (blue) and patellar tendon (red) with standard deviation (± s.d.). [colour figure]

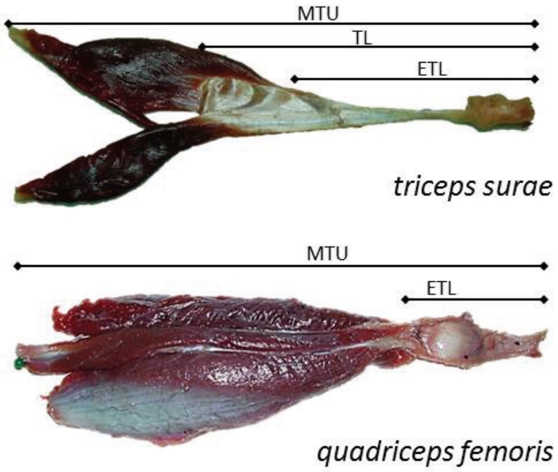
Figure 4 - Load-displacement curves of (A) the Achilles tendon (n = 14) and (B) the patellar tendon (n = 8). The area between the loading and unloading curve is the hysteresis. Each curve represents a different specimen.

Figure 5 - Average stress values at 2%, 3%, 4% and 5% strain (± s.d.) for the Achilles tendon (blue squares) and patellar tendon (red diamonds). [colour figure]

Figure 6 - Dynamics of gibbon leaping (A) and bipedalism (B), illustrating the COM fluctuations (top), knee and joint angle kinematics (middle), and power profiles of the COM (bottom) during the stance phase. 180 degrees corresponds to full knee extension. Data taken from (Vereecke et al., 2006; Vereecke and Aerts, 2008; Channon et al., 2010a).



[Figure 1 - colour]



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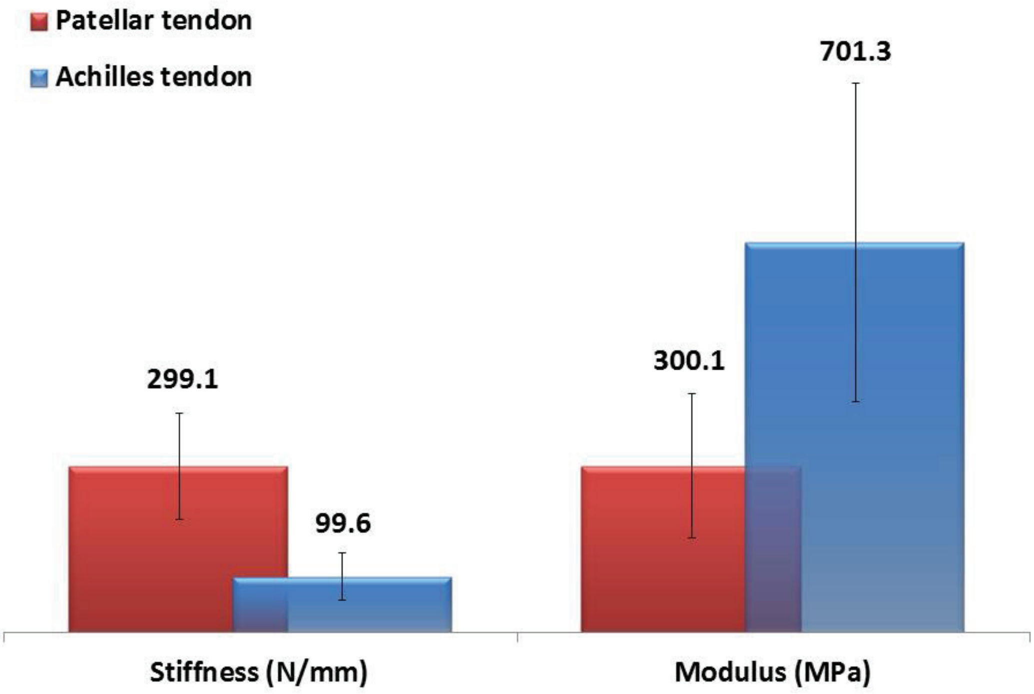
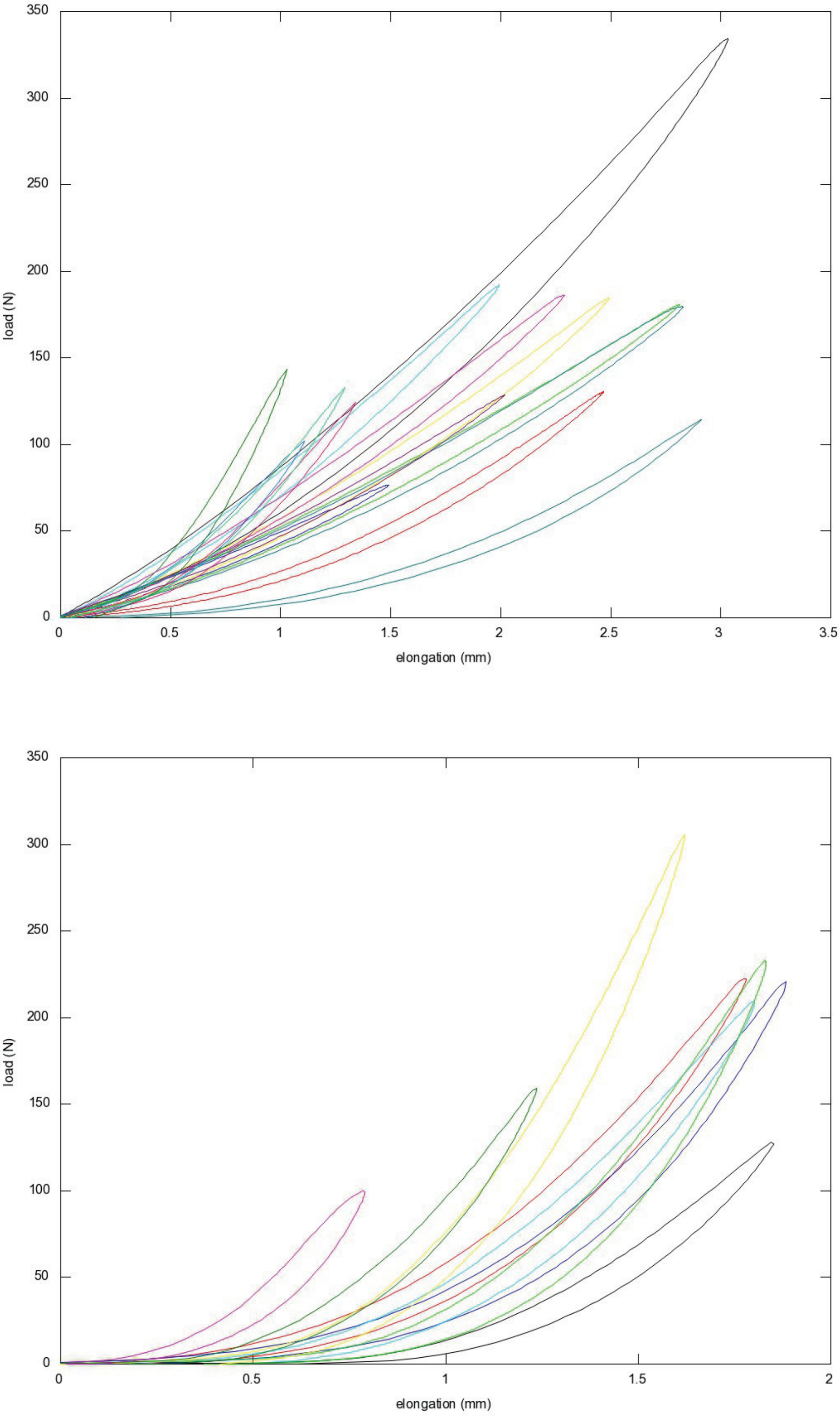
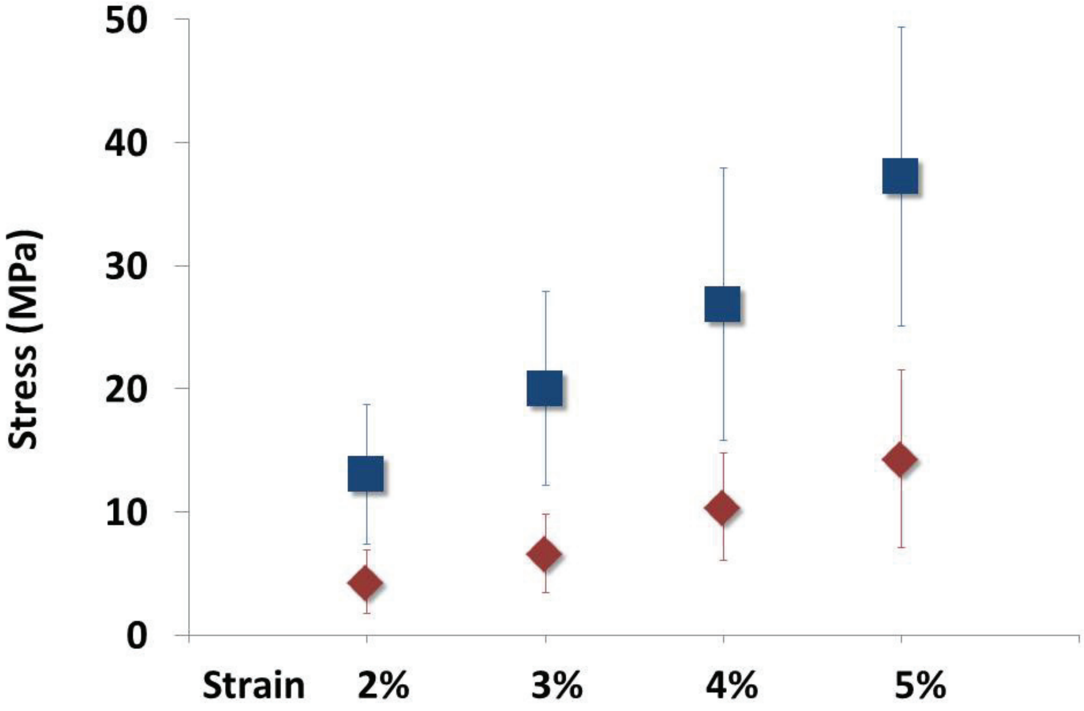


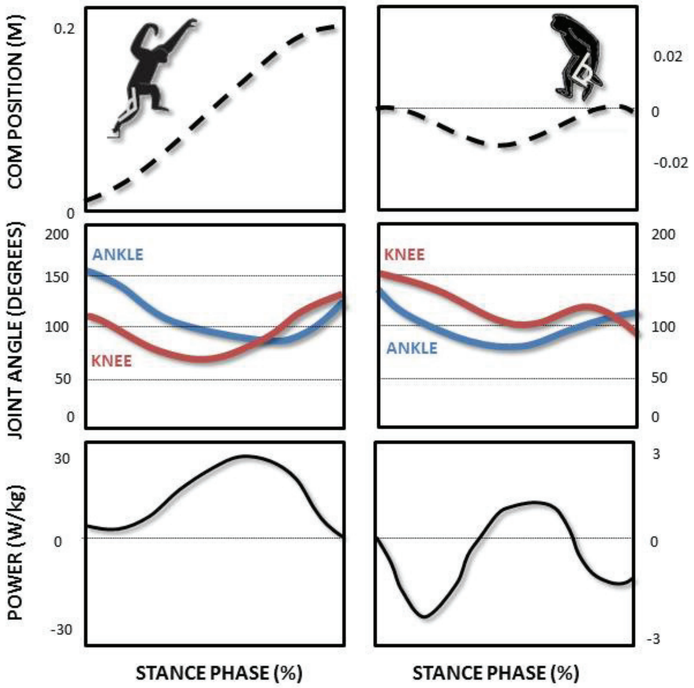
[Figure 3 - colour]



[Figure 4A and 4B]



[Figure 5]


COM POSITION (M)
0.2
0
0.02
0
-0.02
JOINT ANGLE (DEGREES)
200
150
100
50
0
ANKLE
KNEE
KNEE
ANKLE
POWER (W/kg)
30
0
-30
3
0
-3
STANCE PHASE (%)
STANCE PHASE (%)

[Figure 6]

Table 1 – Subject properties and tendon sample collection.

Specimen	**Species**	**Mass** *(kg)*	**Sex**	**Age** *(years)*	**AT** *n*	**PT** *n*	**Source**
Hl1	*Hylobates lar*	10.6	m	26	1	0	National Museums Scotland, UK
Hl2	*Hylobates lar*	-	m	adult	1	1	National Museums Scotland, UK
Hl3	*Hylobates lar*	4.5	m	35	1	0	National Museums Scotland, UK
Hl4	*Hylobates lar*	4.5	f	adult	1	1	Cotswold Wild Animal Park, UK
Hl5	*Hylobates lar*	6.5	f	22	1	0	Wild Animal Park Planckendael, B
Hl6	*Hylobates lar*	8.2	m	adult	1	1	Cotswold Wild Animal Park, UK
Hm1	*Hylobates moloch*	-	m	adult	1	1	National Museums Scotland, UK
Hm2	*Hylobates moloch*	5.8	m	19	1	1	Port Lympe, UK
Hp1	*Hylobates pileatus*	-	f	25	1	1	Twycross, UK
Hp2	*Hylobates pileatus*	5.2	m	41	1	1	Paignton Zoo, UK
Ss1	*Symphalangus syndactylus*	11.5	f	35	1	0	Marwell Zoo, UK
Ss2	*Symphalangus syndactylus*	8.5	f	9	1	1	Twycross Zoo, UK
Ss3	*Symphalangus syndactylus*	12.5	f	32	1	0	Zoo Antwerp, B
Ss4	*Symphalangus syndactylus*	13.4	m	adult	1	0	National Museums Scotland, UK
Total					**14**	**8**	

Note: cause of death is unknown for most specimens, yet none of the specimens included in this study demonstrated musculoskeletal pathologies that could have affected soft-tissue properties. Abbreviations: AT = Achilles tendon, PT = patellar tendon, f = female, m = male.

Table 2 – Average dimensions of the triceps surae and quadriceps femoris in gibbons and humans (taken from literature, see table legend).

	Triceps surae/Achilles tendon		**Quadriceps surae/Patellar tendon*****	
	Gibbon *(n =14)*	**Human** *(range)*	**Gibbon** *(n = 8)*	**Human** *(range)*
FL (mm)	31	43-70’	58	63^-105”
PA (degrees)	24	17-25#	24	13-28”
PCSA (mm^2)	967	20,210’	1,910	16,280-23,180°
scaled PCSA	278	1098	548	884-1259
MTU (mm)	183	267^	206	>413***
TL (mm)	139	-	131	-
ETL (mm)	74	171-256*	25	~78-91***
TCSA (mm^2)	10	43-67*	34	95°-164**
PCSA/TCSA	100	302-470	56	99.3-244
TL/MTU	0.76	-	0.64	-
ETL/MTU	0.40	0.64-0.80	0.12	0.19-0.22***
ETL/FL	2.4	2.4-4.9	0.4	0.7-1.4***
FL/MTU	0.17	0.16-0.26	0.28	0.21-0.32
RC (%)	9.4	-	3.4	-

Human data taken from: *(Peltonen et al., 2010; Peltonen et al., 2012), #(Padhiar et al. 2008; Lichtwark et al., 2007), ’(Morse et al. 2005); ^(Wickiewicz et al., 1983); ”(Erskine 2009); °(O’Brien et al., 2010a; O’Brien et al., 2010b); **(Hansen et al., 2006); "(Waugh et al., 2012). ***Note that the patellar tendon length (ETL) and quadriceps MTU reported for humans are estimations based on available data in literature of the patellar tendon and quadriceps dimensions, but corrected for the length of the patella to enable comparison with the gibbon data, where patellar tendon includes both quadriceps and patellar tendon portion (resp. proximal and distal to patella) and the patella. The human patella ETL is calculated by adding the length of the patella (35.7 mm; Baldwin and House 2005) to the length of the patellar tendon (41.5**-55 mm”), the quadriceps MTU is calculated by adding muscle belly length (322 mm^), patella length (35.7 mm; Baldwin and House 2005) and ETL (55 mm”).