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Soleus fascicle length changes are conserved between young and old adults at their preferred walking speed

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ABSTRACT

Older adults have been shown to naturally select a walking speed approximately 20% slower than younger adults. We explored the possibility that a reduction in preferred speed in older adults represents a strategy to preserve the mechanical function of the leg muscles. We examined this question in the soleus muscle in eight healthy young (25.8 ± 3.5 years) and eight healthy older adults (66.1 ± 2.3 years) who were paired so that their preferred speed differed by ~20%. Soleus muscle fascicle lengths were recorded dynamically using ultrasound, together with simultaneous measurements of soleus EMG activity and ankle joint kinematics while (a) older adults walked on a treadmill at a speed 20% above their preferred speed (speeds matched to the preferred speed of young adults), and (b) young and older adults walked at their preferred treadmill speeds. Analyses of mean muscle fascicle length changes revealed that, at matched speeds, older adults had a statistically different soleus fascicle length pattern compared to young adults, where the muscle's stretch-shorten cycle during stance was diminished. However, older adults walking at their preferred speed exhibited a more pronounced stretch-shorten cycle that was not statistically different from young adults. Conserving muscle length patterns through a reduction in speed in older adults may represent a physiologically relevant modulation of muscle function that permits greater force and power production. Our findings offer a novel mechanical explanation for the slower walking speed in older adults, whereby a reduction in speed may permit muscles to function in a mechanically similar manner to that of younger adults.

1. Introduction

One of the primary characteristics of gait in older adults (OA) is a reduction in preferred walking speed. Indeed, others have reported around 20% lower habitual walking speeds in healthy community dwelling older adults (1.0–1.3 m/s) compared to young adults (YA) (1.3–1.5 m/s) [1,2]. This age-related reduction in walking speed reflects a reduced motor capacity that may be linked to a greater incidence of falls [3] and a comparatively high metabolic rate in older adults for a given speed [4]. Examining the muscular mechanisms linked with a reduced walking speed in older adults may prove important for understanding and treating gait deficits associated with aging.

The underlying muscular mechanisms responsible for a reduced walking speed in OA compared to YA remain unclear. Previous literature has reported alterations in the structural and functional properties [5] of skeletal muscle and tendon linked with aging, such as a loss of muscle mass (sarcopenia), in particular in the lower limbs [6], reduced pennation angle and fascicle lengths [7] and lower tendon Young's modulus and stiffness [8]. These changes in muscle–tendon properties have important implications for the force and power capacity and efficiency of muscle during walking [9,10] and it is logical to assume that they contribute to the altered gait mechanics and control in OA [11]. Yet, exactly how these muscle–tendon characteristics influence speed selection in OA is not known. Is it possible, for instance, that a slower self-selected walking speed in OA represents a strategy to preserve the muscle's mechanical milieu at a level similar to those of YA? It has been proposed that humans and other species select speeds that lead to optimal

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function of skeletal muscles including minimization of force, mechanical power and energy expenditure [12–15]. A conservation of muscle function at preferred walking speeds across the age span would suggest that the slower speeds selected by OA may be a strategy to maintain optimal muscle mechanical function.

The focus of this study was to explore the aforementioned question by assessing how the soleus muscle functions (1) when OA walk at speeds matched to the faster preferred speed of YA and (2) during walking at preferred speeds in YA and OA. Specifically, we examined the differences in soleus muscle fascicle length changes between YA and OA given that this property is known to be intimately linked to muscle function [10]. We hypothesized that the soleus would lengthen less during the early part of stance (dorsiflexion) and shorten less during the latter part of stance and early swing when the muscle is active (plantar-flexion) in OA compared to YA when walking at matched speeds, similar to that reported for the stretch-shorten cycle of the medial gastrocnemius muscle [16], but that these differences would diminish when OA use their preferred walking speed. A corollary hypothesis was, therefore, that the muscle fascicle length change that occurs during stance in OA is greater when walking at their preferred speed compared to a faster-than-preferred speed. The soleus muscle represents a muscle of choice in addressing this question since it is amenable to dynamic *in vivo* imaging [17,18], because the plantar flexors, and the soleus in particular, have been identified as the primary source of mechanical work during gait [19], and finally due to the finding that the primary locus of gait impairment in OA is at the ankle plantar flexors [20].

2. Methods

2.1. Subjects

Sixteen healthy male subjects free from previous lower-limb injuries and musculo-skeletal disorders were recruited for this study. They were divided in two groups of eight by age: YA 25.8 $\pm$ 3.5 years, mean $\pm$ SD; OA 66.1 $\pm$ 2.3 years, mean $\pm$ SD. The YA group was composed of the same subjects recruited for a separate parallel study on soleus mechanics during walking and running [18]. Anthropometric characteristics including tibia length, weight and height were not statistically different between groups (0.41 $\pm$ 0.03 m, 1.75 $\pm$ 0.06 m and 70.3 $\pm$ 9.2 kg, mean $\pm$ SD for YA *vs* 0.40 $\pm$ 0.02 m, 1.74 $\pm$ 0.06 m and 72.1 $\pm$ 9.4 kg, mean $\pm$ SD for OA, respectively).

All subjects provided written, informed consent prior to participating in the study and all of the procedures were approved by the Human Research Ethics Committee at The University of Western Australia.

2.2. Self-selected walking speed and gait kinematics

Subjects performed over-ground and treadmill walking trials. Their preferred over-ground speed was assessed by timing participants walking 10 m along a carpeted surface. A minimum of 5 trials were used to assess mean preferred speeds. For the instrumented treadmill trials (Bertec, Columbus, OH, USA), preferred walking speed was assessed by permitting subjects to freely self-adjust the treadmill speed, starting at a speed 30% slower than their preferred over-ground speed and incrementing speed by 0.01 m/s until they reach their preferred speed. This procedure was repeated five times from which a mean self-selected treadmill speed was determined and used in subsequent tests. All participants attended a familiarization session on the treadmill prior to data collection.

Older adults were paired with younger adults so that the preferred walking speed between each pair differed by 19 $\pm$ 2%. Each subject was tested at their preferred treadmill speed, while OA were also tested at a speed 20% greater than their preferred speed, thus matching within 0.16 m/s the preferred speed of their paired YA. This permitted a case-matched comparison of the soleus muscle function (1) between preferred speeds in YA and OA and (2) between preferred speeds in YA and a 20% faster-than preferred speed in OA that matched the preferred speed of YA (thus controlling for relative speed in OA).

Three-dimensional gait analysis was performed on each subject during their treadmill walking trials. To-this-end, 22 retro-reflective markers were attached to the subject's pelvis and lower limb body landmarks and motion was collected using an 8-camera VICON MX motion capture system (Oxford Metrics, UK; 100 Hz). Marker placement and joint modeling were in accordance with the UWA lower body model [21]. All marker trajectories were filtered using a zero-lag 4th order low pass Butterworth filter with a 6 Hz cut-off frequency, which was defined using a custom residual analysis algorithm (MATLAB, The MathWorks Inc., USA). To determine the stance and swing phases, individual leg ground reaction forces were collected from the treadmill force plates at a frequency of 2000 Hz and synchronized with the motion data. Ankle joint angles were defined following the ISB guidelines [22] with negative values representing plantaflexion and positive values representing dorsiflexion (0° represents a neutral angle with the foot perpendicular to the tibia). Knee joint angles were defined with negative values representing extension and positive values flexion (0° knee fully extended).

2.3. Muscle length changes and activation

While the subjects walked on the treadmill, dynamic B-mode ultrasound images of the soleus muscle (Telemed, EchoBlaster128, Lithuania; image capture 70–80 Hz) were collected using a 7.5 MHz linear array low-profile probe (transducer field width = 60 mm) attached to their right calf using an elastic bandage (Elastoplast Sport, Beiersdorf, Australia). The probe placement was standardized across subjects using a location over the medial gastrocnemius (MG) where the MG muscle–tendon junction was visible in the distal portion of the scan [18]. Soleus muscle fascicle lengths were measured in the mid-region of the ultrasound scan and calculated as the distance between the fascicle endpoints, defined as the intersection of the fascicle with the superficial and deep aponeurosis. Fascicle endpoints were digitized manually using ImageJ software [23] by two investigators (one investigator analyzed all OA data). The digitized data were filtered using a 4th order zero-lag 5 Hz low-pass Butterworth filter (MATLAB, The MathWorks, Natick, MA). An analysis of muscle fascicle lengths across the stride on a sub-set of trials from all YA participants indicated minimal and non-significant differences between investigators; cross correlations were 0.97–0.99 with zero lag and the average difference in length from all data points was 0.9 mm. A rigid cluster composed of three non-collinear retro-reflective spherical markers was fixed to the ultrasound probe to verify that its movement relative to tibia was minimal during walking. The probe movement relative to the tibia across the stride was within 5.2°, 2.8° and 4.9° for movement in the tibia's sagittal plane, frontal plane and coronal plane, respectively. Fascicle lengths were normalized by dividing them by the length of the resting fascicle at 8° of dorsiflexion. This joint posture was selected as it represents the mean joint angle corresponding to the soleus muscle slack length (the length above which passive forces first appear) in YA [18]. Resting fascicle lengths were recorded with subjects seated in a dynamometer (Biodex, M3, Shirley, NY, USA)

Table 1
Spatio-temporal parameters in young adults (YA) and old adults (OA) for preferred and matched walking speeds (mean values ± SD).

	YA	OA (preferred)	OA (matched)
Testing speed (m/s)	1.14 ± 0.16	0.96 ± 0.17*	1.15 ± 0.22§
Stance time (s)	0.71 ± 0.05	0.69 ± 0.05	0.65 ± 0.04§
Swing time (s)	0.44 ± 0.04	0.49 ± 0.05	0.45 ± 0.04§
Duty factor	0.62 ± 0.03	0.59 ± 0.02	0.59 ± 0.01
Stride frequency (Hz)	0.87 ± 0.05	1.18 ± 0.10*	1.09 ± 0.07*,§
Stride length (m)	1.31 ± 0.17	0.82 ± 0.18*	1.06. ± 0.26*,§

* Significantly different from YA ($p < 0.05$).
§ Significantly different from OA preferred ($p < 0.05$).

with the foot rigidly strapped to a customized plate allowing an accurate adjustment of joint angle. Although we did not directly assess muscle slack lengths in OA, previous studies have reported that there are no differences in the ankle angle at which passive force in plantar flexors develop between YA and OA [24]. Therefore, this method was adopted to represent a functionally relevant assessment of muscle length changes relative to resting muscle lengths.

During the treadmill walking trials surface electromyography (EMG) from the soleus muscle was simultaneously measured (Noraxon, Scotsdale, AZ, USA or Motion Lab Systems, Baton Rouge, LN, USA; 2000 Hz) with the motion and ultrasound data using the VICON system. EMG signals were high-pass filtered (4th order Butterworth, cut-off 30 Hz), rectified and low-pass filtered (4th order Butterworth, cut-off 7 Hz) to obtain an EMG linear envelope. The EMG linear envelope recorded during rest (non-weight bearing) was subtracted from the walking values and the signal was subsequently normalized to the peak value across the stride.

2.4. Statistical analysis

A minimum of five non-consecutive gait cycles were used to compute subject mean muscle fascicle length, EMG linear envelope and joint kinematics. Spatial–temporal gait parameters including stride length, stride frequency, duty factor, stance and swing times were calculated (Table 1). Continuous muscle and joint kinematics in the sagittal plane data were normalized to 101 data points for each of the five strides and used to compute mean subject data, which in turn were used to compute mean group data used in descriptive statistics and group comparisons.

Analysis of the muscle fascicle length pattern was performed using a one-tailed unpaired Student's *t*-test to determine significant differences in the amount of active lengthening and shortening, as well as average normalized muscle fascicle lengths across the stride and in stance and swing separately. Muscle lengthening was defined as the increase in length from the time the muscle began to lengthen after heel-strike to the maximum fascicle length in stance; shortening was defined as the decrease in length between the maximum fascicle length in stance to the minimum fascicle length (observed just after toe-off and in conjunction with a return to baseline muscle activity). To account for the false discovery rate due to multiple comparisons, additional *post hoc* testing was performed on muscle fascicle length measurements using the Benjamini method [25] (see Table 2). Statistical procedures (paired Student's *t*-test) were also used in the same manner described above to determine if significant differences arise due to changing speed among the OA participants (analyses were performed both on the group and on each individual). Secondary to our analysis of muscle length, a two-tailed Student's unpaired *t*-test was used to determine significant differences in joint angles and mean EMG linear envelope between the two groups. The significance level was assessed at $p < 0.05$. Effect sizes were calculated using Cohen's d method. Data are reported as mean ± SD unless otherwise stated.

3. Results

3.1. Comparison of muscle mechanics and joint kinematics at matched walking speeds in YA and OA

In the YA, from early stance, the soleus muscle lengthened by 10.6 ± 8.4% (normalized muscle lengths) and subsequently shortened rapidly during the second half of stance by 23.7 ± 4.5%. In contrast, OA exhibited significantly less lengthening during early/mid-stance (3.7 ± 3.3% normalized muscle lengths; $p < 0.05$) and less shortening during the second half of stance and early swing (14.9 ± 5.7% normalized muscle lengths; $p < 0.05$). Significantly shorter mean normalized fascicle length across the total gait cycle (0.86 ± 0.16 YA *vs* 0.73 ± 0.09 OA) and both in stance (0.86 ± 0.16 YA *vs* 0.74 ± 0.09 OA) and swing phases (0.86 ± 0.16 YA *vs* 0.74 ± 0.09 OA) independently were also found in OA compared to YA (Table 2 and Fig. 1a). A Cohen's d analysis indicated that the effect of age on the above variables were large (Table 2).

Absolute resting lengths (mm) were not significantly different between YA (37.7 ± 5.3 mm) and OA (37.9 ± 6.9 mm). Absolute muscle fascicle lengths at heel-strike (33.2 ± 4.9 mm and 30.7 ± 5.9 mm for YA and OA, respectively) were also not significantly different.

No significant differences were present in ankle and knee kinematics between YA and OA walking at matched speeds (Table 3). However, the mean EMG linear envelope value in OA was significantly higher ($p < 0.05$) than in YA during the overall gait cycle at walking speeds matched to the YA and showed a large effect size (Table 3 and Fig. 1c).

3.2. Effect of speed on muscle fascicle length in OA

Significantly greater lengthening during stance (7.6 ± 5.8% normalized muscle lengths) and greater shortening during plantar-flexion in late stance and early swing (19.0 ± 8.8% normalized length) were observed when OA walked at their preferred speed (Table 2). Mean muscle fascicle normalized lengths across the stride (0.84 ± 0.10), stance (0.86 ± 0.09) and swing phases (0.81 ± 0.14) likewise increased significantly between faster than preferred and

Table 2
p-Values relative to the variables analyzed to assess differences in normalized fascicle lengths pattern. Analyses were conducted on the entire stride, as well as the stance and swing phases independently. Significance was initially set at $p < 0.05$ and subsequently adjusted for multiple comparison error using the Benjamini *post hoc* method [25] using the 5 muscle fascicle length parameters. Effect sizes calculated with Cohen's d method are reported in brackets.

	Stance phase			Swing phase	Total stride
	Mean length	Lengthening	Shortening	Mean length	Mean length
YA–OA (preferred)	0.482	0.217	0.099	0.311	0.396
YA–OA (matched)	0.034* (1.05)	0.025* (1.01)	0.002* (1.2)	0.022* (1.18)	0.026* (1.13)
OA (preferred)–OA (matched)	0.001* (1.48)	0.027* (0.87)	0.117	0.002* (1.13)	0.001* (1.34)

YA = young adults. OA = old adults.
* Denotes significant differences after *post hoc* analysis.

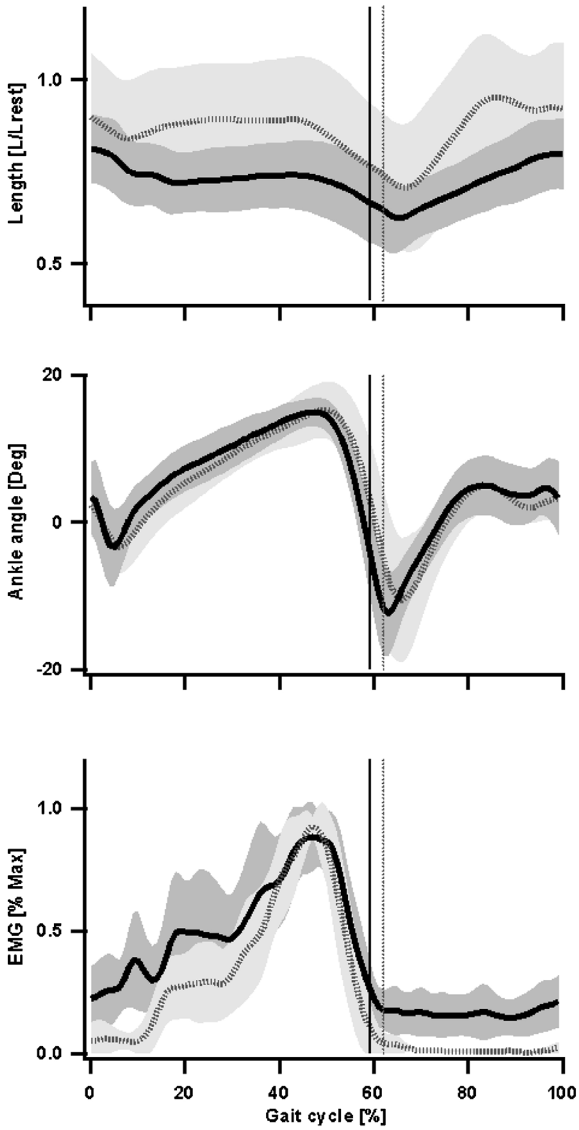

Fig. 1. Comparison of matched walking speeds in young adults (YA) and old adults (OA): (a) normalized muscle length, (b) ankle joint angle and (c) normalized EMG linear envelope as a percent of gait cycle (heel-strike to heel-strike). YA dotted lines and OA solid lines, respectively. The shaded regions represent the SD of the mean and the vertical lines represent toe off.

preferred walking in OA (Table 2). The effect sizes of the differences in muscle lengths due to speed in OA were large (Table 2).

When assessed on an individual basis, the increase in muscle lengthening and shortening observed in OA during the stance phase between walking at their preferred speed and a 20% faster speed was statistically different in 7 of the 8 OA (based on an average of 5 strides per speed).

Table 3
Mean values ± SD of joint kinematics and soleus EMG for young adults (YA) and old adults (OA) for preferred and matched walking speeds. Values are relative to the whole gait cycle. Effect sizes calculated with Cohen's d method are reported in brackets.

	YA	OA (preferred)	OA (matched)
Ankle angle (max)	15.9 ± 3.8°	15.8 ± 3.6°	15.2 ± 2.0°
Ankle angle (min)	−12.9 ± 7.2°	−10.7 ± 5.2°	−13.1 ± 5.9°§ (0.46)
Knee angle (max)	71.9 ± 8.5°	69.0 ± 4.5°	69.9 ± 5.1°
Knee angle (min)	−0.3 ± 3.6°	2.2 ± 8.2°	1.2 ± 6.4°
Mean EMG	0.23 ± 0.06	0.32 ± 0.06* (1.9)	0.38 ± 0.11* (1.8)

* Significantly different from YA ($p < 0.05$).
§ Significantly different from OA preferred ($p < 0.05$).

3.3. Comparison of muscle mechanics and joint kinematics at preferred walking speeds in YA and OA

The overall normalized muscle fascicle length changes during the stance and swing phases were not different between YA and OA walking at the matched speed (Table 2 and Fig. 2a). No significant differences were found in the normalized fascicle lengthening or shortening, nor in the mean fascicle length across the total gait cycle, or the mean lengths in the stance and swing phases between the two groups (Table 2). As with the normalized length data, the pattern of absolute fascicle lengths in the two groups was not significantly different in any parameter.

No significant differences were found in ankle and knee range of motion or minimum and maximum angles between YA and OA (Table 3). The average value of the normalized EMG linear envelope

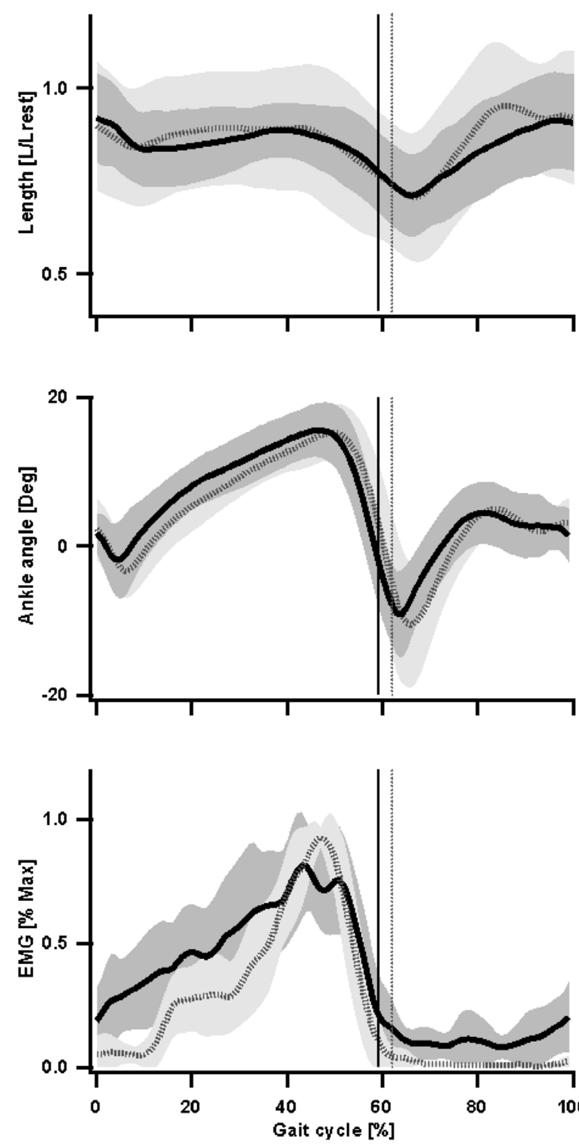

Fig. 2. Comparison of preferred walking speeds in young adults (YA) and old adults (OA): (a) normalized muscle length, (b) ankle joint angle and (c) normalized EMG linear envelope as a percent of gait cycle (heel-strike to heel-strike). YA dotted lines and OA solid lines, respectively. The shaded regions represent the SD of the mean and the vertical lines represent toe off.

across the stride was higher in OA than in YA and showed a large effect size ($p < 0.05$, Table 3 and Fig. 2c).

4. Discussion

In accordance with our hypothesis, there were marked differences in the soleus fascicle length patterns between the two age groups when OA were asked to match the preferred speed of YA. More specifically, when OA walked 20% faster than their preferred speed there was a lack of a stretch-shorten cycle during the stance-phase, whereby the soleus fascicles remain close to isometric, unlike the stretch-shorten cycle observed in YA. Surprisingly, we also observed a shorter average muscle fascicle length in OA compared to YA at matched walking speeds. Because no significant differences were found in the range of motion of the ankle between groups, this finding is likely explained by a higher stretch of the Achilles tendon in OA, thus mitigating the strain in the muscle fibers themselves. This difference in tendon behavior is supported by the fact that OA have shown to have a more compliant Achilles tendon than YA [8].

A similar reduction in fascicle stretch-shorten behavior has also been observed previously in the medial gastrocnemius muscle during walking at 1.1 m/s between YA and OA [16], and thus appears to be a general characteristic of the triceps surae with aging. The possibility that the gastrocnemius muscle influences the soleus muscle function *via* its action at the knee has recently been investigated [26]. Gastrocnemius–soleus interaction could have influenced the change in the length pattern observed between preferred and fast walking in OA, however, given that the knee angles between these speeds were not significantly different this effect is likely small.

Also in accordance with our hypothesis, when OA walked at their preferred speed the soleus muscle fascicles exhibited a greater stretch-shorten cycle during the stance phase (compared to when they walked at a 20% faster speed) and an overall length pattern that was comparable to that of YA walking at their preferred speed. Interestingly, not only is the pattern of muscle fascicle lengths matched at preferred speeds, but an increase in the average muscle fascicle lengths in OA between fast and preferred speeds resulted in mean muscle fascicle lengths that were also matched. It has previously been argued that YA select walking speeds that result in optimal energetics and muscle mechanics [12,13]. Albeit a single muscle analysis, the modulation of active soleus muscle fascicle lengths between fast and preferred walking speeds in OA supports our theory that slower walking in OA may be a strategy adopted to allow their muscles to function mechanically similarly to those of YA.

What could be the possible benefit of maintaining a stretch-shorten cycle of the soleus muscle during walking? It is well accepted that muscles undergoing active stretching produce higher force for a given level of activation [10]. It has also been well documented that eccentric muscle activity is metabolically less expensive than concentric or isometric activity [27]. Maintaining a stretch-shorten-cycle in OA through a reduction in speed may thus lower relative muscle activation and energy use, and in turn reduce fatigue and the energy cost associated with walking. It has also recently been shown that the soleus muscle functions across the ascending limb of its force–length curve during walking in YA [18]. Therefore, an increase in muscle fascicle length during stance increases its length-dependent force capacity as higher forces are required; it has been argued that this can represent a strategy to simplify the control of force regulation during gait [18]. Furthermore, deactivating the soleus muscle as it shortens on the ascending limb of the force–length curve in the second half of stance will result in a more rapid decay of muscle force compared to if the muscle functions isometrically. A rapid decay of force will increase the rate of elastic energy return in the Achilles tendon and thus the ability to power the ankle joint *via* the release of stored elastic energy during toe-off. It should also be noted that an increase in mean muscle fascicle length at the preferred speed in OA may improve the overall force capacity of the muscle. We do not know where the soleus functions on its force–length curve in OA, but given the increased compliance of the Achilles tendon reported in OA [8] it is reasonable to assume that the muscle fibers function at shorter lengths and thus possibly also on the ascending limbs of the force–length curve.

Greater relative soleus muscle activation was present in OA compared to YA (Table 3 and Figs. 1b and 2b) walking at both matched and preferred speeds, which is consistent with previous studies [28]. A higher relative activation across the stance-phase may be required to achieve the necessary force and moment production due to a loss in force capacity (specific tension; [29]), or may represent force–length–velocity affects, although the nature of these remain unclear. The higher average relative muscle activity may also represent a general elevation in co-contraction in OA that is required to maintain stability [30]. Older adults likewise have significantly higher activation during the swing phase compared to YA, where the muscle is inactive. Therefore, a co-contraction strategy may also be adopted in OA to increase their limb stability during the swing phase. Interestingly, the higher swing-phase activation, coupled with higher Achilles tendon compliance [8], may help explain the smaller fascicle lengthening during the swing phase in OA.

The present study focused on length changes in a single region of one muscle. The extent to which these findings extend to other muscles and other regions of the soleus muscle are not known, and thus whether they reflect a general mechanism remains unclear. Furthermore, it remains possible that normalizing muscle fascicle lengths to optimal fascicle lengths in OA could alter the functional assessment of the fascicle length pattern, although the overall direction of the length change will remain unchanged.

Despite these aforementioned limitations, given that the soleus muscle has been reported to be one of the most important muscles responsible for generating the mechanical work of walking [19], and since muscle length patterns are central in dictating the muscle's mechanical performance [10], the conservation of muscle fascicle length pattern through a reduction in speed in OA may indeed represent a physiologically relevant modulation of muscle function. While we cannot rule out that changes in muscle fascicle length patterns result from a reduction in speed brought about by other factors, our work on the soleus muscle offers a novel mechanical explanation for the slower walking speed in OA, whereby a reduction in speed permits muscles to function in a similar manner to that of YA.

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Conflict of interest

All authors reported no conflict of interest.

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