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Perspective Article

Adaptation of the tendon to mechanical usage

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Abstract

Tendons primarily function as contractile force transmitters, but their mechanical properties may change dependent upon their level of mechanical usage. Using an ultrasound-based technique we have assessed tendon mechanical properties *in vivo* in a number of conditions representing different levels of mechanical usage. Ageing alters tendon mechanical properties; stiffness and modulus were lower in older adults by 10 and 14%, respectively, compared to young adults. Increased levels of exercise loading in old age can however partly reverse this process, as tendon stiffness and modulus were found to increase by 65 and 69%, respectively. Complete unloading due to bed rest or spinal cord injury both reduce tendon stiffness and modulus, however, only chronic unloading due to spinal cord injury seems to cause tendon atrophy. Alterations in tendon mechanical properties due to changes in the levels of loading have implications for the speed of force transmission, the muscle's operating range and the likelihood of tendon strain injury.

Keywords: Tendon, Ageing, Resistance Training, Unloading

Tendons form the structural link between muscle and bone and due to their anatomical location their primary role is to transmit contractile force to the bone, facilitating joint movement. Tendons are not however completely rigid tissues, they do elongate when subjected to a tensile load imposed upon them by muscle contraction. The degree to which tendons elongate to a given level of muscle force depends upon their dimensions and their mechanical properties, for review see reference[1]. The mechanical and material properties of various animal and human tendons have been assessed using *in vitro* techniques[2,3]. However, these tests may not accurately represent the mechanical properties of intact tendons functioning *in vivo*. The reasons for this include difficulties in securely fixing tendons in the clamps without inducing stress concentrations, or without allowing the specimen to slip incurring elongation errors. *In vitro* tests however, have provided the first indication that just like muscle and bone, tendons may be sensitive to the level of mechanical usage[4-12]. In recent years a technique has been established that allows the assessment of human tendon mechanical properties *in vivo*[13]. This technique uses B-mode ultrasonography to image the tendon in real-time. A reference point on the tendon is visualised and its displacement during an isometric contraction can be measured and assumed to represent the elongation of the tendon. The forces acting on the tendon can be estimated from dynamometry-based measurements of joint torque and by taking into account a number of other factors. Recently we have applied this *in vivo* technique to assess the adaptation of the tendon to different situations or levels of mechanical usage. Firstly, by using a cross-sectional design, we have investigated the effects of ageing on the tendon, a situation that may also encompass a certain level of reduced loading. Secondly, we have assessed the response of elderly tendons to increased levels of loading by a programme of high-intensity resistance training. Thirdly, the effects of decreased use on the tendon have been investigated by 90 days unloading in healthy adults and by chronic unloading due to spinal cord injury.

The author has no conflict of interest.

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Methods for studying human tendon mechanical properties *in vivo*

The general procedure for the assessment of tendon mechanical properties involves applying ultrasound scanning in the sagittal plane to image the displacement of a reference

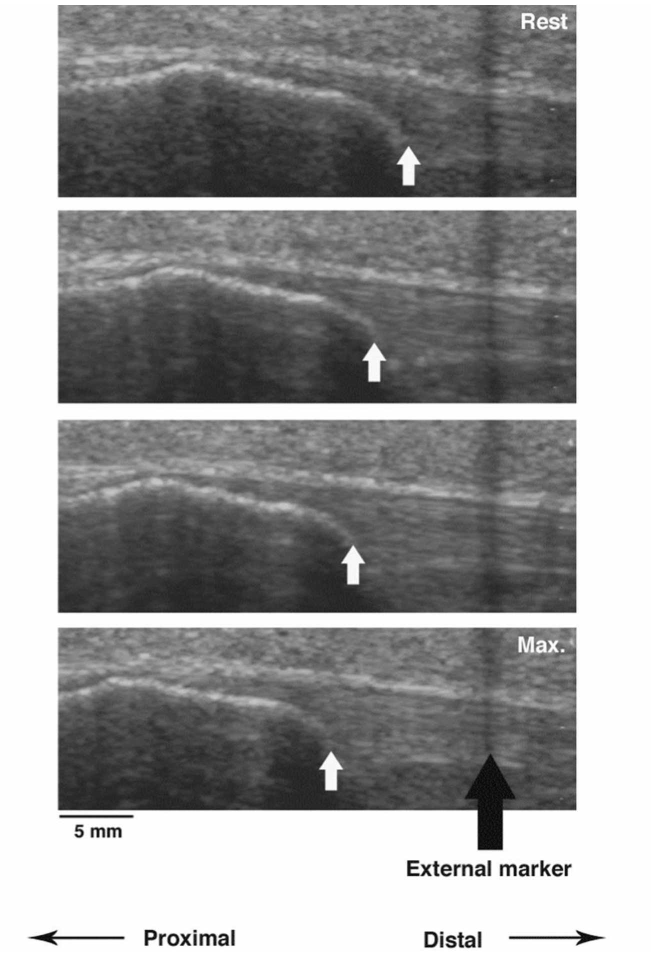

Figure 1. Example sagittal-plane ultrasound scans of the patellar tendon at rest and during an isometric contraction of increasing intensity. The white arrows indicate the contraction-induced displacement of the apex of the patella.

point during an isometric contraction (Figure 1). The reference point in the experiments described is either the myotendinous junction (in the case of the gastrocnemius tendon) or the apex of the patella (in the case of the patellar tendon). The displacement of this reference point gives the elongation of the tendon (Figure 1). An echo-absorptive external marker is fixed to the skin, casting a shadow on the ultrasound image and provides an indication of transducer movement in relation to the scanned structure (Figure 1). Subjects perform a maximal isometric contraction increasing their torque linearly in 3-4 s. In some instances, when maximal torque is reached superimposed electrical stimulation is applied in order to obtain maximal tendon force despite voluntary muscle activation deficits. Both tendon force (estimated from the measured joint torque) and tendon elongation data can be captured continuously over the ~4 s contraction enabling a number of data points to be used in constructing the force-elongation curve. The tendon length and cross-sectional area (CSA) can be assessed using either ultrasound or magnetic resonance imaging (MRI). The tendon forces can be estimated from the measured joint torque and by taking into account a number of factors[13,14]. These factors include MRI-based measurements of the tendon moment arm length and an estimation of the opposing torque generated by the antagonist muscles. Tendon stiffness is calculated from the gradient of the tendon force-elongation curve. Tendon stiffness can be normalized to the dimensions of the tendon to yield the tendon Young's modulus, which provides a measure of the tendon's material properties and enables comparisons across tendons of different sizes and anatomical location.

The effects of ageing on human tendon mechanical properties

The effects of ageing on the tendon may be regarded as somewhat unclear from the findings of some *in vitro* experiments. Some studies suggest that tendons become stiffer with ageing[15]. However, when the effects of ageing are separated from the effects of maturation, a clearer picture emerges with the majority of studies showing a decrease in tendon stiffness with ageing[9,10,16]. Using a cross-sectional design, we investigated the influence of ageing on human tendon mechanical properties *in vivo*[17]. The gastrocnemius tendon was studied in six older adults (69-80 years) and six young adults (20-26 years). Tendon elongation at maximal tendon force was 13 mm in young adults and 21 mm in older adults. Despite much higher tendon forces generated by the young adults (tendon force of 375 N in young adults and 151 N in older adults), the tendon elongated much less, which indicates a reduced stiffness in the tendons of older adults. Indeed tendon stiffness was lower in the elderly by ~10% compared to young adults when measured in the highest force region ($P<0.05$). The tendon Young's modulus in the corresponding stress region was lower in older adults by 14% compared to young adults ($P<0.05$). The lower tendon Young's modulus in older adults indicates that the lower stiffness is not due to differences in the size of the tendon, but is due to intrinsically weaker tendon material properties. The lower stiffness in older adults is likely to have implications for the shortening of the contractile element and the velocity of force transmission. The more compliant tendon of the elderly may allow the muscle fibres to shorten more. Most human muscles (including the gastrocnemius muscle) act on the ascending limb of the sarcomere length-tension relation[18], thus more fibre shortening would shift the muscles' operating range to the left, away from the optimal region, causing a reduction in force (Figure 2A). However, the number of sarcomeres in-series will also influence this theoretical effect and may vary between young and older adults. The more compliant tendon of older adults may result in a slower transmission of contractile forces to the skeleton, which will be seen as a slower rate of torque development at the level of the whole joint system.

The effects of increased loading in old age on human tendon mechanical properties

Given the lower tendon stiffness experienced in old age and the associated functional implications outlined above, strategies to mitigate or partially reverse this deficit in mechanical stiffness are of paramount importance. High intensity resistance training has emerged as an effective method for increasing muscular strength in older adults[19-21]; however, its impact on elderly human tendon mechanical properties is unknown. *In vitro* studies suggest that tendons respond to levels of loading above those experienced physiologically by increasing their tensile stiffness[11,12]. In order to investigate the influence of increased loading in old age on the mechanical properties of the patellar tendon, we recruited nine older adults to a resistance training group and nine older adults to a non-training control group[14]. The resistance training involved knee-extension and leg-press exercises performed using a load corresponding to 80% of the 5-repetition maximum (the maximum load that could be lifted and lowered 5 times only). The duration of the training programme was fourteen weeks with sessions three times each week. After the intervention period, tendon strain at maximal tendon stress (42 MPa) decreased from 10% to 6% in the training group ($P<0.01$), with no change in tendon strain in the control group (Figure 3). Tendon stiffness measured in the highest force region increased by 65% after training (pre: 2187 $N.mm^{-1}$; post: 3610 $N.mm^{-1}$; $P<0.01$), but was unchanged in the control group (pre: 2247 $N.mm^{-1}$; post: 2255 $N.mm^{-1}$; $P>0.05$). The tendon Young's modulus measured over the corresponding stress region increased by 69% (pre: 1.3 GPa; post: 2.2 GPa; $P<0.01$), but remained unchanged in the control group (1.3 GPa; $P>0.05$). These results show that the tendons of older adults can adapt to increased levels of loading by increasing their tensile stiffness and modulus. Therefore it is suggested that ageing-induced reductions in tendon stiffness can be at least partially mitigated by resistance training. The increased levels of loading did not alter the tendon dimensions and as indicated by the increase in Young's modulus the changes were due to alterations in the tendon's material properties. This agrees with findings from animal studies, showing that tendon stiffness increases following increased loading without any change in tendon size in adults[22], whilst immature tendons adapt to the same stimulus primarily through tendon hypertrophy, for review see reference[23]. Increased tendon stiffness has been reported from other animal studies where exercise has been used to increase the level of tendon loading above that experienced under normal physiological conditions[11,12,24-26]. The increased tendon stiffness found after the resistance training intervention might be expected to increase the velocity of force transmission and in support of this concept, we observed a 27% increase in the rate of torque development. The increased tendon stiffness post-intervention may also have implications for the muscle's operating range. It might be speculated that the muscle fibres would shorten less, causing a shift towards the optimal sarcomere operating range (assuming the muscle acts on the ascending limb; Figure 2B). However, in the same subject group, we found that the estimated sarcomere operating range of the vastus lateralis muscle remained constant after the exercise intervention[27]. This was attributed to changes occurring in the muscle fascicles and in the tendon that would have opposite effects on the sarcomere operating range, which interact in order to maintain the muscle's operating range constant.

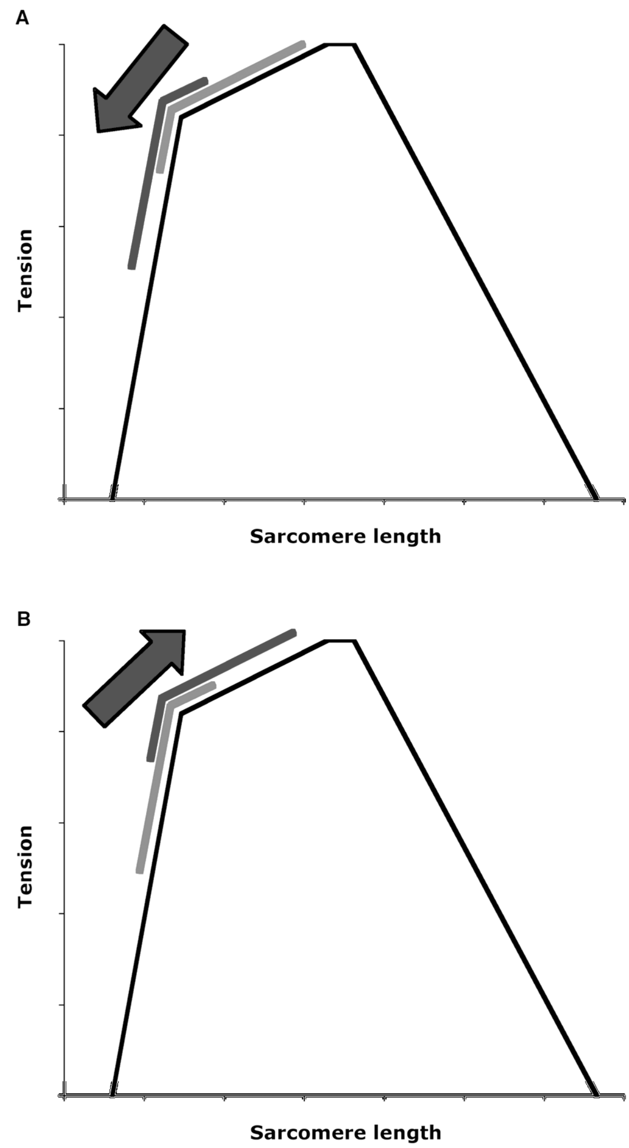

Figure 2. Schematic sarcomere length-tension relations to illustrate theoretical changes in a muscles' operating range with changes in the stiffness of the in-series tendon. Assuming all other conditions remained constant, a reduction in tendon stiffness would result in greater sarcomere shortening and a left shift of the sarcomere length-tension relation (A), whereas an increase in tendon stiffness would result in less sarcomere shortening and a right shift of the sarcomere length-tension relation (B).

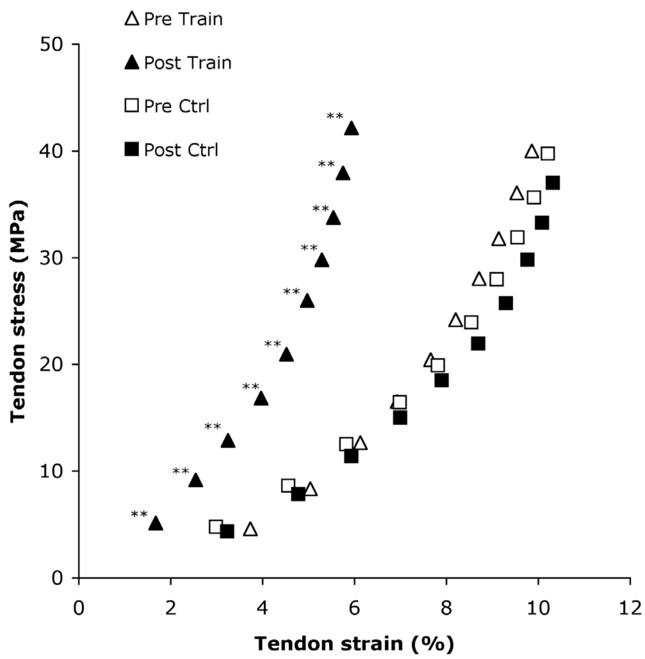

Figure 3. Patellar tendon stress-strain curves for older adults pre- and post-intervention in exercise training (Train) and control (Ctrl) groups. Data are means, ** denotes a significantly ($P<0.01$) reduced tendon strain post-training. Modified from the data presented in reference[14].

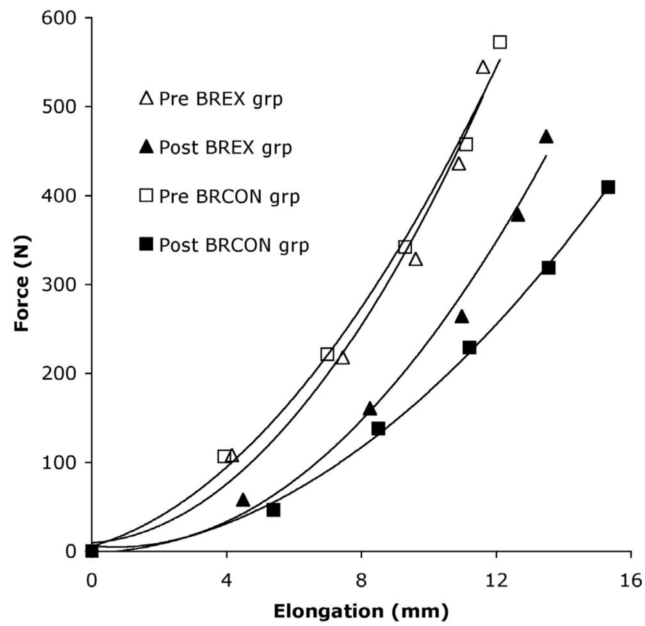

Figure 4. Gastrocnemius tendon force-elongation curves pre- and post-intervention in a group of healthy adults undergoing 90 days of bed rest only (BRCON group) and a group subjected to 90 days of bed rest in combination with exercise countermeasures (BREX group). Data are means. Modified from the data presented in reference[33].

Tendon strain injury may occur once the tendon strains to a given extent, therefore the reduction in patellar tendon strain for any given level of tendon stress found after resistance training (Figure 3), may reduce the likelihood of injury for older adults.

The influence of 90 days' unloading with and without exercise countermeasures on human tendon mechanical properties

As discussed in the above sections, the tendon responds to increased levels of loading by increasing its tensile stiffness, but is the reverse true – does tendon stiffness reduce in response to unloading? Animal models suggest that collagenous tissue stiffness is reduced following periods of unloading, causing greater deformations for the same given load[4-6,8,28,29]. One example of a situation where humans are subjected to unloading is during spaceflight. Astronauts onboard the International Space Station are exposed to the microgravity environment for a minimum duration of 90 days. Given the known detrimental consequences of microgravity exposure on muscle and bone and the possible detrimental consequences on the tendon indicated from animal models, it is important to provide intermittent loading to prevent or attenuate the decline in these tissues. The European Space Agency (ESA) together with the Centre National d'Etudes Spatiales (CNES) and the Japanese National Space Development Agency (NASDA) conducted a microgravity simulation study at the MEDES Institute for Space Medicine and Physiology in Toulouse, France (long-term bed rest study 2001-2002). Bed rest (with a 6 deg head-down tilt) was used to simulate the effects of microgravity exposure for a period of 90 days. Volunteers were allocated to two experimental groups: a group that underwent bed rest only (*BRCON group,* $n=9$; age: 32±4 years) and a group that underwent bed rest while performing exercise countermeasures (*BREX group,* $n=9$; age: 33±5 years). Exercise was performed every third day in the 6 deg head-down tilt position using a gravity-independent flywheel resistive exercise device. This exercise device enables loading in both concentric and eccentric contraction phases via the inertia of rotating flywheels and has been specifically developed for use in space[30-32]. Two exercises were performed, (**i**) the leg-press for the hip, knee and ankle extensors and (**ii**) the calf-raise for the ankle extensors. In this study we investigated two research questions: (**1**) does 90 days of unloading reduce tendon stiffness? and (**2**) can any potential reductions in tendon stiffness with unloading be prevented by intermittent exercise loading? We studied the gastrocnemius tendon mechanical properties pre- and post-intervention[33]. Following 90 days of unloading only (*BRCON group*), tendon elongation was greater by ~3 mm ($P<0.05$) compared to pre-intervention values despite the tendon force being 163 N lower than that generated before the period of unloading ($P<0.01$; Figure 4). Tendon stiffness decreased after unloading by 58% ($P<0.01$) measured over the force interval 250-500 N. The dimensions of the tendon were unaltered by unloading, which is reflected by the fact that the corresponding tendon Young's modulus decreased after unloading by 57% from 266 to 114 MPa ($P<0.01$). Therefore, 90 days of unloading reduces gastrocnemius tendon stiffness due to a change in tendon material properties, with no measurable tendon atrophy. The reduction in tendon stiffness after unloading is likely to reduce the velocity of force transmission and in support of this notion we observed a 38% decrease in the rate of torque development in a sub-sample of participants. The reduced tendon stiffness following unloading means that for any given level of force production the tendon elongation would be greater post-intervention, suggesting that muscle fibres would shorten more. The gastrocnemius muscle acts on the ascending limb of the sarcomere length-tension relation[34] and theoretically, if all other conditions remain constant by unloading, the reduced tendon stiffness would result in a left-shift of the length-tension relation, thus causing a decline in force (Figure 2A). In the volunteers who underwent 90 days of bed rest whilst performing exercise countermeasures every third day (BREX group), tendon elongation increased by 1.9 mm ($P<0.05$) despite a decrease in tendon force by 78 N ($P<0.01$; Figure 4). Following the intervention period, tendon stiffness decreased by 37% ($P<0.01$) over the force interval 250-500 N. The tendon dimensions were unaltered, which is reflected by the fact that the corresponding tendon Young's modulus decreased by 38% from 303 to 187 MPa after unloading combined with exercise training ($P<0.01$). Although the exercise performed did attenuate the detrimental effects of unloading on the mechanical properties of the tendon (decline in tendon stiffness: 58% in BRCON group vs 37% in BREX group), it did not completely prevent them. During gravitational loading experienced on Earth, the plantarflexor tendons are subjected to high repeated loads associated with a "spring-like" action due to the continuous application-removal of muscle forces required to withstand body weight and to propel the body forwards. It is therefore likely that during unloading, the exercise volume (loading level, frequency and duration) needs to exceed a threshold level in order to completely prevent alterations in tendon mechanical properties.

The influence of chronic unloading due to spinal cord injury on human tendon mechanical properties

In order to elucidate the effects of chronic unloading on tendon mechanical properties, we assessed the patellar tendon in individuals with spinal cord injury (SCI) and compared these results to age-matched able-bodied (AB) controls[35]. Lesion duration was between 1.5 to 24 years in the individuals with SCI. Electrical stimulation was applied to induce muscle contraction in both groups. Tendon elongations and strains were actually very similar between SCI and

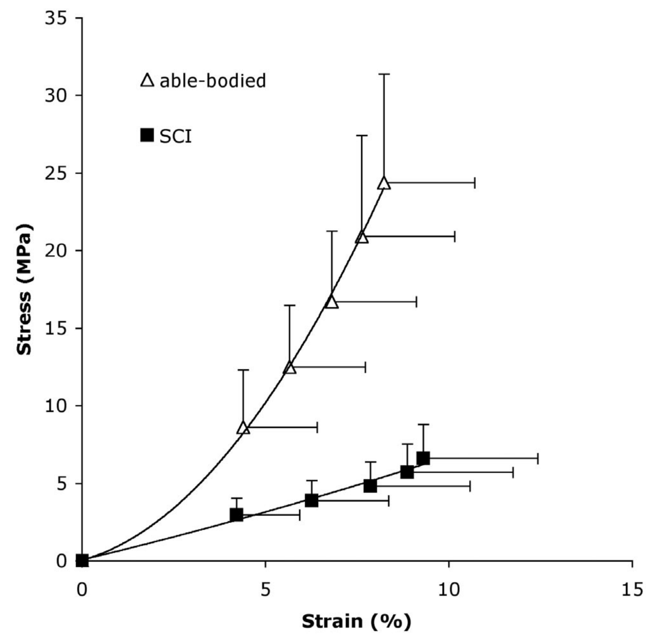

Figure 5. Patellar tendon stress-strain curves in people with spinal cord injury (SCI) and able-bodied aged-matched controls (AB). Data are means and SD. Modified from the data presented in reference[35].

AB subjects (maximal tendon elongation: SCI group 4.1 mm; AB group 3.4 mm; maximal tendon strain: SCI group 9.3%; AB group 8.2%; Figure 5), despite 76% lower tendon forces and 70% lower tendon stresses in the SCI subjects at maximal stimulation intensity (tendon force: SCI group 675 N vs. AB group 2833 N; $P<0.01$; tendon stress: SCI group 7.4 MPa vs. AB group 24.3 MPa; $P<0.01$; Figure 5). Tendon stiffness was lower by 77% in the SCI group (SCI group 143 $N.mm^{-1}$ vs. AB group 434 $N.mm^{-1}$; $P<0.01$) and although tendon length was not different between the two groups, the tendon CSA was smaller by 17% in the SCI group. The tendon Young's modulus was 59% lower in the SCI compared to the AB group (SCI group 67 MPa; AB group 164 MPa; $P<0.01$). These results indicate that consistent with our results from 90 days of unloading in healthy adults, chronic unloading due to spinal cord injury is associated with a decline in tendon stiffness due to alterations in the material properties of the tendon. However, in contrast to findings from 90 days of unloading, chronic unloading is associated with tendon atrophy. It is evident from the decline in tendon mechanical and material properties with chronic unloading that the tendon is more susceptible to strain injury and rupture following a reduction in mechanical usage.

Conclusions

Human tendons are sensitive to changes in the level loading they experience. Tendon stiffness is reduced with ageing, due to a change in the tendon's material properties in the absence of tendon atrophy. These ageing-induced declines can be at least partially mitigated with the increased loading provided by high intensity resistance training. Following 14 weeks of resistance training older adults increased tendon stiffness due to a change in the material properties of the tendon without any tissue hypertrophy. Unloading due to simulated microgravity and chronic unloading due to SCI both lead to reductions in tendon stiffness and Young's modulus. Only chronic unloading seems to cause a certain degree of tendon atrophy. These changes in tendon mechanical properties with alterations in the level of mechanical usage have important implications for the muscle's operating range, the speed of force transmission and the possibility of tendon strain injury.

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