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Age-related differences in Achilles tendon properties and triceps surae muscle architecture in vivo

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Stenroth L, Peltonen J, Cronin NJ, Sipilä S, Finni T. Age-related differences in Achilles tendon properties and triceps surae muscle architecture in vivo. *J Appl Physiol* 113: 1537–1544, 2012. First published October 4, 2012; doi:10.1152/japplphysiol.00782.2012.—This study examined the concurrent age-related differences in muscle and tendon structure and properties. Achilles tendon morphology and mechanical properties and triceps surae muscle architecture were measured from 100 subjects [33 young (24 ± 2 yr) and 67 old (75 ± 3 yr)]. Motion analysis-assisted ultrasonography was used to determine tendon stiffness, Young's modulus, and hysteresis during isometric ramp contractions. Ultrasonography was used to measure muscle architectural features and size and tendon cross-sectional area. Older participants had 17% lower ($P < 0.01$) Achilles tendon stiffness and 32% lower ($P < 0.001$) Young's modulus than young participants. Tendon cross-sectional area was also 16% larger ($P < 0.001$) in older participants. Triceps surae muscle size was smaller ($P < 0.05$) and gastrocnemius medialis muscle fascicle length shorter ($P < 0.05$) in old compared with young. Maximal plantarflexion force was associated with tendon stiffness and Young's modulus ($r = 0.580$, $P < 0.001$ and $r = 0.561$, $P < 0.001$, respectively). Comparison between old and young subjects with similar strengths did not reveal a difference in tendon stiffness. The results suggest that regardless of age, Achilles tendon mechanical properties adapt to match the level of muscle performance. Old people may compensate for lower tendon material properties by increasing tendon cross-sectional area. Lower tendon stiffness in older subjects might be beneficial for movement economy in low-intensity locomotion and thus optimized for their daily activities.

aging; muscle structure; tendon biomechanics

IN OLDER PEOPLE, MUSCLE STRENGTH and power are important determinants of independent living and are associated with functional status and fall incidence (18, 53). Aging is associated with a marked loss in muscle force (41, 49) and power (50), as well as changes in tendon properties (44) and muscle architecture (38). Tendinous tissue properties and muscle architecture have a marked effect on muscle function (42), but the role of these changes in lowered muscle function with aging is not clear as there are inconsistent findings in the area of aging and muscle-tendon complex properties.

Research examining the association between aging and tendon properties is inconclusive. Studies have shown similar (23, 25) or lower (39, 44) Achilles tendon stiffness and similar (9, 11) or lower (23, 25) patella tendon stiffness in old compared with young subjects. No consistent differences in tendon cross-sectional area (CSA) have been found (9, 11, 36, 44). Findings of age-related differences in muscle architecture are also inconclusive as others report differences in pennation angle and fascicle length in triceps surae (38, 43) but others fail to observe such differences (23, 24). Discrepancy between the studies in the association between aging and muscle-tendon complex properties could be related to small sample size or methodological differences. We aim to avoid these problems with a representative sample of healthy young and old subjects and using state-of-the-art methods.

A study examining age-related differences in muscle and tendon is the first step toward understanding the role of mechanical properties of muscle-tendon complex on age-related decline in muscle performance. It is important to study both muscle and tendon in the same study to prevent sampling-related bias when trying to conclude how aging affects muscle-tendon complex properties.

This study was set to examine differences in Achilles tendon properties and triceps surae muscle architecture between healthy old and young individuals. Both men and women were studied because of possible sex differences in tendon properties (45), and a substantially larger sample size was used compared with previous studies to account for individual variation. Therefore, this study will significantly increase the knowledge on aging muscle-tendon complex. We hypothesized that Achilles tendon stiffness and Young's modulus would be lower, Achilles tendon CSA similar, triceps surae muscle size and pennation angle lower, and muscle fascicle length lower in gastrocnemius medialis but not in soleus in old compared with young individuals. We further hypothesize that men and women do not differ in muscle architecture, but women have lower tendon mechanical properties and smaller muscle size and tendon CSA.

METHODS

Subjects. Thirty-three 18- to 30-yr-old young (18 men and 15 women) and 67 70- to 80-yr-old elderly (33 men and 34 women) subjects were recruited to the study (Table 1). Young subjects were university students. Older subjects were recruited from the University of Third Age or from weekly meetings of retired people.

Using telephone interviews an equal number of healthy sedentary and active older subjects were recruited to obtain a representative sample of aged people with varying physical activity levels. Sedentary was defined as a person exercising for fitness and health one or less times per week. Active was defined as a person who exercised three or more times per week (30 min or more with intensity sufficient to cause sweating or breathlessness).

Subjects did not train for competitive sports or participate in other scientific studies at the time of testing. Subject exclusion criteria were Achilles tendon pain, history of Achilles tendon rupture or surgery, neurologic and progressive severe illnesses, insulin-treated diabetes, fracture within the previous year, immobilization for 1 wk during the last 3 mo, daily use of painkillers, use of immunosuppressive drugs or anticoagulants, medical treatment for cancer within the last year, severe visual or hearing impairment and mini mental state examina-

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Table 1. *Subject characteristics*

	Age, yr	Height, cm	Body weight, kg	BMI, kg/m^2	Plantarflexion MVC, N
Young (n = 33)	24.1 ± 2.4	174 ± 9**	69.5 ± 10.0	23.0 ± 2.3**	1,398 ± 356**
Old (n = 67)	74.6 ± 3.4	166 ± 9	69.8 ± 10.2	25.2 ± 2.6	859 ± 291
Men (n = 51)	56.8 ± 24.9	176 ± 6††	75.9 ± 8.1††	24.6 ± 2.7	1,210 ± 379††
Women (n = 49)	59.1 ± 23.4	161 ± 6	63.3 ± 7.8	24.4 ± 2.8	857 ± 347
YM (n = 18)	23.7 ± 2.0	181 ± 6	75.4 ± 9.0	23.1 ± 2.6	1,541 ± 376
OM (n = 33)	74.8 ± 3.6	173 ± 5	76.1 ± 7.7	25.4 ± 2.4	1,029 ± 232
YW (n = 15)	24.5 ± 2.8	166 ± 4	62.5 ± 5.6	22.8 ± 1.8	1,226 ± 246
OW (n = 34)	74.3 ± 3.3	159 ± 5	63.7 ± 8.6	25.1 ± 2.9	694 ± 246

Values are expressed as means ± SD. YM, young men; OM, old men; YW, young women; OW, old women; BMI, body mass index; MVC, maximal voluntary contraction. Asterisks are for young vs. old; daggers are for men vs. women: **, ††$P < 0.01$.

tion score of 23 or lower. Self-reported health status and medication were confirmed by a physician for the older subjects and a research nurse for the younger participants during a clinical examination.

Participants were informed about the procedures used in the study and they all signed a written consent prior to the study. The local ethical committee approved all methods and the study conformed to the standards set by the latest revision of the Declaration of Helsinki.

Measurements. Achilles tendon CSA and length, triceps surae muscle architecture and gastrocnemius CSA were first measured with ultrasonography (US; Aloka Pro Sound alpha 10). Achilles tendon mechanical properties where then measured in an ankle dynamometer during plantarflexion contractions using ultrasonography combined with motion analysis. All measurements were taken from the right leg by the same experienced researcher.

Achilles tendon cross-sectional area and length. Subjects lay prone on a table with the ankle kept at 90° by hand while Achilles tendon CSA was measured with a 3.6-cm linear probe (UST-5411, Aloka, Japan) and an acoustic gel pad (SonarAid, Geistlich Pharma). Ultrasound image of Achilles tendon CSA was taken at rest from transverse plane, four centimeters proximal from the proximal margin of calcaneal tubercle (Achilles tendon insertion site) which is approximately the narrowest site of free Achilles tendon (48). CSA was outlined using a polygon selection tool (Fig. 1). The most distal point of gastrocnemius medialis (GM) muscle-tendon junction (MTJ) and the distal insertion of Achilles tendon were visualized using ultrasonography and marked on to the skin. Achilles tendon resting length was measured as the distance between these two points using a ruler.

Muscle architecture. Muscle architecture was measured from GM and soleus (SOL) and the measurements were performed within 10 min of the subject lying down to prevent fluid redistribution affecting the results (10). Imaging was done at 50% of GM muscle length using a 6-cm linear probe (UST-5712, Aloka, Japan). Imaging locations were optimized for fascicle imaging and were mid muscle in the medial-lateral direction for both GM and SOL (22). For both muscles an acoustic gel was used between the skin and the probe, and the probe was held gently over the skin without applying pressure to the tissues underneath. From the images GM and SOL muscle thickness, fascicle length, and pennation angle were measured. Muscle thickness was measured by drawing a perpendicular line from the deep to superficial aponeurosis at the center of the image (Fig. 1). Muscle fascicle length was measured by drawing a line along a clearly visible muscle fascicle between deep and superficial aponeurosis. If the fascicle was not apparently straight, the curvature of the fascicle was taken into account by drawing the line with multiple points. If necessary, fascicle length was measured by extrapolating the excursion of the fascicle from superficial to deep aponeurosis (15). Fascicle pennation angle was measured as the angle between muscle fascicle and deep aponeurosis. Normalized fascicle length in the direction of muscle pull (referred to later as normalized fascicle length) was calculated by multiplying fascicle length with cosine of the pennation angle divided by the length of the tibia measured with a ruler. This allowed us to compare the functional fascicle length between the study groups.

Muscle anatomical CSA. Gastrocnemius (lateral and medial head) anatomical CSA was measured at 50% of GM length using panoramic US-scan with a 3.6-cm linear probe (UST-5411, Aloka, Japan). This method has been described and validated for quadriceps muscles, and is reproducible and suitable for group comparisons (2). A sequence of images was taken in extended field-of-view mode and the ultrasound device combined these images to one panoramic view of the gastrocnemius muscles. Soleus muscle was not included in the muscle cross-sectional measurement because the borders of that muscle are hard to identify from panoramic images, especially from older subjects. For the CSA analyses a polygon selection tool was used to outline the muscles manually (Fig. 2).

Image analysis for tendon morphology, muscle architecture, and muscle CSA were made using an open source computer program (ImageJ 1.44b, National Institutes of Health). Analyses were done twice by the same investigator on separate days, and a mean was used for further analysis (intraclass correlation ranged from 0.910 to 0.996 and typical error ranged from 0.9 to 6.5%).

Tendon mechanical properties. Plantarflexions were performed in a custom-made dynamometer (University of Jyväskylä) operated in a fixed position (48). Subjects were seated in the dynamometer with the right ankle at 90° of flexion, knee fully extended and hip at 60° of

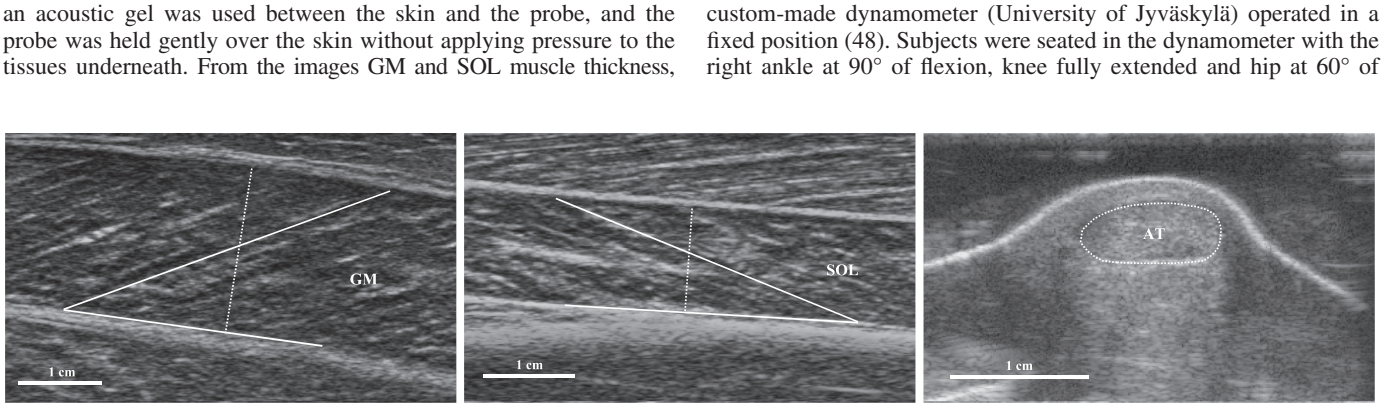

Fig. 1. From *left* to *right*: gastrocnemius medialis (GM) muscle architecture, soleus (SOL) muscle architecture and Achilles tendon (AT) cross-sectional area (outlined). Fascicle length (solid line along fascicles), pennation angle (angle between solid lines) and muscle thickness (dotted line) are drawn in the images of GM and SOL. The images shown are from a young woman.

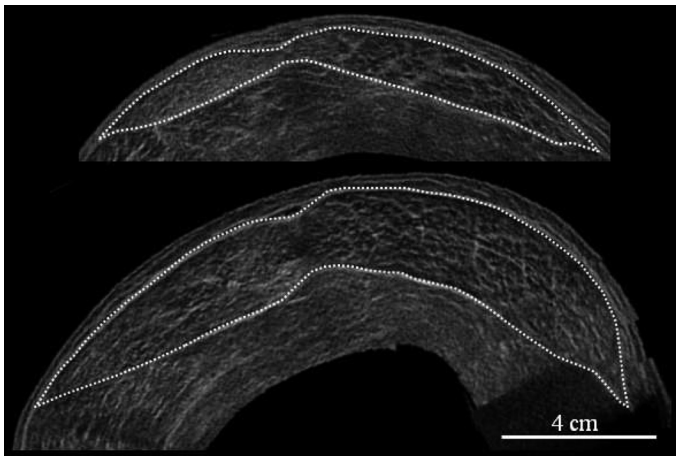

Fig. 2. Gastrocnemius muscle cross-sectional area outlined from an old (*top*) and a young (*bottom*) male subject.

flexion (full extension 0°). The seat was set individually as close to the pedal as possible in knee extended position, which minimized ankle joint rotation during maximal plantarflexion as the subject was tightly fixed between the pedal and the back rest. Velcro straps held knee extended and foot attached to the pedal. A monitor was placed in front of the subjects where they could follow the force signal in real time.

In practice trials subjects performed a series of plantarflexions by pushing the pedal with the ball of their foot following verbal commands. Each contraction in the series lasted for 1 s with rise and fall of the force occurring at the same rate. These contractions have been shown to provide better reproducibility of force production than slower contractions without affecting stiffness or hysteresis (47). Two to three sets of five to eight contractions were performed with an instruction to use half of their maximal force. Maximal voluntary contraction (MVC) force of the plantarflexors was measured three times (3-s contractions) with strong verbal encouragement. The maximal reaction force of the pedal obtained in MVC measurements is hereafter referred to as MVC force.

The best MVC was used to calculate 80% of MVC force. Practice trials and MVC measurements were considered to stabilize Achilles tendon mechanical properties before the actual measurement (32). Tendon properties were calculated from a set of five to eight plantarflexions to a peak force level of at least 80% MVC (Fig. 3). A horizontal line on the screen at the 80% MVC level served as a visual guide.

To derive the force-elongation relationship of the Achilles tendon, plantarflexion force, heel displacement, MG MTJ displacement and movement of the ultrasound probe were simultaneously measured and synchronized with a TTL pulse as described later. The tendon stress-strain relationship was calculated using the tendon force-elongation relationship and anthropometric data.

Plantarflexion force was measured with a force transducer (Precision TB5-C1, Raute, Nastola, Finland) installed to the pedal of the dynamometer. Force signals were sampled with a 16-bit AD-board (Power 1401, CED) at 1 kHz. Achilles tendon force was calculated by multiplying the measured reaction force with the ratio between the externally measured lever arms of the foot and the Achilles tendon. For measuring foot lever arm, subjects placed their right foot on to a paper that had a scale printed on it. The foot longitudinal axis was perpendicular to the scale. The vertical projections of the outermost tip of the medial malleolus and the head of the first metatarsal were marked on to the paper and the distance between these point was determined as the lever arm of the foot. Achilles tendon lever arm was defined as the distance from the center of the Achilles tendon to the outermost tip of the medial malleolus in sagittal plane measured using a ruler.

Displacement of the both ends of the Achilles tendon during the trials was measured to determine Achilles tendon length. The displacement of the distal end of the Achilles tendon in the sagittal plane was measured using a potentiometer installed under the heel with a sampling frequency of 1 kHz. The potentiometer measures the linear distance of the heel from the pedal and is able to detect heel displacement of under 0.1 mm. The displacement of the proximal end of the Achilles tendon was recorded with US at a sampling frequency of 70 Hz using a 6-cm linear array probe (UST-5712, Aloka, Japan). The probe was positioned over the GM MTJ, 2 cm medial from the border between medial and lateral gastrocnemius and secured with an elastic band. An acoustic gel pad (SonarAid, Geistlich Pharma) was used between the probe and the skin. Automatic tracking software was used to analyze MTJ displacement in the US image. The software is based on a pyramidal implementation of the Lukas-Kanade feature tracking (8). Nine tracking points were placed along the aponeurosis between GM and SOL, just proximal to the GM MTJ. The tracking algorithm has been previously shown to have a repeatability of 98% (35). Trials were analyzed twice and the mean was used for further analyses.

2D motion analysis was performed to measure the small movement of the ultrasound probe in the sagittal plane. Four reflective markers were placed on the handle of the probe to enable tracking of linear and rotational movements. A single high-speed video camera (InLine 250, Fastec Imaging) recorded movement perpendicular to the axis of motion at 60 Hz. The reflective markers were digitized from the video files using Peak Motus 2000 software (Peak Performance Technologies) and their location in relation to the laboratory coordinate system was determined using a rigid calibration object.

Tendon length during the trials was quantified by combining GM MTJ displacement in ultrasound frame, ultrasound probe movement, and heel displacement. GM MTJ location at the ultrasound image coordinate system was transformed to laboratory coordinate system using the location and orientation information of the ultrasound probe obtained from motion analysis. The location of the Achilles tendon insertion to the calcaneus in laboratory coordinate system was determined using the data from potentiometer and the measured distance from under the foot to the proximal margin of calcaneal tubercle. As both ends of the MG, tendon was determined in the same coordinate system; it was possible to determine the tendon length as the distance between those two points and elongation by subtracting tendon length at rest. Data synchronization and calculations were made in Matlab software (version R2010b9, The MathWorks) using custom-made

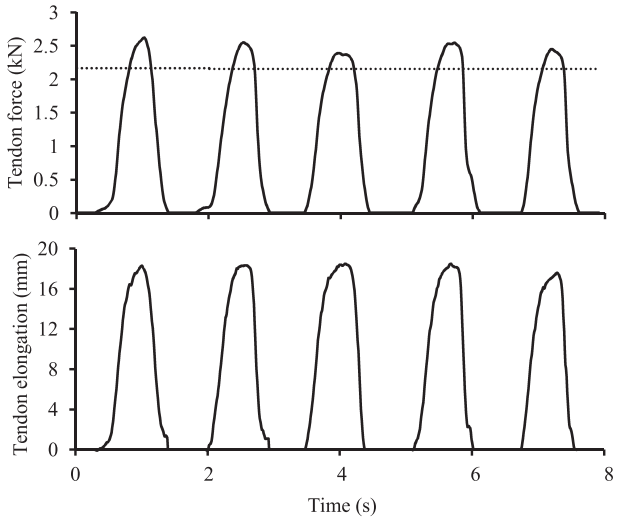

Fig. 3. An example of a trial from which tendon properties were calculated. Tendon force at the top and tendon elongation at the bottom. Horizontal line marks the 80% maximal voluntary contraction (MVC) force level.

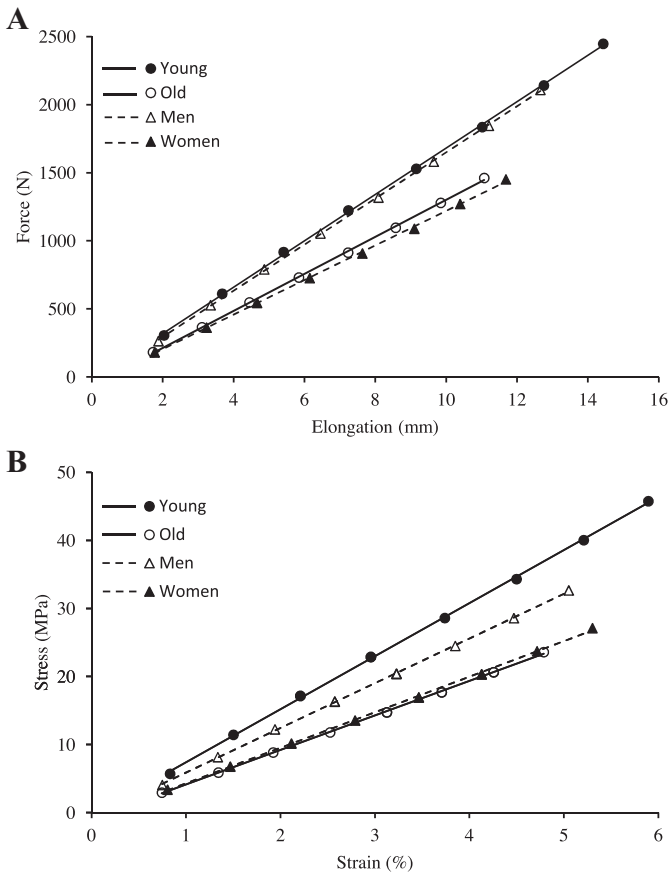

Fig. 4. Mean Achilles tendon force-elongation (*A*) and stress-strain (*B*) plots for young ($n = 33$), old ($n = 67$), men ($n = 51$), and women ($n = 49$). Lines are linear fits and represent Achilles tendon stiffness and Young's modulus, respectively. Values are calculated at 10% MVC increments from 10 to 80% MVC.

scripts. For each of the contractions, tendon force and elongation data were time normalized and averaged to produce one force-elongation relationship for every subject.

Tendon stiffness and Young's modulus were calculated between 10% and 80% of MVC force. This range was chosen since it was not possible for the subjects to produce MVC force with repeated contractions. Within this region, force-elongation curves were linear (Fig. 4*A*; $r = 0.999$). Stiffness was calculated as the slope of the force-elongation relationship and Young's modulus as the slope of the stress-strain relationship using the least-squares fit method. Stress was calculated by dividing tendon force by free tendon CSA (measurement described earlier), and strain was calculated by normalizing tendon elongation to tendon length at rest. Tendon hysteresis was calculated by using the full force-elongation curves and was defined as the percentage difference in the area under the curve for the loading and unloading phases.

Statistical analyses. Differences between the study groups (old vs. young and men vs. women) were tested using two-way ANOVA. Age, sex, and the age × sex interaction were considered independent variables. Homogeneity of variances was tested using Levene's test and normality of distributions was tested using Kolmogorov-Smirnov test. If homogeneity or normality assumptions were violated, the results of the variance analysis were confirmed using nonparametric tests. Only the results from variance analysis are reported since the results from nonparametric tests were in accordance with the variance analysis. For comparing tendon elongation and strain between the groups in similar absolute force values we chose to use a value that has real life relevance and used the mean peak Achilles tendon force value reported for walking (16) that is 1.32 kN. For comparison of tendon stiffness and Young's modulus between young and old subjects with similar muscle strengths we used subjects that had MVC force at a range mean ± SD of MVC forces of the whole population. Student's two-tailed independent samples *t*-test was used for this comparison. The degree of association between variables was tested using Pearson's product-moment correlation. The level of statistical significance was set at $\alpha = 0.05$ for all tests.

RESULTS

Significant interactions between age and sex were not found for any variables. The individual group means are presented in the Tables 1, 2, and 3.

Muscle architectural features and size. SOL pennation angle was larger in men compared with women (18%, $P < 0.001$). Fascicle length in GM was shorter in old compared with young (7%, $P < 0.05$). Muscle thickness was significantly lower in old compared with young in SOL and in GM (9%, $P < 0.05$ and 13% and $P < 0.001$, respectively). Gastrocnemius muscle CSA was 15% smaller in old compared with young subjects ($P < 0.01$) and 12% smaller in women compared with men ($P < 0.01$, Table 3). GM and SOL normalized fascicle length was significantly different between men and women (GM 0.108 ± 0.020 vs. 0.118 ± 0.021, $P < 0.05$; SOL 0.094 ± 0.020 vs. 0.116 ± 0.030, $P < 0.01$), but there was no difference between young and old (GM 0.115 ± 0.020 vs. 0.112 ± 0.022, $P = 0.327$; SOL 0.103 ± 0.028 vs. 0.106 ± 0.027, $P = 0.548$).

Tendon properties. Achilles tendon CSA was 16% larger in old compared with young subjects ($P < 0.001$) and 21% larger in men compared with women ($P < 0.001$, Table 2). Achilles tendon stiffness was lower in old compared with young subjects (17%, $P < 0.01$) and women compared with men (25%, $P < 0.001$). Young's modulus was lower in old compared with young subjects (32%, $P < 0.001$) and women compared with men (19%, $P < 0.01$ Fig. 4, Table 3). There was a significant

Table 2. *Achilles tendon properties*

	Resting length, cm	CSA, mm^2	Stiffness, N/mm	Young's Modulus, GPa	Hysteresis, %
Young ($n = 33$)	18.7 ± 2.6*	53.49 ± 9.75**	170 ± 37**	0.79 ± 0.20**	3.0 ± 5.2
Old ($n = 67$)	17.4 ± 2.6	61.98 ± 12.64	141 ± 48	0.54 ± 0.18	2.5 ± 5.1
Men ($n = 51$)	19.2 ± 2.4††	64.58 ± 12.79††	171 ± 45††	0.68 ± 0.22††	2.3 ± 4.2
Women ($n = 49$)	16.3 ± 2.0	53.56 ± 9.09	129 ± 38	0.55 ± 0.21	3.1 ± 5.9
YM ($n = 18$)	19.7 ± 2.6	56.53 ± 9.64	186 ± 37	0.86 ± 0.20	1.4 ± 3.7
OM ($n = 33$)	19.0 ± 2.2	68.97 ± 12.24	164 ± 47	0.59 ± 0.17	2.8 ± 4.4
YW ($n = 15$)	17.4 ± 1.9	49.84 ± 8.83	151 ± 29	0.71 ± 0.18	5.0 ± 6.0
OW ($n = 34$)	15.9 ± 1.9	55.20 ± 8.83	120 ± 39	0.48 ± 0.18	2.3 ± 5.7

Values are expressed as means ± SD. CSA, cross-sectional area. Asterisks are for young vs. old; daggers are for men vs. women: *$P < 0.05$; **, ††$P < 0.01$.

Table 3. *Muscle architectural features and gastrocnemius cross-sectional area*

	SOL angle, °	SOL fl, mm	SOL thickness, mm	GM angle, °	GM fl, mm	GM thickness, mm	G CSA, cm^2
Young (n = 33)	20.24 ± 5.47	41.10 ± 9.91	13.85 ± 2.63*	24.90 ± 3.95	47.51 ± 6.68*	19.73 ± 2.64*	22.56 ± 4.69**
Old (n = 59/67)	18.77 ± 4.36	39.84 ± 7.90	12.54 ± 2.99	23.78 ± 3.96	43.96 ± 7.17	17.18 ± 2.72	19.13 ± 4.42
Men (n = 48/51)	21.12 ± 4.63††	39.36 ± 8.01	13.56 ± 2.66†	24.57 ± 4.13	45.97 ± 7.33	18.59 ± 3.18†	21.54 ± 4.90††
Women (n = 44/49)	17.32 ± 4.20	41.22 ± 9.23	12.40 ± 3.12	23.65 ± 3.80	44.09 ± 6.89	17.37 ± 2.52	18.89 ± 4.27
YM (n = 18)	20.92 ± 5.82	40.67 ± 9.04	14.26 ± 2.63	25.04 ± 4.05	47.70 ± 6.84	20.17 ± 2.54	24.35 ± 4.61
OM (n = 30/33)	21.17 ± 3.94	38.72 ± 7.47	13.15 ± 2.62	24.40 ± 4.18	45.25 ± 7.61	17.81 ± 3.22	20.12 ± 4.46
YW (n = 15)	19.46 ± 5.12	41.58 ± 11.12	13.38 ± 2.64	24.74 ± 3.96	47.30 ± 6.74	19.23 ± 2.74	20.54 ± 4.01
OW (n = 29/34)	16.21 ± 3.21	41.04 ± 8.30	11.88 ± 3.26	23.17 ± 3.68	42.67 ± 6.56	16.55 ± 1.95	18.16 ± 4.23

Values are expressed as means ± SD. Number of subjects (n), SOL/GM; SOL/GM angle, soleus/gastrocnemius medialis pennation angle; fl, fascicle length; G CSA, gastrocnemius muscle cross-sectional area. Asterisks are for young vs. old; daggers (†) are for men vs. women; *, †, ‡$P < 0.05$; **, ††$P < 0.01$.

difference in elongation and strain at 80% MVC force between old and young subjects (old vs. young: 11.1 ± 3.4 vs. 14.4 ± 3.1 mm, $P < 0.001$ and 4.8 ± 1.5 vs. 6.0 ± 1.5%, $P < 0.001$), but not between men and women (men vs. women: 12.7 ± 3.3 vs. 11.7 ± 3.9 mm, $P = 0.451$ and 5.1 ± 1.4 vs. 5.3 ± 1.8%, $P = 0.191$). We also compared elongation and strain at tendon force of 1.32 kN corresponding to the peak tendon force in walking (16) and found that there was a significant difference between old and young and between men and women in both elongation and strain (old vs. young: 9.6 ± 2.4 vs. 8.1 ± 2.4 mm, $P < 0.01$ and 4.1 ± 1.0 vs. 3.4 ± 1.3%, $P < 0.01$; men vs. women: 8.4 ± 2.4 vs. 9.9 ± 2.3 mm, $P < 0.01$ and 3.4 ± 1.0 vs. 4.5 ± 1.1%, $P < 0.001$). Stress at MVC force was lower in old compared with young (29.6 ± 9.5 vs. 57.9 ± 14.7 MPa, $P < 0.001$) and women compared with men (35.2 ± 17.5 vs. 42.6 ± 17.0, $P = 0.05$). When comparing old and young subjects with similar MVC forces (at a range mean ± SD, old n = 50 and young n = 19), we observed similar stiffness (old vs. young: 153 ± 42.9 vs. 151 ± 29.0 N/mm, $P = 0.861$) but significantly different Young's modulus (old vs. young: 0.58 ± 0.17 vs. 0.73 ± 0.17 GPa, $P = 0.001$, Fig. 5).

Maximal isometric force. MVC force was 39% lower in old compared with young subjects (859 ± 291 vs. 1,398 ± 356 N, $P < 0.001$) and 29% lower in women compared with men (857 ± 347 vs. 1,210 ± 379 N, $P < 0.001$).

Associations between variables. The correlation coefficient between tendon stiffness and MVC force and between Young's modulus and MVC force was significant in combined data (r = 0.580, $P < 0.001$ and r = 0.561, $P < 0.001$, respectively; Fig. 5). In old subjects there was a significant correlation between stiffness and MVC (r = 0.549, $P < 0.001$) and between Young's modulus and MVC (r = 0.376, $P = 0.01$). In young subjects a significant correlation was found between stiffness and MVC (r = 0.535, $P = 0.001$). Tendon stiffness correlated significantly with gastrocnemius muscle CSA and body weight (r = 0.219, $P < 0.05$ and r = 0.278, $P < 0.01$, respectively), but Young's modulus was not correlated with either muscle CSA or body weight. Neither MVC force nor gastrocnemius muscle CSA was associated with tendon CSA.

DISCUSSION

This study provides novel information about changes in the muscle-tendon complex due to aging with the largest number of subjects to date measured with state-of-the-art methods of determining tendon properties. There were four main findings from this study: *1*) Achilles tendon stiffness and Young's modulus were lower in healthy old men and women compared with young subjects; *2*) Achilles tendon CSA was larger in old compared with young subjects despite lower tendon stiffness, maximal plantarflexion force, and gastrocnemius muscle CSA; *3*) Achilles tendon mechanical properties correlated with muscle force-producing capacity even in old age; and *4*) Achilles tendon stiffness did not differ between young and old individuals with similar strengths.

Achilles tendon CSA. To our knowledge the current study is the only one to show larger Achilles tendon CSA in old men and women compared with young. Our finding is supported by a previously study by Magnusson et al. (34) that showed larger Achilles tendon CSA in old compared with young women using MRI. The observed difference in tendon CSA in the current study cannot be attributed to body weight or tendon length, since body weight was similar between old and young and tendon length was smaller in old compared with young. Habitual exercise-related tendon hypertrophy (27, 51) also

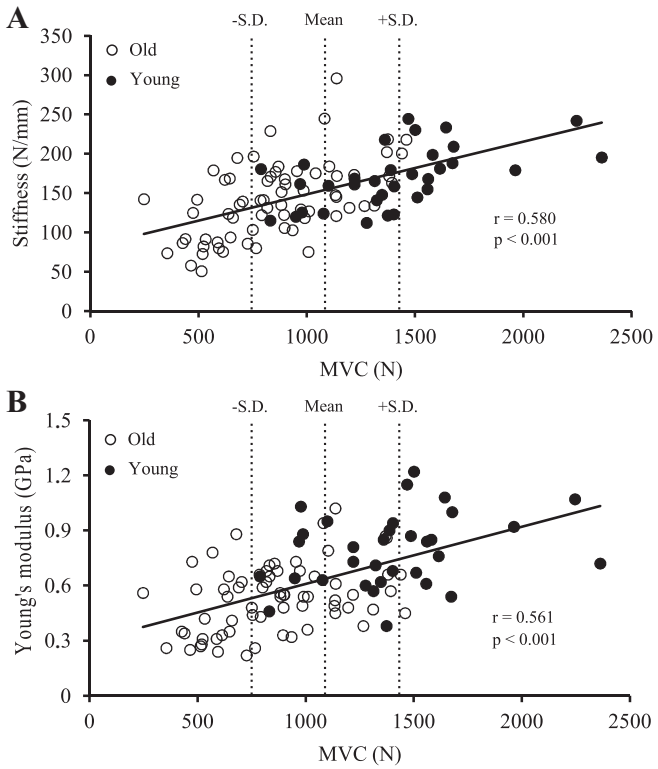

Fig. 5. Correlations between MVC force and stiffness (*A*) and MVC force and Young's modulus (*B*). Mean ± SD range of MVC force is marked with dotted lines. Within that range tendon stiffness did not differ, but Young's modulus was significantly different between young and old subjects.

seems an unlikely explanation because aging is associated with a decrease in moderate to vigorous physical activity (6) and the magnitude of tendon loading seems to be a key factor related to adaptive responses (4). One possibility is that a decrease in the loading of the tendon could increase extracellular water content and thus increase tendon CSA in old subjects (26). Another possible explanation for larger tendon CSA in old subjects is that pathological processes related to high levels of circulating cholesterol (7) could cause a large decrease in tendon material properties that has to be compensated by increased tendon CSA to maintain appropriate tendon stiffness. Some of the old subjects used statin medication for high levels of cholesterol, but we did not observe a difference in tendon CSA between statin users and nonusers (users: 19 old men and 13 old women). In women, estradiol concentration can affect tendon dimensions (17) and prevention of decrease in estradiol concentration by hormone replacement therapy (HRT) might hinder the growth of tendon CSA in older women. In the current study six old women reported receiving HRT and exclusion of those women would increase the mean value of tendon CSA from 55.20 to 56.01 mm^2. Finally, an age-related increase in tissue dimensions is also evident in other connective tissue structures, such as increased endosteal and periosteal diameter of the proximal femur in connection with decreased bone mass (3), which preserves bone strength and is also inversely related to estradiol levels (1), as is tendon CSA (17).

Muscle architecture and size. The trends found in muscle architecture are consistent with previous results that have found age-related differences in triceps surae muscle architecture (38, 40, 43). Although we found statistically significant differences between old and young only from GM fascicle length, the lack of other age-related differences in muscle architecture is supported by the findings of Karamanidis and Arampatzis (23, 24). Similar normalized fascicle lengths in GM and SOL between young and old suggest similar capability for muscle shortening and thus similar working range of triceps surae muscles between these groups. Muscle size was significantly lower in old compared with young as indicated by lower muscle thickness in SOL and in GM and lower gastrocnemius CSA. In general it seems that the muscle architecture of triceps surae in older subjects in this study was quite well preserved despite marked changes in muscle force and size. In conjunction with previous literature, our findings suggest that there is a trend for decreased pennation angle and muscle fascicle length with aging but these changes are necessary to maintain functionality of the muscle as muscle size decreases. Discrepancy in previous findings is probably caused by differences in subjects groups. The old subjects in this study were all living independently and attending regularly in social activities and thus do not represent the most frail elderly people.

Achilles tendon mechanical properties. Our findings of age-related differences in Achilles tendon mechanical properties are in accordance with the studies that measured Achilles tendon elongation as a displacement of GM myotendinous junction (39, 44). The studies that have reported similar Achilles tendon properties in old and young subjects have measured the elongation as the elongation of outer tendon and aponeurosis (23, 25). This methodological difference can be the factor causing this discrepancy. Two studies have examined age-related differences in patella tendon properties measuring only the outer tendon (9, 11), and both fail to find differences between old and young in tendon mechanical properties. It is possible that Achilles and patella tendon respond to aging differently as they are morphologically and functionally different. We admit that SD in mean values of hysteresis was large although similar than previously reported (13, 31), causing statistical power to detect group differences to be low. The differences in group means were not large enough to have any real life significance, and thus it can be concluded that the hysteresis values were similar between age groups and sexes. The mean hysteresis for the whole population was 2.7%, which is smaller than reported previously in vivo (13, 19, 31, 55). We did not observe a toe region, and the tendon force-elongation relationship was linear in the region where tendon properties were calculated (10–80% MVC, $r = 0.999$). This was probably due to initial force acting on the Achilles tendon in the seated position and the fact that we excluded the lowest 10% of MVC force from the stiffness and Young's modulus analysis. The relatively small values of hysteresis may thus be due to the fact that the crimped pattern of collagen fibers was already straightened in this joint configuration. In this experimental setting, the Achilles tendon acted almost totally elastically without a viscous component that would increase hysteresis.

When we compared young and old individuals with similar force production capacity we found that tendon stiffness was similar. We also found that tendon stiffness and Young's modulus correlated with muscle strength which has been previously shown in young (54). These findings indicate that aging does not affect the tendon's ability to adjust its mechanical properties to the requirements set by the muscle, but it may be that the strategy for the adjustment is changed due to aging, as tendon CSA was higher in old subjects. Increasing tendon CSA does not seem to be the mechanism for relatively fast adaptation of mechanical properties (28, 52) but might be involved in habitual loading (12, 27) and aging. Finally, lower stress and strain in old compared with young subjects at similar relative force levels may decrease the likelihood of tendon injury in old individuals.

Implications of different tendon properties between young and old. We hypothesize that in low-loading situations such as in walking the lower Achilles tendon stiffness in old individuals allows more elastic energy utilization, muscle fascicles to operate closer to the optimal length and slower speed of fascicle length change when triceps surae muscles are active than if they had similar tendon stiffness as young. Since the amount of elastic energy stored in tendon is $E = 1/2\, kx^2$ (where k is stiffness and x is elongation), the tendon with smaller stiffness loaded with equal force will store more energy. The amount of energy the tendon releases at unloading is dependent on hysteresis and there is no evidence that hysteresis is different between old and young. It has been estimated that in young, muscle fascicles of GM work at slightly longer length than optimal in walking (5, 20), and it could be that the lower Achilles tendon stiffness in old individuals allows muscle fascicles to shorten the amount needed to reach optimal length. In gastrocnemius lateralis, it has been shown that in walking when the muscle is active, fascicle length remains unchanged in older subjects and lengthens in younger subjects (37). Slower contraction velocity is beneficial for the force generation according to the force-velocity relationship. These hypotheses are logical since older individual are likely to use only walking for ambulation and young individuals are more likely

to use both walking and running and the differences in tendon properties would reflect adaptations to the tasks of daily living. Further studies are needed to verify these hypotheses.

Methodological aspects. One of the strengths of this study is that the sample size is the largest to date for studies that have measured tendon properties in vivo. This is important for group comparisons of measures that have large individual variation. State-of-the-art methods were also used to measure Achilles tendon properties. The method combines ultrasonography, motion analysis, heel movement measurement, and force measurement to obtain tendon force-elongation data. A similar method was recently suggested for measuring tendon properties in vivo (21). This method accounts for possible probe movement or heel movement during contractions, which can result in 40% and 30% overestimations of tendon elongation, respectively (21, 33). Strain rate was also matched between young and old subjects to prevent this parameter from influencing tendon properties (46).

Calculation of Achilles tendon force is problematic because not all the plantarflexion force is transmitted through the Achilles tendon, and coactivation of dorsiflexion muscles would decrease measured plantarflexion force and thus calculated Achilles tendon force. Estimation of the proportion of force that is transmitted through the Achilles tendon is difficult because of possible individual variations in plantar flexor activation strategies (14). In this study there was no attempt to correct for coactivation of tibialis anterior or other muscles for several reasons. In a study conducted in our lab coactivation was always less than 5% during isometric plantarflexion (48). Further, the correction of coactivation-induced force relies on the assumption that force and surface EMG are linearly related, which may not be the case (30). Several muscles contribute to ankle joint torque, and it is not possible to measure the activity of them all. We used relatively fast contractions for the measurements of tendon properties and thus we could not average EMG activity over a sufficiently long time period to obtain reliable measures of muscle activity. Finally, correction of the coactivation of muscles requires measurement of force-EMG relationship and it can be assumed that there is also coactivation in several muscles when trying to measure this relationship. Besides the beforementioned facts tendon force calculation relies on knowledge of the lever arms' lengths. The joint rotations observed in this study would cause only negligible changes in Achilles tendon lever arm length (29) and foot lever arm length was confirmed in a pilot study using plantar pressure measurement (Pedar-X, Novel). Thus constant lever arm lengths were considered sufficient approximation for this study.

Future studies and conclusions. Muscle and tendon interaction and the effects of tendon properties on muscle function warrant more attention. In particular it would be interesting to investigate how changes in tendon properties due to training or aging relate to muscle function and economy in different types of movement and in different age groups. In future studies it would also be interesting to examine whether tendon adaptation mechanisms are different between young and old people and to clarify why aging seems to be related to an increase in tendon dimensions.

In conclusion, we showed that there can be substantial age-related differences in tendon properties with only minor differences in muscle architecture. This will probably have effects on the muscle-tendon complex function between young and old people in activities requiring approximately similar force production but not in activities where similar muscle forces are used in relation to the muscles force production capacity. We suggest that discrepant finding for age-related differences in tendon are due to methodological differences and for muscle architecture possible differences in subject groups. It seems that muscle architecture or tendon properties are not responsible for functional deficit in older people. Muscle size and intrinsic properties of muscle tissue are likely to be the main causes of lowered functional capacity. Although it was shown that Achilles tendon stiffness and Young's modulus are lower in older participants, it may be that tendon tissue is optimized to functional requirements rather than deteriorated. The current results suggest that tendon mechanical properties are matched to the force producing capacity of the muscle and adapt to loading rather than the effects of aging. Tendon stiffness was shown to be strength dependent but age independent. In the case of Achilles tendon, changes in tendon properties with aging may actually enhance the function of the muscle-tendon complex in low-loading conditions such as walking.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: L.S., S.S., and T.F. conception and design of research; L.S. performed experiments; L.S., J.P., and N.J.C. analyzed data; L.S. interpreted results of experiments; L.S. prepared figures; L.S. drafted manuscript; L.S., J.P., N.J.C., S.S., and T.F. approved final version of manuscript; J.P., N.J.C., S.S., and T.F. edited and revised manuscript.

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