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Slower Walking Speed in Older Men Improves Triceps Surae Force Generation Ability

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Abstract

Purpose: Older adults walk slower than young adults, but it is not known why. Previous research suggests that ankle plantarflexors may have a crucial role in the reduction of walking speed. The purpose of this study was to investigate age-related differences in triceps surae muscle–tendon function during walking to further investigate the role of plantarflexors in the age-related reduction of walking speed. **Methods:** Medial gastrocnemius and soleus muscle fascicle lengths were measured using ultrasound imaging during walking from 13 young (25 ± 4 yr) men at preferred walking speed and from 13 older (73 ± 5 yr) men at preferred speed and at the young men's preferred speed. Muscle–tendon unit lengths were calculated from joint kinematics, and tendinous tissue lengths were calculated by subtracting muscle lengths from muscle–tendon unit lengths. In addition, ground reaction forces and electromyographic activity of medial gastrocnemius and soleus were measured. **Results:** In both medial gastrocnemius and soleus, it was observed that at preferred walking speed, older men used a narrower muscle fascicle operating range and lower shortening velocity at the estimated time of triceps surae peak force generation compared with young men. Fascicles also accounted for a lower proportion of muscle–tendon unit length changes during the stance phase in older compared with young men. Significant differences in triceps surae muscle function were not observed between age groups when compared at matched walking speed. **Conclusions:** In older men, walking at preferred speed allows triceps surae muscles to generate force with more favorable shortening velocity and to enhance use of tendinous tissue elasticity compared

with walking at young men's preferred speed. The results suggest that older men may prefer slower walking speeds to compensate for decreased plantarflexor strength.

Key Words: aging, ultrasound, fascicle, tendon, gastrocnemius, soleus

Older adults tend to walk slower than young adults. The slowing of preferred walking speed is a well-established feature of aging, and although several mechanisms have been proposed to explain the age-related reduction in the preferred walking speed, a consensus has not been reached (29).

Preferred walking speed is a good predictive tool of health-related outcomes in older adults (22). It predicts adverse health outcomes (32), development of mobility disability (1), and mortality (40). Thus, it would be of interest to better understand the causes of the reduction in preferred walking speed with aging.

Reduced ankle plantarflexion peak power in the late push-off phase of walking is a consistent finding in both healthy and mobility-limited older compared with young adults (10,23,30), and it seems that impairments in plantarflexor force and power generation contribute to a reduction in preferred walking speed in older adults (29). Tendinous tissues (TT; tendon and aponeurosis) elasticity greatly affects muscle function of the main plantarflexor, triceps surae, because of a large tendon to muscle fiber length ratio (41). Using ultrasound imaging, it has been revealed that TT elasticity is used in triceps surae to enhance power generation during the push-off phase of walking (11,21).

On the basis of previous modeling and experimental studies, there seems to be an optimal TT stiffness to maximize muscle efficiency or power generation in cyclic contractions (24,27). Several *in vivo* human studies have linked aging with a decrease in Achilles tendon or triceps surae TT stiffness (9,20,28,34,38). Thus, age-related changes in triceps surae TT elastic properties may contribute to reduced plantarflexor performance in walking in older adults. In fact, we showed earlier that 6-min walking test results positively correlate with Achilles tendon stiffness in older adults (39). In addition, recent studies using ultrasound imaging and musculoskeletal modeling have started to unfold more complex interactions between Achilles tendon mechanical properties and triceps surae muscle function in which age-related Achilles tendon interfascicular adhesions coupling gastrocnemius and

soleus muscle function may contribute to the reduced plantarflexor performance in walking in older adults (15,16).

Two previous studies have examined differences in triceps surae muscle fascicle behavior between young and older adults in walking using ultrasound imaging. At the preferred walking speed of older adults ($1.1 \text{ m}\cdot\text{s}^{-1}$), Mian et al. (31) found that fascicle lengthening contributed less and TT lengthening more to muscle–tendon unit (MTU) lengthening in older compared with young adults in lateral gastrocnemius, which is consistent with the previously reported age-related decrease in Achilles tendon stiffness. Panizzolo et al. (36) exploited an approach where older adults walked at their preferred speed and in addition at a speed matched to the preferred speed of young adults. The results showed that soleus muscle fascicle length and length changes were similar between the groups when older adults were allowed to walk at their preferred speed. This result suggests adaptation of preferred walking speed in older adults to preserve soleus muscle fascicle mechanical behavior.

This study investigated triceps surae muscle–tendon function in young and older men to gain insight into the mechanisms that may underlie reduced plantarflexor force and power generation in older adults in walking and, therefore, possibly also reduced preferred walking speed. The purpose of the study was to compare triceps surae muscle–tendon function (fascicle length and velocity and TT length changes) between young and older men at matched (young men’s preferred walking speed) and preferred walking speeds. In addition, triceps surae muscle–tendon function was compared within older men between the two walking speeds. On the basis of previous literature, we hypothesized that when the groups were compared at matched walking speed, TT in triceps surae muscles would elongate more in older compared with young men because of lower stiffness, leading to greater muscle fascicle shortening amplitude and shortening velocity in older men to compensate for greater tendon stretch. We also hypothesized that when young and older men were compared at preferred walking speeds, there would be no differences in triceps surae muscle–tendon function between the groups.

Methods

Subjects.

Thirteen young (YOUNG, 20–31 yr old) and 13 older (OLDER, 67–81 yr old) men volunteered for the study. The sample size was considered sufficient based on previous study using similar methodology (36) providing approximately 80% statistical power. YOUNG were recruited using e-mail advertisements among university students, and OLDER were recruited from local meetings of older people. All subjects were community living and were able to walk without pain or discomfort. The

ethics committee of the University of Jyväskylä approved the study, and all participants signed an informed consent before participation in the study. The study was conducted according to the principles set by the Declaration of Helsinki.

Walking trials.

Subjects were asked to walk over a 10-m force platform at their preferred walking speed. They started walking 3 m before and stopped walking 3 m after the force platform to ensure that walking speed was stable over the force platform. The trials were timed using photocells at the start and end of the force platform, and the average walking speed was calculated from the measured time. The average walking speed of three consecutive trials with walking speeds within $\pm 5\%$ was defined as preferred walking speed. In addition to the preferred walking speed, OLDER performed trials at a speed that matched the mean preferred speed of YOUNG within $\pm 5\%$. Therefore, all YOUNG were tested before OLDER. In both preferred and matched speed trials, data were recorded from at least three trials. In addition, all subjects performed one trial with maximal walking speed from which only the time of the trial was recorded.

Muscle fascicle length and pennation angle.

Muscle fascicle length and pennation angle of medial gastrocnemius (MG) and soleus muscles were simultaneously measured. An ultrasound probe (7.5 MHz linear array probe with 60-mm field width; Telemed, EchoBlaster128, Lithuania) was attached over the MG muscle visualizing both MG and soleus muscles simultaneously (7). Images were collected at 80 Hz and stored on a PC. Muscle fascicle length and orientation and orientation of the aponeurosis between MG and soleus were tracked from the ultrasound images using an automatic tracking algorithm (8) in MATLAB (MathWorks Inc., Natick, MA). The algorithm produces the orientation of the tracked anatomical feature (fascicle or aponeurosis) in relation to the probe orientation. This information was used to calculate the pennation angle of the fascicles (angle between muscle fascicles and the aponeurosis). Soleus muscle fascicle data from one older subject were not analyzed because of inadequate image quality.

Reference lengths of muscle fascicles were measured in neutral anatomical position (knee extended and ankle angle at 90°) for the normalization of the fascicle lengths during walking. The reference lengths were measured three times in a resting condition while subjects were seated in a dynamometer, and the mean value was used for normalization. The neutral anatomical position was chosen for reference length measurements because it has been previously used to represent optimal fascicle length (26), i.e., the plateau region of the sarcomere force–length relationship. Operating length was defined as the normalized fascicle length at a specific instant of time or over a

time range, and operating range was defined as the range of normalized fascicle lengths over a given time range.

Maximal voluntary contraction force.

Plantarflexion maximal voluntary contraction force was measured at 2000 Hz (Cambridge Electronic Design, Cambridge, UK) in a custom-built dynamometer (University of Jyväskylä, Finland) where subjects were seated with knee extended and ankle angle at 90°. After a standardized warm-up, three isometric maximal voluntary contractions lasting approximately 3 s were performed. The highest force generation obtained was taken as plantarflexion strength. Force produced against the dynamometer's footplate was chosen as a measure of muscle strength rather than ankle joint moment because it was considered that this measure reflects the maximal capacity for force generation in the push-off phase of walking taking into account possible differences in forefoot length between the subjects.

MTU and tendon length.

During walking, sagittal plane ankle and knee joint angles were measured at 2000 Hz (Cambridge Electronic Design) using custom-built electrogoniometers (University of Jyväskylä, Finland) attached over the lateral side of the joints. MTU lengths for both MG and soleus were calculated from the joint kinematics using regression equations defined by Hawkins and Hull (18). TT (including both proximal and distal free tendon and aponeurosis) lengths for both MG and soleus were calculated as $L_{TT} = L_{MTU} - L_{FAS} \cos(\text{pennation angle})$, where L_{MTU} is MTU length and L_{FAS} is muscle fascicle length (17). MTU and TT lengths were normalized by dividing them by their corresponding reference lengths, which were determined in the same way as the muscle fascicle reference lengths.

Muscle activity.

To determine muscle activity in walking and in MVC tests, EMG was measured from MG and soleus using a telemetric EMG system (Noraxon Inc., Scottsdale, AZ). After shaving and preparing the skin with fine sandpaper and alcohol wipes, two electrodes (Ambu A/S, Ballerup, Denmark) were attached over the skin with 22-mm interelectrode distance according to SENIAM recommendations (19). The data were sampled at 1500 Hz, preamplified, and sent wirelessly to an A/D converter (Cambridge Electronic Design). EMG data from one older subject were lost because of technical problems in data collection.

Ground reaction forces.

Three-dimensional ground reaction force (GRF) values were recorded using two custom-built 10-m-long (University of Jyväskylä, Finland) force platforms positioned side by side that allowed reaction

forces to be measured separately for both legs. The data were collected at 2000 Hz (Cambridge Electronic Design). GRF values were normalized by dividing the forces by body weight.

Data analysis.

Data analyses were performed in MATLAB (MathWorks Inc.). All data were interpolated to 1000 Hz and synchronized. EMG data were band-pass filtered between 20 and 450 Hz using a fourth-order zero-lag Butterworth filter. GRF values were low-pass filtered at 40 Hz, and joint kinematics and ultrasound data were low-pass filtered at 15 Hz (fourth-order zero-lag Butterworth filter). Stride cycles were separated based on vertical GRF data and interpolated to 1000 data points. Data from each stride were averaged within a subject, and the mean data were used in further analysis. An exception to this was EMG data from which root mean squared (RMS) values during the stance and push-off phases were calculated from each stride, normalized to maximal 500-ms RMS obtained during MVC tests, and then averaged across strides. For visualization, moving 100-ms RMS windows were used to produce EMG envelopes. To calculate fascicle, MTU, and TT velocities, subject's mean data were interpolated back to units of time using the mean duration of the included strides, and velocities were calculated by numerical differentiation of lengths with respect to time.

The start of the push-off phase was identified from the anterior–posterior GRF as the instant at which the force changed from negative to positive. Selected variables were calculated from the whole stance phase (hereafter referred to as stance) or from the push-off phase (hereafter referred to as push-off). TT peak length was used as a surrogate measure of the instant of MTU peak force. TT maximal elongation was calculated as the difference between maximal and minimal length during the whole stride. Strain was calculated by dividing maximal elongation by TT reference length.

The number of strides included in the analysis per subject was 25 ± 7 , 28 ± 8 , and 23 ± 8 for YOUNG, OLDER preferred speed, and OLDER matched speed, respectively. A different number of strides were included from separate trials. To ensure that the reported walking speeds reflected the average stride of each individual, walking speed was calculated as the weighted mean of the trials where the number of included strides from each trial was used as the weights.

Statistical analysis.

Data were first checked for normality using the Shapiro–Wilk test and for homogeneity of variance using the Levene test. Differences between YOUNG and OLDER were tested using independent-samples t-test, and differences between preferred and matched speed within OLDER were tested using paired samples t-test. For nonnormally distributed variables, the Mann–Whitney U-test and the Wilcoxon signed rank test were used for between- and within-group comparisons, respectively. Associations between preferred walking speed and parameters related to triceps surae muscle–

tendon function were tested using the Pearson product–moment correlation. Regression analysis was used to test the effect of age on the associations. The level of statistical significance was set at $P < 0.05$. Statistical analyses were performed using IBM SPSS Statistics (version 20.0.0.2, IBM Corp., Armonk, NY).

Results

Subject characteristics.

Sample means of YOUNG and OLDER were relatively similar in height, but OLDER were slightly heavier and had higher body mass index compared with the sample means of YOUNG (Table 1).

OLDER were on average 32% weaker in body weight–normalized plantarflexion strength compared with the YOUNG (1.3 vs 1.9 N per body weight, $P = 0.001$). No significant differences were observed between YOUNG and OLDER in fascicle, MTU, or TT reference lengths that were used to normalize the data.

Table 1 Subject characteristics

	Young (n = 13)	Older (n = 13)
Age (yr)	25 ± 4	73 ± 5
Height (cm)	179 ± 6	176 ± 5
Body mass (kg)	79 ± 7	88 ± 9
BMI (kg·m ⁻²)	25 ± 2	29 ± 3
Plantarflexion strength (N per body weight)	1.86 ± 0.43	1.30 ± 0.33**
MG fascicle reference length (mm)	52.9 ± 8.6	49.1 ± 5.4
MG MTU reference length (mm)	477 ± 24	469 ± 24
MG TT reference length (mm)	427 ± 18	423 ± 22
Soleus fascicle reference length (mm)	45.0 ± 12.5	41.1 ± 5.0
Soleus MTU reference length (mm)	321 ± 16	316 ± 16
Soleus TT reference length (mm)	280 ± 18	281 ± 16

Values are expressed as mean ± SD. Sample descriptors (age, height, body mass, and BMI) were not statistically tested for group difference. BMI, body mass index.

**Significantly different from young adults ($P < 0.01$).

Spatiotemporal gait parameters.

Spatiotemporal parameters of walking are reported in Table 2. The preferred speed was 18% slower in OLDER compared with YOUNG ($P < 0.001$), but the matched speed in OLDER was similar to the preferred speed of YOUNG ($P = 0.946$). Similarly, other spatiotemporal gait parameters significantly differed between YOUNG and OLDER at preferred speed ($P < 0.05$) but not at matched speed ($P > 0.05$). Maximal walking speed was 13% slower in OLDER compared with YOUNG (2.01 ± 0.22 vs 2.31 ± 0.39 m·s⁻¹, $P = 0.024$).

Table 2 Spatiotemporal gait parameters

	Young Preferred	Older Preferred	Older Matched
Walking speed (m·s ⁻¹)	1.35 ± 0.16	1.11 ± 0.12**	1.35 ± 0.02††
Stride frequency (Hz)	0.92 ± 0.05	0.85 ± 0.06**	0.93 ± 0.05††
Stride length (m)	1.47 ± 0.14	1.30 ± 0.11**	1.46 ± 0.07††
Duty factor (% stride)	62.8 ± 1.0	64.2 ± 1.8*	63.3 ± 1.6††

Values are expressed as mean ± SD.

*Significantly different from young adults, P < 0.05.

**Significantly different from young adults, P < 0.01.

††Significantly different from older preferred, P < 0.01.

Muscle fascicle lengths.

In both YOUNG and OLDER, after initial shortening, MG fascicles were relatively isometric through the first half of stance after which the fascicles shortened during push-off. For soleus, fascicle shortening started earlier, already during the first half of stance. There was also more pronounced lengthening of soleus muscle fascicles during the first half of stance in OLDER, which was not evident in YOUNG (Fig. 1).

Muscle fascicle operating lengths are shown in Figure 2. Both MG and soleus muscles operated at a narrower range in OLDER compared with YOUNG in stance at preferred speed (MG = 7.5% ± 2.7% vs 12.0% ± 4.8% of reference length, P = 0.014; soleus = 4.9% ± 1.7% vs 8.5% ± 3.9% of reference length, P = 0.007). However, no significant differences were observed between the age groups at matched speeds. Also, operating ranges did not significantly differ between YOUNG and OLDER when calculated from push-off only. In OLDER, increase in walking speed significantly increased the operating range in MG both in whole stance and push-off, and in stance only in soleus (MG stance 7.5% ± 2.7% vs 9.3% ± 3.1% of reference length, P = 0.003, MG push-off 6.6% ± 2.6% vs 7.8% ± 3.1% of reference length, P = 0.016, soleus stance 4.9% ± 1.7% vs 6.5% ± 1.7% of reference length, P < 0.001).

YOUNG and OLDER did not significantly differ in mean fascicle length during stance or push-off or in fascicle lengths at peak TT length. In OLDER, walking speed did not have a significant effect on MG mean fascicle length during stance, MG, or soleus mean fascicle length during push-off or MG or soleus fascicle length at peak TT length.

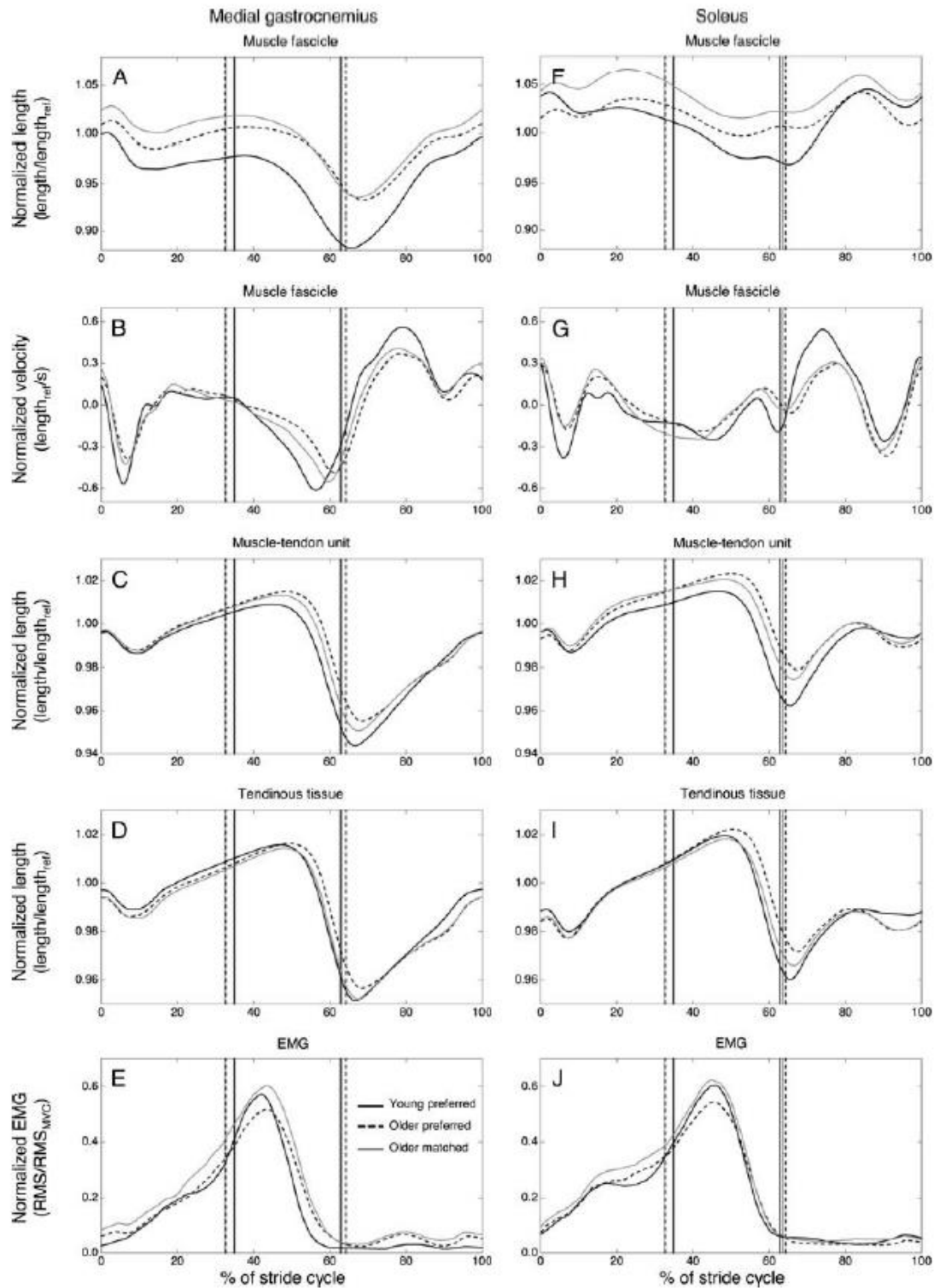


Figure 1 Group mean normalized muscle fascicle lengths (A, F) and velocities (B, G), MTU (C, H) and tendinous tissue lengths (D, I), and EMG (E, J) envelopes. The left column shows results from MG (A–E) and the right column from soleus (F–J). Vertical lines represent start of push-off phase and toe-off, respectively. SD values are omitted for clarity.

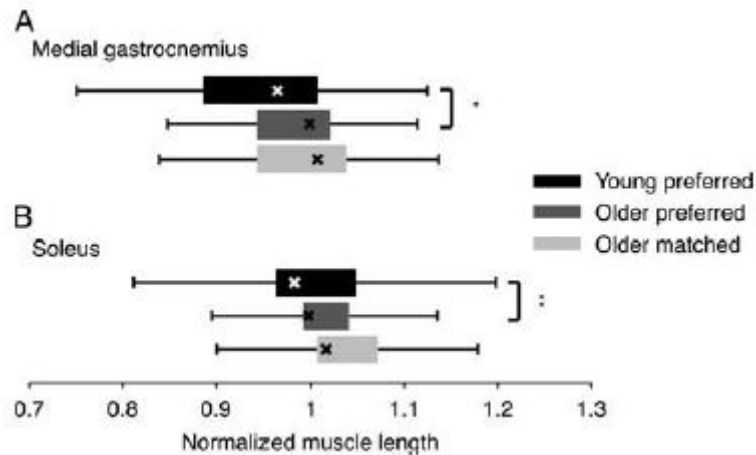


Figure 2 Normalized MG (A) and soleus (B) fascicle operating lengths during the stance phase. Whiskers represent the SD values of lower and upper limit. Crosses mark fascicle lengths at peak tendonous tissue elongation. Fascicle lengths are normalized to resting length at 90- ankle angle and knee extended.

MTU and tendonous tissues lengths.

MTU lengths were derived from joint angles, and thus joint angles are not separately reported. MTU peak length and length at toe-off were significantly longer in OLDER compared with YOUNG in both muscles at preferred speed (peak length: MG = 1.015 ± 0.009 vs 1.009 ± 0.010 , $P = 0.044$, soleus = 1.023 ± 0.011 vs 1.016 ± 0.014 , $P = 0.022$; length at toe-off: MG = 0.964 ± 0.013 vs 0.953 ± 0.113 , $P = 0.032$, soleus = 0.983 ± 0.014 vs 0.967 ± 0.0178 , $P = 0.021$), but the range during stance did not differ between the groups. At matched speed, no significant differences were observed between YOUNG and OLDER in MTU lengths or ranges. MG MTU range significantly increased in OLDER when walking speed was increased from preferred to matched (0.051 ± 0.012 vs 0.055 ± 0.012 , $P = 0.043$).

TT maximal elongation and strain did not differ between the groups, nor did they change with speed in OLDER. Pooling the data from both groups and both speeds of OLDER resulted in the following mean TT maximal elongation and strain values: MG = 27.2 ± 5.3 mm and $6.4\% \pm 1.2\%$; soleus = 16.3 ± 4.7 mm and $5.9\% \pm 1.7\%$.

Muscle fascicle and MTU shortening velocities.

Soleus peak shortening velocity during push-off was significantly higher at the faster compared with slower walking speed in OLDER (0.35 ± 0.16 vs 0.29 ± 0.14 reference length per second, $P = 0.010$), and a similar tendency was observed in MG (0.63 ± 0.23 vs 0.57 ± 0.16 reference length per second, $P = 0.066$). Fascicle shortening velocity at peak TT length was significantly lower in OLDER compared with YOUNG at preferred speed (MG = 0.11 ± 0.10 vs 0.25 ± 0.23 reference length per second, $P = 0.048$; soleus = 0.06 ± 0.12 vs 0.20 ± 0.15 reference length per second, $P = 0.020$) but not at matched

speed (MG $P = 0.545$, soleus $P = 0.208$). Soleus fascicle shortening velocity at peak TT length was significantly higher at the faster compared with slower walking speed in OLDER (0.13 ± 0.15 vs 0.06 ± 0.12 reference length per second, $P = 0.004$), but a statistically significant difference was not observed in MG ($P = 0.094$).

Muscle–tendon interaction.

In both MG and soleus, muscle fascicle length changes were clearly decoupled from the length changes of the MTU. Contributions of muscle fascicle to MTU length changes during stance were significantly lower in OLDER compared with YOUNG at preferred speed in both muscles (MG = 0.26 ± 0.10 vs 0.16 ± 0.05 , $P = 0.012$; soleus = 0.23 ± 0.08 vs 0.15 ± 0.04 , $P < 0.001$; Fig. 3). Significant differences were not observed when YOUNG and OLDER were compared at matched speeds. Increase in walking speed significantly increased muscle fascicle to MTU length change ratio in OLDER (MG = 0.16 ± 0.05 vs 0.19 ± 0.07 , $P = 0.013$; soleus = 0.15 ± 0.04 vs 0.21 ± 0.08 , $P = 0.002$).

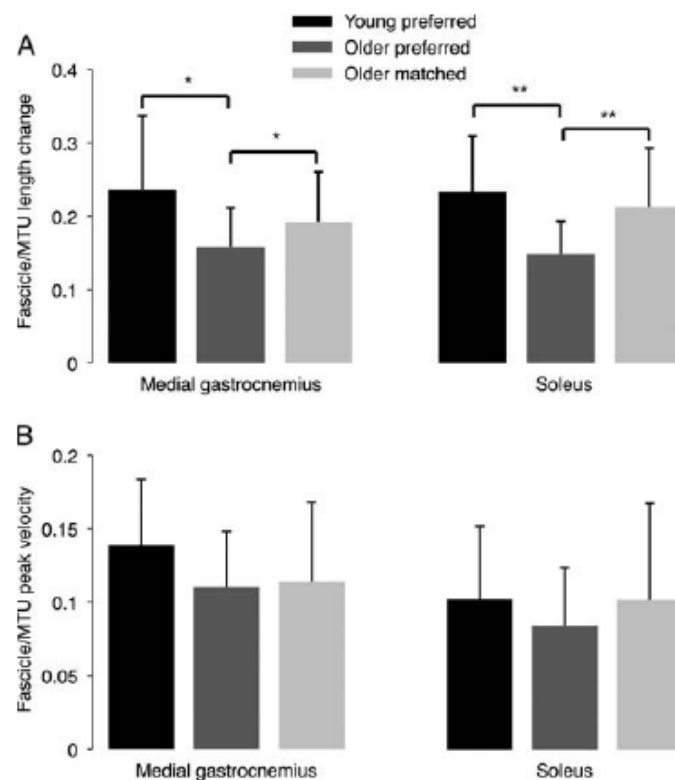


Figure 3 Ratio of muscle fascicle to MTU length change during stance (A) and ratio of muscle fascicle to MTU peak shortening velocity during push-off (B).

Muscle fascicle velocities were clearly different from MTU velocities. Muscle fascicle relative to MTU peak shortening velocities during push-off did not significantly differ between YOUNG and OLDER or

within OLDER between different walking speeds in either muscle (Fig. 3). Pooling both groups and velocities together, MTU peak shortening velocities during push-off were on average 8 and 11 times greater than the peak shortening velocity of the muscle fascicles in MG and soleus, respectively.

EMG.

RMS EMG activity of MG and soleus did not significantly differ between YOUNG and OLDER at either walking speed when compared during stance or push-off. However, EMG activity significantly increased in both stance and push-off in both muscles in OLDER as they increased their walking speed from preferred to matched speed (MG stance = 0.32 ± 0.12 vs 0.38 ± 0.16 RMS/RMS_{MVIC}, $P = 0.011$; push-off = 0.39 ± 0.17 vs 0.47 ± 0.23 RMS/RMS_{MVIC}, $P = 0.026$; soleus stance = 0.36 ± 0.18 vs 0.40 ± 0.19 RMS/RMS_{MVIC}, $P = 0.001$; push-off = 0.43 ± 0.23 vs 0.49 ± 0.23 RMS/RMS_{MVIC}, $P = 0.001$).

GRF.

Peak propulsive and resultant forces during push-off significantly increased in OLDER with increase in walking speed (propulsive = 0.16 ± 0.03 vs 0.19 ± 0.03 body weights, $P < 0.001$; resultant = 1.03 ± 0.07 vs 1.05 ± 0.08 body weights, $P = 0.012$). However, both peak propulsive and resultant forces during push-off remained significantly lower in OLDER compared with YOUNG at matched speed (propulsive = 0.19 ± 0.03 vs 0.22 ± 0.04 body weights, $P = 0.011$; resultant = 1.05 ± 0.08 vs 1.14 ± 0.08 body weights, $P = 0.045$).

Associations between preferred walking speed and triceps surae muscle–tendon function.

A significant positive correlation was observed between preferred walking speed and body weight–normalized plantarflexion strength ($r = 0.562$, $P = 0.046$). Preferred walking speed was also significantly correlated with MG mean fascicle velocity during push-off ($r = -0.461$, $P = 0.018$), mean soleus fascicle velocity during push-off ($r = -0.534$, $P = 0.006$), minimum soleus fascicle velocity during push-off ($r = -0.599$, $P = 0.002$), soleus fascicle velocity at estimated peak force generation ($r = -0.653$, $P < 0.001$), soleus fascicle to MTU length change ratio during stance ($r = 0.412$, $P = 0.041$), soleus muscle fascicle operating range during stance ($r = 0.603$, $P = 0.001$), and MG TT peak strain ($r = 0.399$, $P = 0.043$). Linear regression analysis showed that age only had a significant effect ($P < 0.05$) on the previously mentioned relationships for MG mean fascicle velocity during push-off and soleus fascicle to MTU length change ratio during stance.

Discussion

The current study examined triceps surae muscle–tendon function in young and older men during walking. No significant differences were observed between the young and the older men at matched walking speed in any triceps surae muscle–tendon function parameters. Only peak GRF values during push-off were significantly lower in older compared with young men. However, at their preferred walking speeds, older men used a narrower fascicle operating range and had lower fascicle shortening velocity at estimated peak force generation, and fascicle length changes accounted for a lower proportion of MTU length changes compared with young men. These findings may partly explain why older adults prefer to walk at a slower speed.

The results of the current study did not support our first hypothesis. We did not observe differences in TT elongation between young and older men when the groups were compared at the matched speed, which we expected based on previous studies that showed lower Achilles tendon stiffness in older compared with young adults (9,20,34,38). However, our finding is consistent with the results of Csapo et al. (9), showing lower stiffness but similar MG fascicle shortening in older compared with young women in isometric contractions with similar force generation relative to maximal. It could be that aponeuroses, the stiffness of which can vary according to level of muscle force (4), serves to preserve TT length changes despite possible differences in free tendon stiffness between the age groups. We also hypothesized that contractile conditions in triceps surae muscles would be less optimal for force generation according to muscle force–velocity properties in older compared with young men at matched walking speed. The results did not support this hypothesis as no significant differences were observed between the age groups. Thus, it can be concluded that the results do not support the idea that differences in TT behavior or triceps surae muscle fascicle length or velocity between young and older men can explain reduced plantarflexor performance in older men. However, it remains possible that significantly less energy (normalized to body mass) was stored in TT of older compared with young men, as suggested by lower peak resultant GRF and similar TT elongation, contributing to previously observed reduction in ankle plantarflexion peak power at late push-off in older men during walking (10,23). The results, however, supported our hypothesis that force generation ability in older men improves at preferred walking speed, as fascicle shortening velocity at the estimated time of peak force generation was lower in older men at preferred compared with young adult's preferred walking speed, thus improving muscle force generation ability.

The results of the current study differed from previous studies examining triceps surae muscle fascicle behavior in young and older adults in walking (31,36). Previous studies have shown differences in either fascicle length change pattern or operating length between the age groups when compared at matched walking speeds (31,36). A possible reason for the discrepancy between the current and the previous studies is that in the current study, spatiotemporal gait parameters were matched between the groups at matched walking speed, whereas in the previous studies, older adults adopted greater stride frequency and shorter stride length to walk at the same speed as young adults, which may have an effect on muscle function despite the matched walking speed. It could be that the older men in the current study were in better physical condition compared with the older adults in the previous studies that reported differences in spatiotemporal gait parameters at matched walking speed between young and older adults. This may in turn explain the discrepancy in the findings related to spatiotemporal gait parameters.

The finding that triceps surae muscle–tendon function was not significantly different between young and older men at matched walking speed but differences were observed at preferred speeds suggest that triceps surae muscle–tendon kinematics are mainly determined by walking speed without significant effects of age. This was supported by the significant correlations observed between preferred walking speed and triceps surae fascicle shortening velocities, soleus operating range, and muscle–tendon interaction and MG TT strain. Age had significant effect on these associations only in few variables, in which cases the significant age effect was caused by significant correlations within older but not young men. Hence, the associations between walking speed and muscle–tendon function were not different between the age groups or were only evident in older men.

Walking slower than young men’s preferred speed improved triceps surae contractile conditions for force generation by reducing shortening velocity at estimated peak force generation. Thus, at preferred walking speed, older men can generate the same force with lower activation and hence energy cost compared with faster walking speeds. This is highlighted by the results of the current study showing that an increase in walking speed of 22% in older men was accompanied by 19% and 13% increases in MG and soleus RMS EMG, respectively, during push-off, but only a 2% increase in peak resultant GRF. In addition, at preferred walking speed in older men, triceps surae muscles operated within a narrower range, thus possibly performing less mechanical work, and TT elasticity also accounted for a greater proportion of the MTU length changes. These walking speed-related adaptations in triceps surae muscle–tendon function may provide a mechanism to mitigate the age-

related reduction in plantarflexor force generation capacity, and to reduce the energy cost of walking.

We propose that the walking speed-related adaptations in triceps surae muscle–tendon function observed in the current study could play a role in the selection of a slower preferred walking speed in older compared with young adults. In support of the idea that plantarflexor force generation is an important factor in the selection of preferred walking speed in older adults, we observed a significant correlation between preferred walking speed and body weight–normalized plantarflexion strength. Previously, contractile conditions for force generation in triceps surae muscles have been linked to preferred walk-to-run transition speed in young adults in both experimental and modeling studies (11,33), and a similar mechanism could be involved in the selection of preferred walking speed of older adults. Improved contractile conditions for force generation could also play a role in the selection of preferred walking speed via the energy cost of walking. Humans tend to prefer walking speeds that minimize the gross energy cost of walking per unit distance (6,12). Triceps surae muscles may make a relatively large contribution to changes in whole body energy cost in walking with changes in walking speed because it has been shown using EMG-driven simulations that triceps surae were the only muscles of the 11 analyzed lower limb muscles that decreased their force generation ability with increasing walking speed, requiring greater activation to maintain required force generation (3). Thus, improvement in triceps surae contractile conditions for force generation and consequential decrease in muscle activation to maintain required level of force generation may affect the total energy cost of walking and hence drive the selection of slower walking speeds in older adults. In addition, it has been shown that older adults compensate for reduced plantarflexor power and work output during push-off by increasing the use of hip extensors in early stance (10), which may operate with greater reserve capacity (23). However, this distal to proximal shift in muscular strategy, where the power generation of plantarflexors that can use a catapult action because of a long Achilles tendon (21) is replaced by power generation from an MTU with a short tendon, may increase the energy cost of walking because of the unfavorable muscle shortening velocities of the muscles providing the positive power (37). In addition, the distal to proximal shift in muscular strategy in older adults, which is associated with more conserved center of mass trajectory (13), may increase energy cost because of less efficient pendulum-like mechanical energy exchange (35). Hence, improved contractile conditions for force generation in plantarflexors due to slower walking speed may increase the proportion of plantarflexor power output to the total positive power, which may be a more economical strategy. Finally, it should be noted that walking is a complex motor action, and several different muscular strategies can be used in walking. It is also

probable that other factors than those previously mentioned affect the selection of preferred walking speed. For example, it has been previously suggested that older adults may purposefully limit propulsion in push-off to improve balance (14). Thus, it is likely that no single factor is solely responsible for the selection of preferred walking speed.

Limitations.

A limitation of the current study is the two-dimensional nature of ultrasound imaging. Error in the measured fascicles lengths could arise from the out-of-plane motion of the fascicles and from the imaging plane not being completely aligned with the fascicle direction (5). In addition, muscle fascicle lengths were measured from a single location, and thus it is not known how well the results reflect muscle fascicle behavior in other parts of the muscles. However, the measurement location that was used in the current study should represent the general pattern of fascicle length changes, at least for MG (25). Furthermore, these limitations may induce errors in the absolute values but probably do not affect between- or within-group comparisons. Finally, our study was limited by the lack of estimations of MTU mechanics and energetics based on inverse dynamics. These measures would provide important additional insights to muscle function.

Suggestions for future research.

To gain further insight into age-related differences in triceps surae muscle function in walking, a larger range of speeds should be tested from both young and older adults with estimates of joint torques, powers, and muscle forces based on inverse dynamics. These measurements, in combination with measurement of respiratory gases, could provide further evidence for whether the selection of walking speed depends on factors related to energy cost, muscle force generation, or perhaps other factors such as balance, as previously suggested (14). In future studies, it is also important to examine the effects of different exercise interventions on muscle function and walking speed in older adults. Of particular interest could be interventions specifically aimed to strengthen the soleus muscle and to increase TT stiffness. One type of training intervention that could be used for this purpose is high force isometric strength training that has been shown to be effective at increasing Achilles tendon stiffness (2).

Conclusions.

Understanding the mechanisms underlying the age-related decline in preferred walking speed is important to be able to target preventative and rehabilitative strategies more effectively and to better understand the link between reduced walking speed and adverse health outcomes. The

results of the current study suggest that the force generation ability of triceps surae muscles is decreased in older men when increasing walking speed from their preferred walking speed to the preferred walking speed of young men. In addition, this change in walking speed increases the proportion of fascicle to MTU length change, suggesting the less effective use of tendinous tissue elasticity. The reduction in preferred walking speed with aging may provide a means to compensate for the decline in triceps surae muscle strength and to minimize the energy cost of walking. Improving plantarflexor strength could be an effective strategy to improve and maintain walking speed in older age.

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