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Triceps surae muscle-tendon properties in older endurance- and sprint-trained athletes

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Running head: Muscle-tendon properties in older athletes

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Abstract

Previous studies have shown that aging is associated with alterations in muscle architecture and tendon properties. However, the possible influence of different types of regular exercise loading on muscle architecture and tendon properties in older adults is poorly understood. To address this, triceps surae muscle-tendon properties were examined in older male endurance (OE, n=10, age=74.0±2.8) and sprint runners (OS, n=10, age=74.4±2.8) with an average of 42 years of regular training experience, and compared to age-matched (OC, n=33, age=74.8±3.6) and young untrained controls (YC, n=18, age=23.7±2.0).

Compared to YC, Achilles tendon cross-sectional area (CSA) was 22% ($p=0.022$), 45 % ($p=0.001$) and 71% ($p<0.001$) larger in OC, OE and OS, respectively. Among older groups, OS had significantly larger tendon CSA compared to OC ($p=0.033$). No significant between-group differences were observed in Achilles tendon stiffness. In older groups, Young's modulus was 31-44% and maximal tendon stress 44-55% lower than in YC ($p\leq0.001$). OE showed shorter soleus fascicle length than both OC ($p<0.05$) and YC ($p<0.05$).

These data suggest that long-term running does not counteract the previously reported age-related increase in tendon CSA, but instead, may have an additive effect. The greatest Achilles tendon CSA was observed in sprinters followed by endurance runners and older controls, suggesting that adaptation to running exercise is loading intensity dependent. Achilles tendon stiffness was maintained in older groups even though all older groups displayed larger tendon CSA and lower tendon Young's modulus. Shorter soleus muscle fascicles in older endurance runners may be an adaptation to life-long endurance running.

Keywords: Achilles tendon, mechanical properties, muscle architecture, aging, exercise

Introduction

Loss of muscle function with aging is associated with physical limitations and disability (40). Decline in muscle mass is undoubtedly an important contributor to the deterioration in muscle function with aging (16). However, longitudinal studies have shown a clear dissociation in loss of muscle function and cross-sectional area or mass with aging (9, 17), suggesting that other factors may also contribute to the age-related loss of muscle function. Muscle architecture and tendon mechanical properties greatly affect muscle performance (28, 51) and have been found to differ between young and old sedentary adults (36, 37, 44). Thus, age-related alterations in muscle architecture and tendon mechanical properties may partially explain the loss of muscle performance with age that occurs at a disproportionally faster rate than the decline in muscle mass.

Regular exercise is a key aspect supporting healthy aging. Indeed, it has been suggested that older athletes provide a model of exceptionally successful biological aging (46). For example, previous studies have shown that aged athletes with systematic exercise training habits exhibit much better cardiorespiratory, metabolic and bone health than their less active counterparts (22, 49). Regular exercise training, especially strength and sprint exercise, also helps to maintain muscle mass, function (21, 52) and composition (43), thus counteracting the age-related decline in functional performance typically observed in normal populations (9, 39).

In spite of several known beneficial effects of regular exercise on the musculoskeletal system in old age, little is known about the effects of regular participation in planned exercise on muscle architecture and tendon properties in older adults. Two previous studies have compared untrained older adults to older endurance runners. Firstly, Karamanidis and Arampatzis (19) found that muscle architecture and tendon stiffness in medial gastrocnemius and vastus lateralis were largely similar in older endurance runners compared to untrained older adults. The only significant difference was greater medial gastrocnemius pennation angle in endurance runners. Secondly, Couppé et al. (7) recently found that older endurance runners had a greater patella tendon cross-sectional area but similar tendon stiffness compared to untrained peers. These previous studies were conducted on endurance runners and thus knowledge of the long-term effects of different types of exercise loading on muscle architecture and tendon properties in older adults is missing.

Therefore, the aim of this study was to examine the association between different types of life-long exercise and muscle-tendon properties by comparing muscle architecture and tendon properties in older sprint and endurance runners to both age-matched and young untrained adults. Triceps surae muscles were studied because of their important role in locomotion and because they exhibit the greatest functional limitation of all lower limb muscle groups in older adults during locomotion (24). Endurance running provides a model of high volume and moderate intensity loading while sprint running represents a model of low volume but high intensity loading of triceps surae muscles. The hypothesis was that older athletes with a life-long regular running background would exhibit muscle fascicle length, pennation angle, muscle size, muscle strength and tendon mechanical properties in the triceps surae muscle group that are more similar to those of young adults than untrained older adults. In addition, based on previous cross-sectional studies conducted in young adults (1, 2), it was hypothesized that sprint-trained older athletes would be stronger, have stiffer Achilles tendons, lower pennation angle, and longer muscle fascicles compared to endurance-trained older athletes.

Materials and methods

Subjects

Male subjects were recruited in two age categories, one from 18 to 30 years old (untrained young controls, YC, n=18) and the other from 70 to 80 years old. The older cohort was recruited in three groups: untrained older controls (OC, n=33), older athletes competing in endurance running events (OE, n=10) and older athletes competing in sprint running events (OS, n=10).

Untrained young and older control groups were part of a Europe-wide collaborative study called MyoAge (34) and included in the current study to represent general populations of healthy young and older adults. We defined untrained as a person who may be recreationally active but is not training for, or participating in, competitive sport. YC were recruited from among university students using study advertisements via e-mail and bulletin boards. We excluded those who studied sport sciences as well as competitive athletes. OC were recruited from the University of the Third Age or from weekly community meetings of retired people. The aim was to recruit healthy older people who were socially active and free from comorbidity. Using telephone interviews, an equal number of sedentary and physically active (competitive athletes excluded) older subjects were recruited to obtain a representative sample of older people with varying physical activity levels. Sedentariness was defined as exercising for fitness and health one or fewer times per week. Physically active was defined as exercise three or more times per week (30 min or more with intensity sufficient to cause sweating or breathlessness). Results (44) and more detailed description of the recruitment (34) of YC and OC have been presented earlier.

Older athletes were recruited among the participants of the World Master Athletics Indoor Championships held in Jyväskylä, Finland in 2012. Twenty male athletes were recruited based on the events they participated in during the championships. Ten subjects were recruited from sprint running events (60 m, 60 m hurdles, 200 m, 400 m) and 10 were recruited from endurance running events (3 km, ½ marathon and 8 km cross country running). Some subjects in the OS and OE groups participated in several sprint or endurance running events, respectively. Mean results of the subjects competing in the championships were: 60 m 9.13 ± 0.48 (sec, n=8), 60 m hurdles 10.15 (sec, n=1), 200 m 30.64 ± 1.97 (sec, n=7), 400 m 1:13 ± 8 (min:sec, n=3), 3000 m 13:48 ± 60 (min:sec, n=4), ½ marathon 1:43:37 ± 11:34 (hr:min:sec, n=5) and 8 km cross country running 44:19 ± 6:25 (min:sec, n=7). These results correspond to 8, 1, 11, 16, 22 and 16 % slower than the world record times for 75 year old men in 60 m, 60 m hurdles, 200 m, 400 m, 3000 m and ½ marathon respectively. Thus, the participating subjects can be considered to be highly competitive athletes.

Subject exclusion criteria were Achilles tendon pain, history of Achilles tendon rupture or surgery, pain in calf muscles during measurements, neurologic and progressive severe illnesses, insulin treated diabetes, fracture within the previous year, immobilization for one week during the last three months, daily use of painkillers, use of immunosuppressive drugs or anticoagulants, or severe visual or hearing impairment.

The ethics committee of the Central Finland Health Care District approved the study. All participants signed an informed consent prior to participating in the study and measurements were conducted according to the standards set by the latest revision of the Declaration of Helsinki.

Measurements

Training characteristics of OE and OS groups were assessed with self-reported questionnaire. The athletes were asked about their training history (yr.), overall training volume (h/wk.) and amount of endurance (km/wk.), sprint (sessions/wk.) and strength training (sessions/wk.) in their current normal training routines.

Laboratory measurements included assessment of triceps surae muscle architecture and size and Achilles tendon cross-sectional area and mechanical properties. The measurement procedures have been previously described in detail (44) but are briefly described below.

For the measurements of Achilles tendon and both gastrocnemius and soleus muscle architecture and size at rest, the subjects were lying prone facing down with ankle angle at 90°. Tendon cross-sectional area (mm^2) was measured from a B-mode ultrasound image taken 4 cm proximal from the proximal border of the calcaneal tubercle where the free Achilles tendon typically reaches its smallest cross-sectional area (38). Body mass normalized tendon cross-sectional area was calculated by dividing cross-sectional area by body $mass^{2/3}$ (20). Muscle architecture from medial gastrocnemius and soleus muscles was assessed from ultrasound images taken at 50% of medial gastrocnemius length and mid-muscle belly in the medial-lateral direction. Fascicle length (mm), pennation angle (°) and muscle thickness (mm) were measured from the images. In order to take into account between-subject differences in stature, fascicle length was normalized to tibia length. The combined anatomical cross-sectional area (cm^2) of medial and lateral gastrocnemius was measured from a panoramic B-mode ultrasound image taken at 50% of medial gastrocnemius length as a measure of the size of the gastrocnemius muscles. All measurements from ultrasound images were taken twice using an open source computer program

(ImageJ 1.44b, National Institutes of Health, US) and the mean was used for subsequent data analysis.

For the measurement of Achilles tendon mechanical properties, the subjects were seated in a custom built dynamometer with ankle angle at 90°, knee fully extended and hip at 60° of flexion (full extension 0°). After a standardized warm-up, three maximal voluntary contractions (MVC) lasting approximately 3 seconds were performed with strong verbal encouragement to measure plantar flexion strength (Nm). The highest value obtained during MVC trials was used for subsequent analysis. Warm-up and plantar flexion MVCs served to precondition the tendon before the measurement of tendon mechanical properties (30). Achilles tendon mechanical properties were measured from several isometric plantar flexion contractions up to a force level of 80% of MVC. Tendon force was calculated by multiplying measured reaction force by the ratio between Achilles tendon moment arm length and moment arm of the reaction force. Achilles tendon moment arm was defined as the distance from the center of the Achilles tendon to the outermost tip of the medial malleolus in the sagittal plane measured using a ruler. The moment arm of the reaction force around the ankle joint was defined as the sagittal plane distance between the outermost tip of the medial malleolus and the head of the first metatarsal. Achilles tendon elongation (mm) was defined as the change in the distance between the proximal border of the calcaneal tubercle and the medial gastrocnemius muscle-tendon junction. Changes in the location of the calcaneal tubercle in the laboratory coordinate system were measured using a potentiometer that measures heel lift from the dynamometer footplate. Medial gastrocnemius muscle-tendon junction location in the laboratory coordinate system was measured with a combination of B-mode ultrasonography and motion analysis. Ultrasound images of the muscle-tendon junction were collected at 70 Hz and the location of the muscle tendon junction within the image was defined by automatic tracking software (32). The location of the muscle-tendon junction was converted to the laboratory coordinate system using video based motion capture of the ultrasound probe. Two parameters that describe tendon mechanical properties were calculated, tendon stiffness (N/mm) and Young's modulus (GPa). Tendon stiffness characterizes mechanical properties of the tendon and is defined as the slope of the linear portion of the tendon force-elongation curve. We calculated tendon stiffness as a linear fit to force-elongation data from 10 to 80% MVC force since the curves were almost perfectly linear in this region (Fig. 1, $r^2=0.999$ from linear fits to average force-elongation curves). Tendon Young's modulus is the slope of the linear portion of the tendon stress-strain curve and represents tendon stiffness normalized to tendon dimensions. Young's modulus describes the mechanical properties of the material from which a tendon is composed. To derive Young's modulus, Achilles tendon stress (Pa) was calculated by dividing Achilles tendon force (N) by tendon cross-sectional area (m^2) and strain (%) was calculated by dividing elongation (mm) by initial tendon length (mm). Young's modulus was calculated as a linear fit to force-elongation data from 10 to 80% MVC force.

Statistical analyses

Due to inadequate image quality, soleus muscle architecture data were excluded for two subjects from the OS group and three from the OC group, while medial gastrocnemius muscle architecture data were excluded for one subject from OE, and gastrocnemius cross-sectional area data from one subject from OC. Data were first checked for normality with Shapiro-Wilk test and for homogeneity of variance with Levene's test. Differences in muscle and tendon properties between the groups were tested using single factor analysis of variance and Tukey-Kramer post hoc test. Games-Howell post hoc test was used when inhomogeneous variances between the groups were observed and Kruskal-Wallis test with Bonferroni correction for non-normally distributed variables. Differences in training characteristics between OE and OS were tested using Mann-Whitney U-test. The level of statistical significance was set at $\alpha = 0.05$ for all tests. Statistical analyses were performed using IBM SPSS Statistics (version 20.0.0.2). Standardized mean differences between YC and groups of older adults were calculated for main results of the study (Table 2 and 3) as a measure of effect sizes using Hedges' g including a correction for small sample bias (12).

Results

Subject characteristics and training status for the older athletes are reported in Table 1. Older adults in the three different groups were matched for age, height and body mass. YC were significantly taller than OC ($p<0.001$). OC had significantly greater BMI compared to YC ($p=0.006$) and OE ($p=0.009$). Significantly lower plantar flexion strength was found in OC (34%, $p=0.001$) and OE (42%, $p<0.001$) compared to YC but not in OS compared to YC ($p=0.077$). OE and OS groups did not differ in years of training, hours of training per week, or number of strength training sessions per week. Endurance training measured in distance was 8 times greater in OE in comparison with OS ($p<0.001$), and OS did 3 times more sprint training sessions per week than OE ($p=0.006$).

Achilles tendon cross-sectional area was 22, 45 and 71% larger in OC ($p=0.022$), OE ($p=0.001$) and OS ($p<0.001$) compared to YC, respectively (Table 2). Tendon cross-sectional area in OS was significantly larger than in OC ($p=0.033$). Body mass normalized tendon cross-sectional area yielded similar results to the unnormalized values. No statistically significant differences were observed between the groups in Achilles tendon stiffness (Figure 1) but Young's modulus was 31, 35, and 44% smaller in OC ($p<0.001$), OE ($p=0.001$) and OS ($p<0.001$) in comparison to YC, respectively. Maximal tendon force during MVC was significantly lower in OC (35%, $p<0.001$) and OE (38%, $p<0.001$) but not in OS ($p=0.156$) compared to YC. Average tendon stress during MVC was greater in YC than the older groups ($p<0.001$). Tendon elongation at 80% MVC was significantly greater in YC compared to OC ($p=0.014$) but the difference did not reach statistical significance in OE ($p=0.114$) or OS ($p=0.352$). However, effect sizes between YC and OE and OS were greater than the effect size between YC and OC. The groups did not differ significantly in tendon strain at 80% MVC.

Results of soleus and gastrocnemius muscle architecture and size, as well as plantar flexion muscle strength, are presented in Table 3. Soleus fascicle length was significantly shorter in OE compared to YC (absolute $p=0.014$, normalized $p=0.002$) and also compared to OC (absolute $p=0.047$, normalized $p<0.001$). No significant differences were found in soleus pennation angle or muscle thickness. Medial gastrocnemius fascicle length and pennation angle did not differ between the groups. In OC, medial gastrocnemius muscle thickness was significantly smaller in contrast to YC ($p=0.043$) and gastrocnemius cross-sectional area was significantly smaller in contrast to YC ($p=0.011$) and OS ($p=0.011$).

Discussion

We examined selected triceps surae muscle-tendon properties of two differently trained groups of older athletes with an average of 42 years of regular running training, and compared them to untrained age-matched older and young adults. The main findings of the study were that Achilles tendon cross-sectional area was significantly larger in all older adult groups than young adults, and in older sprinters compared to age-matched untrained older adults, while there were no statistically significant group differences in Achilles tendon stiffness. The greater tendon cross-sectional area was also reflected in tendon Young's modulus and tendon average tensile stress during maximal isometric force production, both of which were significantly lower in all older groups compared to young untrained adults. Only minor differences were observed in triceps surae muscle architecture, the most important being significantly shorter fascicle length in soleus muscle in older endurance runners. The current study adds new insight into possible effects of exercise loading on muscle and tendon structure and function in older age. The novelty of the current study is that measurements of triceps surae muscle architecture and Achilles tendon properties were made from top-level older athletes that included both endurance and sprint runners.

Achilles tendon properties

To the best of our knowledge, this is the first study to show greater Achilles tendon cross-sectional area in older adults with a regular exercise training background. Contradicting our hypothesis, the results suggest that long-term exercise did not counteract the age-related increase in Achilles tendon cross-sectional area. Previous cross-sectional studies suggest that Achilles tendon cross-sectional area increases in response to both long-term exercise loading (20, 33) and normal aging (31, 44). The present results suggest that the Achilles tendon responds to regular loading by increasing cross-sectional area in an intensity-dependent manner. Moreover, the increase in cross-sectional area appears to be additive to the increase due to normal aging. This finding supports recent findings by Couppé et al. (7), who showed that regular endurance running was associated with larger patella tendon cross-sectional area in both young and older adults.

A possible explanation for ageing and exercise training to be associated with larger tendon cross-sectional area is that tendon hypertrophy is needed to compensate for an age-related decrease in mechanical properties of the tendon collagen structure. Another possible explanation is that greater tendon cross-sectional area in older adults is observed as a consequence of intratendinous accumulation of lipids or water. These two possible mechanisms are not exclusive and could together explain the observed results. The following paragraphs introduce these proposed explanations in more detail.

In animal models, aging has been linked with an increase in type V collagen and a greater proportion of small collagen fibrils, which probably contribute to concurrently observed reduced ultimate tensile stress (10, 48). Greater tendon cross-sectional area in older adults could be due to a necessary adaptation to reduce maximal tendon stress to safe levels for older tendons that possibly have reduced ultimate tensile stress. To reduce the stress to a safe level, cross-sectional area must be proportional to maximal force acting on the tendon, thus explaining the greater cross-sectional area in older sprint runners compared to older untrained adults observed in the current study.

Greater tendon cross-sectional area in older adults could also serve to maintain sufficient stiffness, which could be important both for protecting the tendon from strain-induced damage and for muscle function. A possible age-related reduction in stiffness of tendon collagen structure may be partly compensated by an age-related increase in collagen cross-links, especially in advanced glycation end product cross-links (6), which stabilize collagen structure and may increase tendon stiffness. Life-long endurance running has been shown to be associated with lower advanced glycation end product cross-link density (7). If older athletes in the current study had a lower density of collagen cross-links, this could explain the requirement for older athletes to have even greater tendon cross-sectional area compared to untrained older adults, in order to maintain tendon stiffness with aging.

Based on current knowledge of tendon adaptation, loading intensity is the main factor determining adaptations in tendon mechanical properties (5). Thus, it seems unlikely that sprint-trained older athletes would have the lowest Achilles tendon Young's modulus among the groups in the current study. A possible explanation could be that larger tendon cross-sectional area in older adults is not an adaptation to lowered tendon Young's modulus. Instead it could be due to accumulation of tendon subcomponents that do not markedly affect tendon mechanical behavior. These could include extracellular lipid deposits and proteoglycans and glycosaminoglycans that attract water. Extracellular lipid deposits within tendon have been associated with aging (14) and this could be common to all older adults irrespective of exercise training. On the other hand, production of proteoglycans and glycosaminoglycans could be increased with exercise training induced tendon loading (15). This would explain the observed lower Young's modulus and stress of the tendon in older adults in the present study, and also explains why greater tendon cross-sectional area was not related to greater tendon stiffness.

Within- and between-operator reliability of Achilles tendon cross-sectional area measurement using ultrasound imaging has been reported to be good (11, 50). In the current study, duplicate analysis of tendon cross-sectional area images produced intraclass correlation 0.989 and typical error 2.1%. However, validity of tendon cross-sectional area measurement using ultrasound imaging is not known, thus the results should be interpreted with some caution. Future studies should try to replicate the findings of the current study, preferably using magnetic resonance imaging, which allows measurements of tendon cross-sectional area along the whole tendon. More research examining tendon composition and collagen structure in older adults is also warranted to explain the mechanisms behind changes in tendon cross-sectional area.

In contrast to our hypothesis that life-long running would mitigate age-related changes in tendon mechanical properties, we found that Young's modulus was significantly lower in older compared to young adults irrespective of training status, with no significant differences between the older groups. There were also no significant between-group differences in initial tendon length or tendon stiffness. Thus, the lower Young's modulus in older compared to young adults can be attributed mainly to the larger tendon cross-sectional area in older adults.

It should be noted that a toe-region with a lower slope of the tendon force-elongation curve at low forces or stresses was not observed (Figure 1). We think that the reason for highly linear force-elongation/stress-strain curves is initial force acting on the Achilles tendon at a 90° ankle angle, and the fact that we calculated the curve starting from 10% MVC force. Lack of toe-region has also been previously observed for Achilles tendon in vivo when elongation is measured from the medial gastrocnemius muscle-tendon junction (27), as done in the present study.

To summarize the findings regarding tendon mechanical properties, Young's modulus of the Achilles tendon was significantly lower in older compared to young adults, irrespective of training status. Despite this, Achilles tendon stiffness was conserved in all groups of older adults. Thus, the lower muscle strength, greater tendon cross-sectional area and conserved tendon stiffness resulted in reduced maximal tendon stress and strain in older adults. Reduced tendon stress and strain could be a necessary mechanism to decrease the probability of tendon injury, as aging may decrease tendon fascicle sliding that possibly leads to greater loading of the fascicles themselves (47). A functional consequence of similar Achilles tendon stiffness but lower muscle strength in older compared to young adults is a limited maximal capacity for elastic energy storage and subsequent utilization during locomotion. This may contribute to the reported greater metabolic cost of transport in older compared to young adults (35).

Triceps surae muscle architecture, size and strength

The present data also suggest that, in general, muscle architecture is not greatly different in older habitual runners in contrast to both untrained older or young adults. Soleus fascicle length was found to be significantly shorter in endurance-trained older adults than young and older untrained adults. Although somewhat speculative, it may be that shorter fascicles observed in long-term endurance runners in the current study are due to adaptation that improves the efficiency of force production in locomotion. Soleus has short muscle fascicles compared to tendon length (51). Consequently, soleus muscle operates mainly as a force rather than a power producer in locomotion (4). Thus, as this muscle does not need to produce large amounts of work, short fascicles may decrease the energy cost of force production due to lower activated muscle volume per unit of force output compared to longer fascicles (29). We recently observed that shorter fascicle length in soleus and gastrocnemius was associated with better mobility in older adults (45), further supporting the suggestion that shorter soleus fascicle length in older endurance runners may be an adaptive response to life-long exercise training.

Another finding of the present study is that long-term endurance running was not associated with greater strength or size of triceps surae muscles compared to untrained older controls. Plantar flexion strength and maximal tendon force in endurance-trained older adults was significantly lower in comparison to young adults. Moreover, the effect sizes for the difference in gastrocnemius thickness and cross-sectional area were comparable to those between young and older controls, which were also statistically significant. Taken together, these results suggest that endurance running is not a sufficient stimulus for maintenance of muscle mass and size with aging.

In contrast, the current data suggest that high intensity loading due to sprint training may be an effective stimulus to counteract the age-related decline in both muscle mass and strength in triceps surae muscles. We observed that gastrocnemius muscle cross-sectional area was significantly larger in sprint-trained older adults compared to untrained older controls. In addition, plantar flexion strength and maximal tendon force were not significantly different from those of young controls, with about half the effect size as in endurance-trained older adults compared to young controls. These findings are supported by previous studies in young adults in which sprint running but not endurance running was associated with greater muscle strength and size in triceps surae muscles (18, 23). It may be that the beneficial effects of sprint training preferentially target gastrocnemius muscle, which contains more fast twitch muscle fibers than soleus (13).

Methodological considerations

The strengths of the current study are that the world-class older athletes measured in the present study had a life-long physical activity background and had performed many decades of regular exercise training. In addition, both the trained and untrained older adults were over 70 years old and thus can be assumed to be affected by primary biological aging.

Limitations of the present study include the cross-sectional study design which does not allow conclusions about cause-effect relationships that a longitudinal study design may allow. Cross-sectional studies can be affected by selection bias. It is possible that subjects with favorable muscle-tendon properties for endurance or sprint running were more likely to participate in such activities. However, we did not observe differences between older trained and untrained subjects in genetically determined variables such as Achilles tendon moment arm, forefoot length or Achilles tendon length, all of which are related to running performance (3, 25, 26, 42). This suggests that selection bias caused by genetic predisposition towards favorable musculoskeletal properties for running did not considerably affect our data, although the possibility of selection bias cannot be completely excluded. Another limitation of the current study is the small sample size. However, it was not possible to obtain a larger sample of older athletes from the highest performance level.

Conclusions

The current findings suggest that triceps surae muscle size, architecture, strength and tendon stiffness are relatively unaffected by long-term running training in older adults. The reason for this finding may be that the triceps surae muscle group is highly loaded in daily activities and thus training produces only a small relative overload to this muscle group. Considering the unparalleled physical performance of the older athletes in the present study, it appears that the measured triceps surae muscle-tendon properties are not the key determining factors in their physical performance. However, relatively high individual variation in these properties suggests that a well-functioning muscle-tendon unit may be achieved via different combinations of muscle and tendon properties. In addition, it is likely that in the current study there were differences between the groups in factors that were not measured but that affect physical performance. These include muscle fiber type, composition, molecular level modifications in contractile proteins and neural activation (8, 21, 41). To further elucidate the importance of muscle architecture and tendon mechanical properties for physical performance, future studies should investigate how aging and physical loading affect muscle-tendon interaction during locomotion.

In conclusion, our data suggest that long-term physical loading induced by either endurance or sprint running does not have a significant effect on Achilles tendon stiffness in older adults. However, the loading patterns associated with sprint and endurance training in older age both appear to increase Achilles tendon cross-sectional area in an intensity dependent manner. Furthermore, the present results suggest that sprint running but not endurance running may mitigate age-related loss of muscle mass and strength in triceps surae muscles. On the other hand, endurance training in older age may alter muscle architecture in a way that is beneficial for movement economy.

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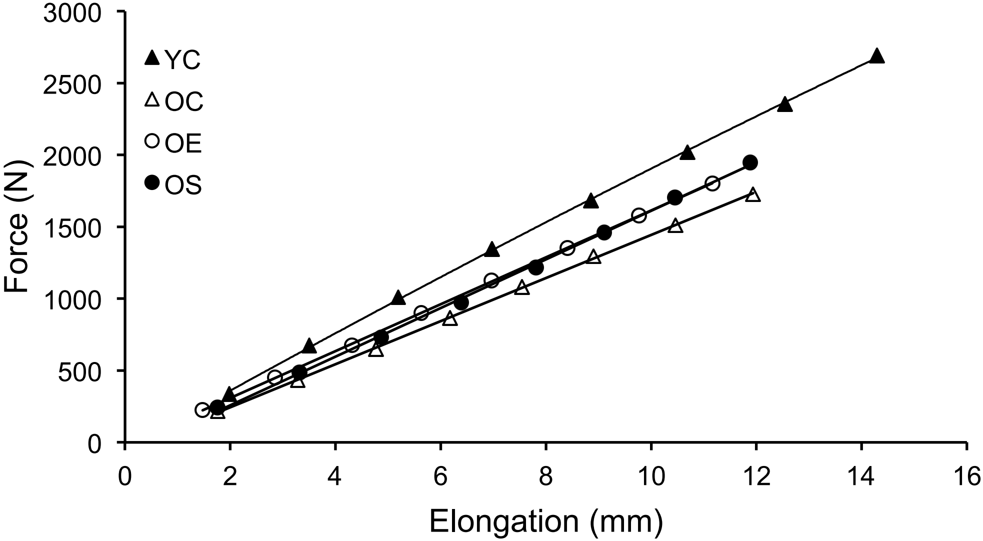
Figure legend

FIGURE 1. Mean Achilles tendon force-elongation (upper) and stress-strain (lower) relationships for young controls (YC), older controls (OC), older endurance runners (OE), and older sprint runners (OS). Lines are linear fits and represent Achilles tendon stiffness and Young's modulus, respectively. Values are calculated at 10% MVC increments from 10 to 80% MVC. Standard deviations are omitted for clarity.


YC
OC
OE
OS
Force (N)
3000
2500
2000
1500
1000
500
0
0
2
4
6
8
10
12
14
16
Elongation (mm)

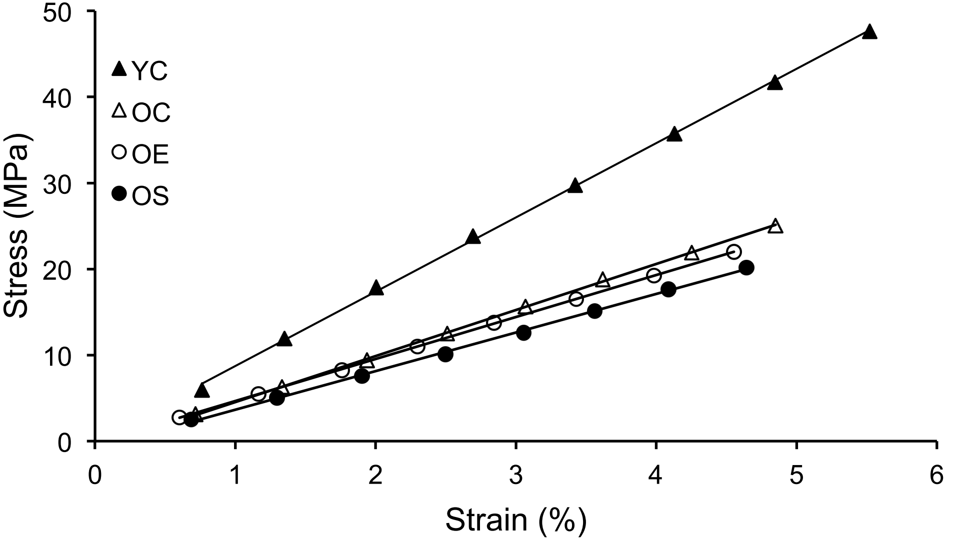

YC
OC
OE
OS
Stress (MPa)
50
40
30
20
10
0
0
1
2
3
4
5
6
Strain (%)

TABLE 1. Subject characteristics and training status of older athletes

	YC	OC	OE	OS
Number of subject	18	33	10	10
Age (yr.)	23.7 ± 2.0	74.8 ± 3.6**	74.0 ± 2.8**	74.4 ± 2.8**
Height (cm)	181 ± 6	173 ± 5**	175 ±7	176 ± 7
Body mass (kg)	75.4 ± 9.0	76.1 ± 7.7	69.9 ± 6.9	74.3 ± 7.1
BMI (kgm^{-2})	23.1 ± 2.6	25.4 ± 2.4**††	22.7 ± 1.6	24.1 ± 1.9
Plantar flexion strength (Nm)	199 ± 56	132 ± 21**	116 ± 25**	153 ± 39
Years of training			39.4 ± 20.9	44.7 ± 19.7
Hours of training per week			6.8 ±3.3	6.2 ± 2.6
Endurance training per week (km)			55.2 ± 8.8	6.5 ± 2.8††
Sprint training sessions per week			0.8 ± 0.7	2.3 ± 1.2††
Strength training sessions per week			0.5 ± 0.2	0.9 ± 0.2

Values are expressed as mean ± SD. * significantly different from YC, † significantly different from OE, **/†† p<0.01. YC young controls, OC older controls, OE older endurance runners, OS older sprint runners.

TABLE 2. Achilles tendon cross-sectional area and mechanical properties

	YC	OC	OE	OS
Cross-sectional area (mm^2)	56.5 ± 9.6	69.0 ± 12.2 (-1.05)* ‡	82.0 ± 19.8 (-1.69)**	96.5 ± 24.9 (-2.26)**
Stiffness (N/mm)	186 ± 37	164 ± 47 (0.49)	172 ± 39 (0.34)	166 ± 35 (0.51)
Young's modulus (GPa)	0.86 ± 0.20	0.59 ± 0.17 (1.46)**	0.56 ± 0.22 (1.40)**	0.48 ± 0.19 (1.85)**
Max. tendon force (kN)	3.4 ± 0.9	2.2 ± 0.6 (1.58)**	2.1 ± 0.4 (1.64)**	2.6 ± 0.8 (0.80)
Max. tendon stress (MPa)	59.3 ± 14.9	33.1 ± 9.0 (2.22)**	26.5 ± 8.3 (2.36)**	30.1 ± 14.3 (1.86)**
Elongation at 80 % MVC (mm)	14.3 ± 2.5	11.9 ± 6.4 (0.42)*	11.2 ± 4.4 (0.88)	11.9 ± 4.2 (0.70)
Strain at 80 % MVC (%)	5.6 ± 1.5	4.8 ± 2.2 (0.42)	4.5 ± 1.8 (0.66)	4.7 ± 1.7 (0.56)

Values are expressed as mean ± SD (effect size compared to YC). * significantly different from YC, ‡ significantly different from OS, */‡ $p<0.05$, ** $p<0.01$. YC young controls, OC older controls, OE older endurance runners, OS older sprint runners, MG medial gastrocnemius.

TABLE 3. Muscle architecture and size

	YC	OC	OE	OS
Soleus fascicle length (mm)	40.6 ± 8.8	38.6 ± 7.6 (0.24) †	31.2 ± 3.9 (1.18)*	35.3 ± 8.3 (0.57)
Normalized soleus fascicle length (mm/mm)	0.102 ± 0.021	0.100 ± 0.021 (0.11) ††	0.073 ± 0.008 (1.55)**	0.083 ± 0.022 (0.83)
Soleus pennation angle (°)	21.0 ± 5.7	21.2 ± 4.0 (-0.05)	23.7 ± 5.3 (-0.46)	21.6 ± 8.3 (-0,08)
Soleus thickness (mm)	14.3 ± 2.6	13.1 ± 2.7 (0.44)	13.4 ± 2.7 (0.33)	12.8 ± 3.7 (0.49)
MG fascicle length (mm)	47.7 ± 6.6	45.0 ± 7.6 (0.35)	45.3 ± 6.5 (0.34)	47.7 ± 7.0 (0.00)
Normalized MG fascicle length (mm/mm)	0.121 ± 0.018	0.117 ± 0.022 (0.17)	0.108 ± 0.015 (0.71)	0.111 ± 0.021 (0.46)
MG pennation angle (°)	24.8 ± 4.0	24.4 ± 4.2 (0.09)	23.3 ± 4.8 (0.34)	24.1 ± 3.5 (0.18)
MG thickness (mm)	20.1 ± 2.5	17.7 ± 3.2 (0.77)*	17.2 ± 3.6 (0.94)	18.6 ± 2.7 (0.55)
Gastrocnemius CSA (cm^2)	24.2 ± 4.5	20.1 ± 4.5 (0.89)* ‡	20.9 ± 3.4 (0.73)	25.1 ± 4.4 (-0.19)

Values are expressed as mean ± SD (effect size compared to YC). * significantly different from YC, † significantly different from OE, ‡ significantly different from OS, */†/‡ $p<0.05$, **/†† $p<0.01$. YC young controls, OC older controls, OE older endurance runners, OS older sprint runners.