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Altered plantarflexor muscle-tendon mechanics and gearing during stretch-shortening contractions in older adults

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ABSTRACT

Ageing is associated with impairments in muscle force-generating capacity and tendon mechanical properties, yet its effects on stretch-shortening cycle (SSC) function remain unclear. We combined in vivo ultrasonography with dynamometric and kinematic measurements to investigate the muscle-tendon mechanisms underpinning SSC performance in older adults. Fourteen young (28 ± 5 years) and fifteen older adults (67 ± 3 years) performed electrically evoked plantarflexion contractions on an isokinetic dynamometer. Pure shortening and stretch-shortening (SSC) contractions were performed at angular velocities of 60 and 150°·s^{-1}. Ankle torque, muscle-tendon unit (MTU) force, fascicle force, fascicle and Achilles tendon (AT) length changes, muscle belly gearing, tendon gearing, and mechanical work were quantified.

Older adults exhibited lower maximal plantarflexor force and AT stiffness than young participants (both $P <$ 0.001). SSCs increased ankle torque, MTU force, and fascicle force in both groups, with a greater enhancement at the higher shortening velocity. The magnitude of SSC-induced force enhancement was similar between groups, with no significant age×SSC interactions for force-related variables. Older adults exhibited greater AT elongation and tendon gearing, but less fascicle shortening, smaller changes in pennation angle, and lower muscle belly gearing.

AT mechanical work increased during SSCs in both groups, whereas fascicle work was reduced only in the young participants.

These findings demonstrate no significant age-related differences in SSC-effect between populations despite marked reductions in maximal force-generating capacity. The comparable SSC-effect could be achieved through altered muscle-tendon interaction strategies characterised by greater AT compliance and modified fascicle behaviour. Ageing, therefore, seems to preserve SSC function while altering the distribution of mechanical work within the MTU.

1. Introduction

Ageing is characterised by several muscle-tendon unit (MTU) structural changes that affect contractile function, including muscle atrophy (~1% per year), and reductions in muscle pennation angle, fascicle length and in-series tendon stiffness (Magnusson and Kjaer, 2019; Narici et al., 2003). These changes, along with an impairment in neural drive, underpin a reduction in muscle strength (~2% per year) and power (~3% per year) (Izquierdo et al., 1999).

Interestingly, however, the above ageing-induced deteriorations in muscle strength and power are contraction-type dependent, affecting mainly isometric and shortening muscle contractions (Power et al., 2013a; Wu et al., 2021). Instead, muscle strength and power during eccentric contractions are well-maintained into old age (Roig et al., 2010a; Power et al., 2013b; Patterson et al., 2024). This is of importance, since daily-life human movements, such as walking and running, are characterised by an active muscle shortening contraction preceded by active muscle lengthening (Monte et al., 2020; Monte et al., 2023; Fukunaga et al., 2001), known as the stretch-shortening cycle (SSC). The SSC is a phenomenon in which muscle force, work and power are enhanced when compared to a typical shortening contraction (hereafter referred to as "the SSC effect"). Different mechanisms may account for the SSC effect, including, but not limited to, energy return from the series elastic component in the muscle (Thys et al., 1975; Monte et al.,

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2021a; Van Roie et al., 2020), pre-activation of muscles due to activation dynamics (Cutlip et al., 2004), and the history-dependent properties of muscle (Patterson et al., 2024; Holzer et al., 2024). However, previous human studies have evaluated SSC performance mainly through functional outcomes such as jumps and hopping (Elam et al., 2021; Werner et al., 2026), demonstrating reductions in muscle mechanical power and SSC effect, (e.g., jump height) in elderly individuals. The muscle-tendon mechanical behaviour underpinning these differences remains poorly understood.

In this regard, one potential determinant of the SSC effect is the uncoupling between muscle fascicle, muscle belly, and muscle–tendon unit length changes during contraction. When a pennate muscle, such as the ankle plantarflexors, shortens actively, the fascicles rotate, increasing the pennation angle, while the tendon accommodates a substantial proportion of the MTU length change (Azizi et al., 2008; Eng et al., 2018; Wakeling et al., 2011). Muscle belly gearing describes the ratio between whole-muscle shortening and fascicle shortening, whereas tendon gearing reflects the uncoupling between muscle belly and muscle–tendon unit length changes (Holt et al., 2016; Monte et al., 2021b). Together, these mechanisms allow fascicles to operate over favourable lengths and shortening velocities, thereby influencing muscle force production and metabolic demand (Monte et al., 2022; Monte and Zamparo, 2023; Maganaris and Paul, 2002; Magnusson et al., 2001). However, whether ageing alters these gearing mechanisms during SSC contractions, and whether such alterations contribute to age-related differences in SSC performance, remains unknown.

Although no human studies have directly investigated the muscle–tendon determinants of the SSC effect in older adults, rodents studies suggest that SSC contractions may preserve power production in aged muscle despite reduced contractile capacity, particularly during rapid shortening (Patterson et al., 2024). However, age-related adaptations in muscle–tendon mechanics differ between rodents and humans. Older rats exhibit increased aponeurosis stiffness and muscle-belly gearing (Holt et al., 2016), whereas older humans typically show reduced tendon stiffness, smaller contraction-induced changes in pennation angle and muscle thickness, and greater intramuscular connective tissue and fat infiltration (Kelp et al., 2021; Randhawa and Wakeling, 2013). In humans, these adaptations have also been associated with reduced muscle-belly gearing during isometric and isokinetic plantar-flexor contractions (Kelp et al., 2021; Randhawa and Wakeling, 2013). These species-specific differences suggest that the mechanisms identified in animal models may not reflect those operating in older humans, leaving the muscle–tendon mechanisms underlying the SSC effect in older adults unclear.

To address the knowledge gap in how ageing affects the muscle–tendon mechanisms underlying the SSC effect in humans, here we combined dynamometry with in vivo ultrasonography during electrically evoked shortening and SSC contractions of the ankle plantar flexors at different velocities in older and younger participants. We examined age-related differences in gastrocnemius fascicle behaviour, Achilles tendon mechanics, and muscle-belly and tendon gearing, as characterising these mechanisms may provide novel insight into functional decline in older age given the central role of the plantarflexors in daily activities involving SSC (e.g., walking). Based on previous human evidence of altered muscle architecture, reduced tendon stiffness and lower muscle-belly gearing with ageing (Magnusson and Kjaer, 2019; Narici et al., 2003; Narici and Maganaris, 2006), we hypothesised that muscle-belly and tendon gearing would be impaired in older adults, limiting their ability to decouple fascicle behaviour from MTU length changes during SSC contractions. Consequently, we expected these alterations in muscle–tendon interaction to reduce the magnitude of the SSC effect, particularly at higher shortening velocities.

2. Methods

2.1. Participants

Fourteen younger participants and fifteen older participants were recruited and provided written informed consent to be involved in the study (see Table 1 for participants' characteristics). Exclusion criteria included any musculoskeletal or neurological impairments in the lower limbs. The experimental protocol was approved by the institutional ethical committee (protocol nr: 2019/SPF00123).

2.2. Experimental design and protocol

Each participant performed three different experimental sessions. In the first and second visits, the participants were familiarised with the experimental procedures. Data were collected in the third visit.

In each experimental session, after preparing the International Physical Activity Questionnaire (IPAQ) to investigate the physical activity level and familiarising themselves with the protocol, participants underwent a standard warm-up (5 min of cycling at a self-selected intensity and cadence). They were then secured to the dynamometer and performed a series of sub-maximal contractions to precondition the MTU structure (Maganaris, 2003; Arnold et al., 2013; Arnold and Delp, 2011).

The participants were fixed on an isokinetic dynamometer (Biodex 4), lying prone with their knee and hip joints fully extended. The right foot was fixed at 0° of plantar/dorsiflexion to the dynamometer footplate, with the ankle and the dynamometer axes of rotation visually aligned (see Fig. 1).

Each participant then performed three maximum voluntary contractions. These contractions served as a reference for setting the proper stimulation intensity and to obtain the maximum voluntary torque and the Achilles tendon stiffness. During the MVCs, the subjects were instructed to gradually increase the torque from zero to the maximum possible value in 2–3 s, maintain the maximum effort for an additional 2 s, and then relax the muscles. Two minutes of recovery were interposed between contractions.

The electrical stimulation intensity needed to elicit 50% of the MVC was then identified using a ramp-stimulation protocol. This contraction intensity was used to represent the typical contraction intensity adopted during walking and jogging (Maganaris and Paul, 2002).Tetanic contractions using the above stimulation intensity were then elicited during two different contraction types: a pure shortening contraction (SHO) and a stretch-shortening contraction (SSC) (see Fig. 1). During the pure shortening condition, the ankle range of motion was limited from 10° of dorsiflexion to 10° of plantarflexion (− 10° and + 10°, respectively). The dynamometer was set to start the shortening action 0.5 s after the electrically evoked contraction reached the target intensity (50% of MVC). The entire stimulation lasted 4 s, and two different angular velocities were tested, 60 and 150°/s (SHO60, SHO150, respectively). During the SSC condition, the starting position for the ankle was set at 0°, rapidly rotating to −10° and then ending at +10° after a subsequent shortening phase. The stretching phase was performed at an acceleration of $400°/s^2$, while the shortening phase was performed at the same angular velocities with the SHO contractions (SSC60 and SSC 150). Five contractions for each experimental condition were performed in a randomised order, and the mean value was used for statistical analysis.

Table 1
Participants characteristics.

	Young (7 M and 7F)	Older adults (8 M and 7F)
Age (years)	28 ± 5	67 ± 3
Stature (cm)	170 ± 13	163 ± 9
Body mass (kg)	66 ± 15	70 ± 18
IPAQ (MET-min/week)	2989 ± 384	2856 ± 256

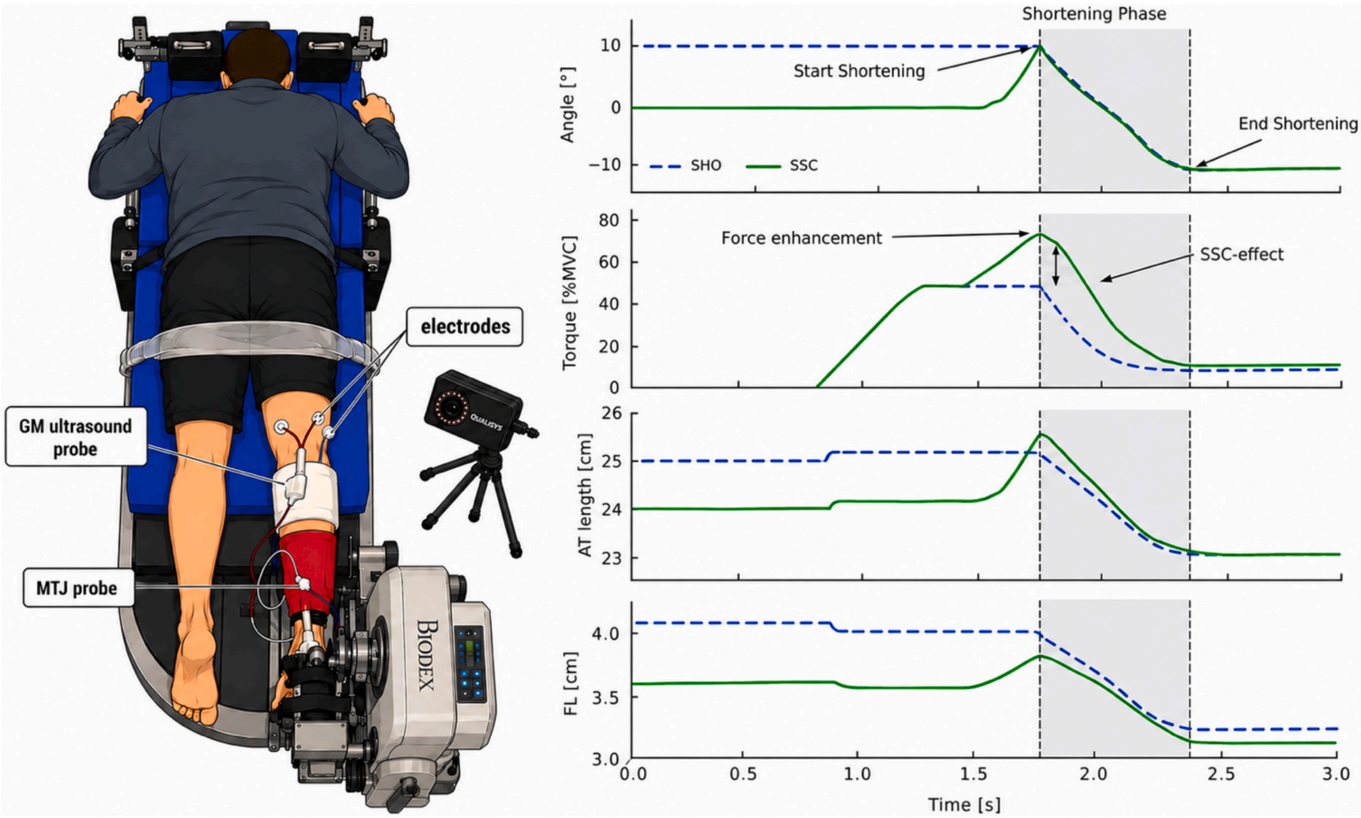

Fig. 1. Participants were secured in a prone position on the dynamometer (left panel). The right panels refer to the original data of a representative young participant. Blue and green lines represent pure shortening and stretch-shortening contractions, respectively. Data analysis was focused on the shortening phase (gray shaded area). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The contraction was repeated when the torque before the contraction starting point was unstable or reached values higher or lower than 50% of MVC, or the rotation was not initiated within the first 2 s of the contraction. We used electrically evoked contractions to minimise the confounding effects of voluntary motor drive and spinal/supraspinal neural mechanisms, thereby enabling a more direct assessment of muscle–tendon mechanical behaviour during SSC contractions.

During the entire experimental protocol, ankle plantarflexion torque was collected using the dynamometer system (operating at 1000 Hz), while ankle kinematic was obtained using a motion capture system (QUALYSIS, operating at 200 Hz). Two ultrasound apparatuses were used to collect the behaviours of the gastrocnemius medialis muscle fascicles (Philips EPIQ 7) and its muscle-tendon junction (i.e., referring to the displacement of the Achilles tendon) (Aixplorer Supersonic). An external digital trigger synchronised all apparatuses and the signals were collected using an analogue-digital converter (BioPac; MP100, Biopac System).

All data collection and image analyses were performed by the same experienced operator (>10 years of experience in ultrasound image analysis) to ensure methodological consistency and maximise intra-rater reliability. Analyses were conducted in a non-blinded manner.

2.3. Data collection

2.3.1. Maximum voluntary contractions

During the MVCs, the kinematic parameters of the right foot were collected using reflective markers placed on: the lateral and medial malleolus, the lateral and medial femoral condyle, the first and fifth metatarsophalangeal joint, and the heel. Five additional markers were placed along the Achilles tendon to reconstruct its line of action. These markers were placed at 0, 1.5, 3 and 4.5 cm proximal to the tendon insertion and in the middle of an ultrasound probe that was placed on the gastrocnemius medialis (GM) muscle-tendon junction, along the muscle-tendon action line, to quantify Achilles tendon elongation (Maganaris and Paul, 2002; Magnusson et al., 2001; Monte and Zignoli, 2020).

2.3.2. Electrically evoked contractions

Tibial nerve electrical stimulation with a constant current was used to evoke plantarflexor muscle contractions. The anode electrode was placed in the distal area of the popliteal fossa, while the optimal cathode position was ensured using single electrical square-wave pulses (20 mA) elicited by a hand-held cathode pen. The highest plantarflexion torque response defined the cathode position. The cathode electrode was then fixed to the skin to reduce the pain exerted during electrical stimulation (Cattagni et al., 2018). Muscle contraction were induced using tetanic electrical stimulation (DS7AH, Digitimer, UK; 50 Hz, square-wave pulses with 1 ms pulse width). During stimulated plantarflexion contractions, a steady plantarflexion torque of 50% of the MVC was reached.

During the evoked SHO and SSC contractions, the Achilles tendon displacement was recorded as described above for the MVCs, while a second ultrasound probe was placed on the most prominent part of the GM muscle, and properly aligned to record fascicle behaviour. Because of technical challenges associated with simultaneously imaging multiple muscles with a single probe during dynamic SSC contractions, ultrasound analyses were limited to the GM muscle and its myotendinous junction.

2.4. Data analysis

2.4.1. Muscle geometry and Tendon stiffness

Kinematic data were filtered using a 6 Hz fourth-order (zero lag) low-pass Butterworth filter, then ankle angle was calculated and utilised to take into account the possible detachment of the heel and correct it (Magnusson et al., 2001; Arampatzis et al., 2006).

The ankle plantarflexion torque measured by the dynamometer was filtered using a 10 Hz second-order (zero lag) low-pass Butterworth filter and converted into internal force by division with the Achilles tendon moment arm, calculated as the minimal distance between the ankle joint center of rotation (identified with a marker positioned on the lateral malleolus) and the Achilles tendon action line (Tecchio et al., 2022).

The elongation of the Achilles tendon during MVC was obtained by tracking the position of the GM myotendinous junction following the closest visible fascicle insertion (Tracker 4.95) and taking into account the possible displacement of the heel (Maganaris and Paul, 2002; Arampatzis et al., 2005; Arampatzis et al., 2004). Force-elongation data for the three investigated contractions were fitted with a second-order polynomial function forced through zero (see Fig. 2). Achilles tendon stiffness was calculated as the slope of the force-tendon elongation curve in the 60–90% of MVC interval.

2.4.2. Muscle and tendon kinetics

Changes in GM fascicle length, muscle thickness and pennation angle during the evoked contractions were detected using a semi-automatic software (UltraTrack v5.5). To assess intra-rater reliability, fascicle and Achilles tendon tracking were repeated in a subgroup of 8 participants (4 young and 4 older adults). Excellent reliability was observed (ICC = 0.97 and 0.96; CV = 3.3% and 3.8% for fascicle length and Achilles tendon displacement, respectively). When the tracking was inaccurate, the operator manually repositioned the reference point. The final parameters were filtered using a 5 Hz fourth-order (zero lag) low-pass Butterworth filter. During these contractions, GM muscle belly length was defined as the linear distance between the medial femoral condyle and the position of the MTJ. Achilles tendon length between the bony insertion and the GM myotendinous junction was quantified taking into account its curvature (Tecchio et al., 2022). GM belly gearing was calculated as the ratio of muscle belly and fascicle length changes, where the changes were the point-by-point differences. For statistical analysis, the maximum length change of each parameter, calculated from the onset until the end of the shortening phase, was utilised. For belly gearing, the mean values during the shortening phase were used for further analysis.

From the estimated Achilles tendon force, the GM MTU force was calculated, accounting for the GM contribution (15.9% based on its relative physiological cross-sectional area (Fukunaga et al., 1996)). MTU work was calculated as the area under the curve of the GM MTU force – MTU length relationship during the shortening phase. Fascicle work was

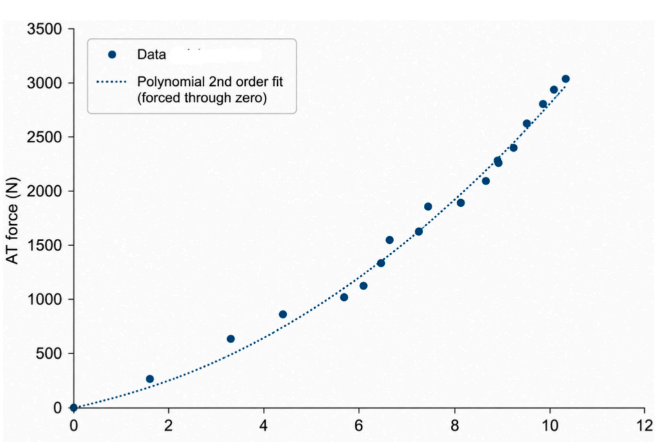

Fig. 2. Experimentally quantified Achilles tendon (AT) force–elongation relationship during maximum voluntary contractions (Raw data) and the modeled force-elongation curve during loading phase.

calculated as the area under the curve of the fascicle force-fascicle length relationship during the shortening phase, where fascicle force was calculated as: Ffas = GM MTU force/cos(pennation angle). The SSC effect was calculated as the ratio between MTU and fascicle work performed during SSC shortening and the work performed during shortening in the corresponding SHO trials.

2.5. Statistics

The Shapiro-Wilk and Levene's tests ($p > 0.05$) were used to check normality of distribution and homogeneity of variance. A three-way repeated-measures ANOVA (main effect of velocity, contraction type and age) was performed to identify significant differences in the dependent variables during active muscle shortening across different conditions. The interaction effect was analysed for the 1st order interaction, avoiding the 2nd order interaction (velocity-contraction-age) for simplicity. A two-way repeated-measures ANOVA was performed to identify changes in the SSC effect (e.g., ratio between data obtained during pure shortening contractions and SSC at the same contraction velocity) (main effect of velocity and age; dependent variable: SSC effect). A Bonferroni-Holm correction was used to adjust the α-levels. For all analyses, effect sizes are reported as partial eta squared (η^2).The statistical analyses were performed using R (v.4.5.1) with the alpha level set at $\alpha = 0.05$. Data are reported as the mean ± standard deviation.

3. Results

The maximum voluntary MTU force of the plantarflexor muscles obtained during the MVCs was 2200 ± 211 N and 1631 ± 104 N for younger and older participants, respectively, while the Achilles tendon stiffness was 140 N/mm and 112 N/mm. Older adults exhibited lower maximum isometric force values ($P < 0.001$) and Achilles tendon stiffness ($P < 0.001$) compared to younger participants.

Fig. 3 reports the values of ankle torque, MTU force and GM fascicle force in all the investigated conditions for both populations, as well as the SSC effect. A significant interaction between velocity and SSC was observed in all the investigated parameters ($P = 0.039$, 0.021 and 0.037 for plantarflexion torque, MTU force and fascicle force, respectively): the higher the velocity, the greater the SCC effect. On the contrary, there was no significant interaction between SCC and age: ankle torque, MTU force and fascicle force were greater during the SSC in both age groups, with no between-group differences in the magnitude of the SSC effect.

Ankle plantarflexion torque, MTU force and fascicle force increased with SSC in both groups (main effect: $P < 0.001$, $\eta^2 = 0.77$; $P < 0.001$, $\eta^2 = 0.81$; $P = 0.012$, $\eta^2 = 0.71$ for ankle torque, MTU force and fascicle force, respectively). However, the absolute values of the investigated parameters were lower in older group (main effect: $P < 0.001$, $\eta^2 = 0.73$; $P < 0.001$, $\eta^2 = 0.80$; $P < 0.001$, $\eta^2 = 0.74$ for ankle torque, MTU force and fascicle force, respectively). The effect of velocity was present in plantarflexion torque (main effect: $P = 0.032$, $\eta^2 = 0.34$) and fascicle force (main effect: $P = 0.041$, $\eta^2 = 0.29$), while MTU force was unaffected by it.

Fig. 4 shows the values of fascicle and tendon mechanical work for all the investigated conditions for both populations, as well as the SSC effect. Significant interactions between SSC and velocity ($P = 0.037$), as well as between SSC and age ($P < 0.001$), were observed in fascicle work. For instance, the SSC effect increased as a function of contraction velocity in both age groups. There was a reduction in fascicle work with SSC for younger participants, but no changes for older adults. Achilles tendon mechanical work showed a significant interaction between SCC and velocity ($P = 0.012$) with a larger SSC effect at higher velocities for both groups. No significant interaction between SSC and age was observed, suggesting a similar effect of SCC on Achilles tendon mechanical work. Fascicle mechanical work was affected by SSC (main effect: $P = 0.012$, $\eta^2 = 0.70$) and by age (main effect: $P < 0.001$, $\eta^2 = 0.89$), while it was unaffected by contraction speed: it was higher for

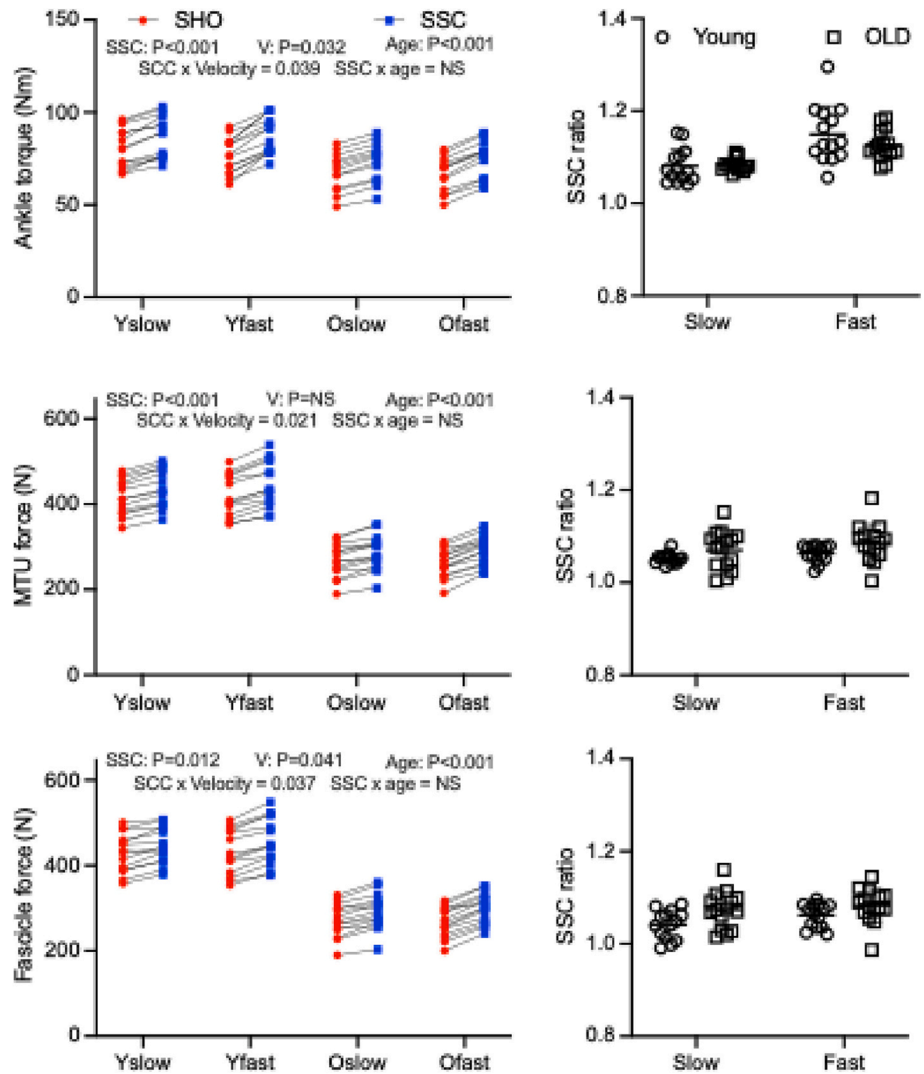

Fig. 3. Left panels refer to individual data reported by young (Y) and older (O) participants in all the investigated conditions. Red and blue dots represent the pure shortening phase and SSC contractions, respectively. Slow and Fast refer the angular velocities of 60 and 150°/s, respectively. SSC, V (velocity) and Age refer to the three-way repeated measure ANOVA results. Interactions between SSC and velocity and between SCC and age are also reported. Right panels refer to the SSC effect (ratio between the values obtained in the SSC condition over SHO condition). Significance bars and associated *P*-values refer to the comparison between young and older adults at each contraction velocity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

young participants when compared to older adults and decreased during SSC in younger subjects only. Achilles tendon mechanical work increased with SSC (main effect: $P < 0.001$, $\eta^2 = 0.90$) in both populations and tended to be reduced in the older group (main effect: $P = 0.055$, $\eta^2 = 0.17$). No effect of contraction velocity was observed.

Fig. 5 reports the changes in fascicle length, pennation angle and Achilles tendon length in all the investigated conditions for both populations as well as the SSC effect. No significant interaction between velocity and SSC was observed across all investigated parameters, whereas a significant interaction between SCC and age was observed for fascicle ($P = 0.022$) and Achilles tendon length changes ($P < 0.001$) (see Fig. 5): changes in fascicle length were reduced in the older group, but the opposite was the case for the Achilles tendon length changes. Changes in fascicle length decreased during SSC in both populations, while changes in Achilles tendon length increased during SSC (main effect: $P < 0.001$, $\eta^2 = 0.81$ and $P = 0.0013$, $\eta^2 = 0.78$ for the changes in fascicle and Achilles tendon lengths, respectively). In contrast, the changes in pennation angle were unaffected by the SCC. Fascicle length and Achilles tendon length were greater in the older group, while the changes in pennation angle were significantly smaller when compared to the young group (main effect: $P = 0.003$, $\eta^2 = 0.71$; $P = 0.038$, $\eta^2 = 0.38$; $P < 0.001$, $\eta^2 = 0.80$ for the changes in fascicle length, pennation angle and Achilles tendon length, respectively). The effect of velocity was present in pennation angle for the younger cohort (main effect: $P = 0.034$, $\eta^2 = 0.31$), but not in the other variables.

Fig. 6 shows the values of belly and tendon gearing for all investigated conditions in both populations, as well as the SSC effect. The SSC effect on tendon gearing was larger in older compared to younger participants, as shown by the interaction between SSC and age ($P < 0.001$). No interaction between SSC and velocity was observed for tendon gearing. There was no interaction between SSC and either velocity or age for belly gearing, suggesting that the responses of both populations were similar between contraction types and velocity. Tendon gearing increased with SSC (main effect: $P < 0.001$, $\eta^2 = 0.90$) and contraction velocity (main effect: $P = 0.018$, $\eta^2 = 0.69$) in both populations, but the effects were higher for older individuals (main effect: $P < 0.001$, $\eta^2 = 0.93$). Belly gearing increased as a function of velocity in younger participants (main effect: $P = 0.022$, $\eta^2 = 0.45$), while decreased with age (main effect: $P < 0.001$, $\eta^2 = 0.88$). No effect of SSC was observed for belly gearing in both populations.

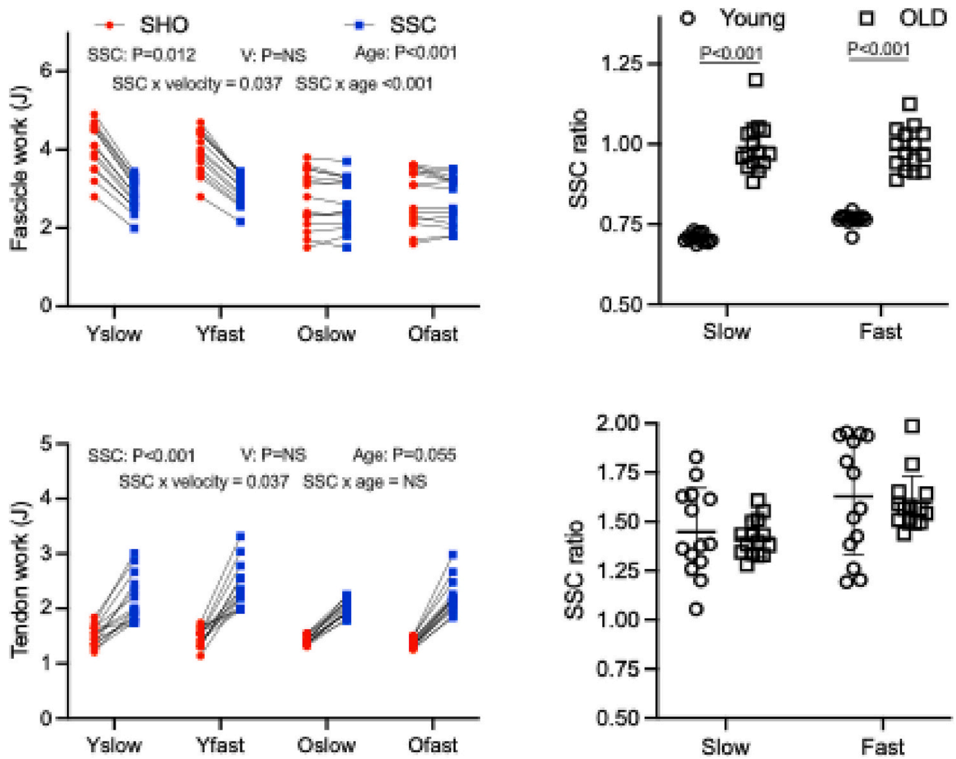

Fig. 4. Left panels refer to individual data reported by young (Y) and older (O) participants in all the investigated conditions. Red and blue dots represent the pure shortening phase and SSC contractions, respectively. Slow and Fast refer the angular velocities of 60 and 150°/s, respectively. SSC, V (velocity) and Age refer to the three-way repeated measure ANOVA results. Interactions between SSC and velocity and between SCC and age are also reported. Right panels refer to the SSC effect (ratio between the values obtained in the SSC condition over SHO condition). Significance bars and associated *P*-values refer to the comparison between young and older adults at each contraction velocity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

The present study investigated whether ageing alters the magnitude of the SSC effect in humans and whether age-related changes in muscle-tendon uncoupling behaviour contribute to explaining these differences. Our findings indicate that, despite a clear age-related reduction in contractile force during pure shortening contractions, no significant age-related difference in the magnitude of the SSC effect was detected. During SSC contractions, ankle plantarflexion torque, MTU force and GM fascicle force were comparable between younger and older participants. Tendon mechanical work was also similar between groups, whereas fascicle work differed with age. The data also show that the SSC effect was velocity dependent in both age groups, with greater enhancements evident at the higher shortening velocity. Finally, despite similar SSC effect between populations, ageing was associated with marked alterations in muscle and tendon behaviour. Specifically, changes in Achilles tendon length and fascicle length were larger in the older participants. These findings indicate that the similar SSC effect observed between groups was accompanied by substantial alterations in the strategy by which the muscle-tendon unit redistributes length changes and mechanical work during SSC contractions. In line with previous literature, older adults exhibited lower maximal isometric force and reduced Achilles tendon stiffness compared to younger individuals, confirming well-established age-related declines in muscle force-generating capacity and tendon mechanical properties (Narici et al., 2003; Magnusson et al., 2001; Ferri et al., 2003; Sarto et al., 2022). Contrary to our initial hypothesis, however, we observed no significant age-related difference in the SSC effect, even at higher shortening velocities, with a comparable enhancement in ankle plantarflexion torque, MTU force, and fascicle force in both age groups. The absence of significant SSC × age interactions suggests that, although muscle-tendons in older humans operate at lower absolute force levels, their capacity to benefit from prior active lengthening remains comparable to that of the younger group.

The similar SSC effect between populations at joint and MTU levels aligns with reports showing maintenance of eccentric strength with ageing at whole-muscle level (Power et al., 2013b; Patterson et al., 2024; Roig et al., 2010b), despite reductions in concentric and isometric muscle strength. As SSC contractions integrate active lengthening and shortening phases, comparable eccentric capacity may contribute to maintaining SSC-induced force enhancement.

At fascicle level, SSC contractions increased fascicle force similarly in the two age cohorts. These findings are consistent with the possibility that pre-activation and lengthening-induced cross-bridge mechanisms remain largely preserved with ageing (Patterson et al., 2024), although neither mechanism was directly assessed in the present study. However, differences emerged in the mechanical work performed by the fascicles, suggesting that the mechanisms underlying force enhancement may be altered with ageing (Patterson et al., 2024). In this regard, our data showed reduced fascicle length changes during SSCs compared with SHOs in both populations, thereby decreasing fascicle shortening speed during SSCs. According to the force-velocity relationship, a decrease in fascicle shortening velocity would allow the fascicles to generate higher contractile forces, likely explaining the increased torques/forces observed throughout the entire shortening phase (Hill, 1964; Barclay, 2015). However, our data suggest that the magnitude of this positive effect is reduced in older participants compared with younger participants, possibly explaining the higher fascicle work observed in older participants during SSC contractions.

The decrease in fascicle work during the SSC in the younger participants is an unexpected result that could be interpreted as a positive mechanism. Holzer et al. (Holzer et al., 2024) defined this mechanism as a “reversed SSC effect”. Since a decrease in fascicle work for a given contraction is associated with a decrease in the metabolic energy

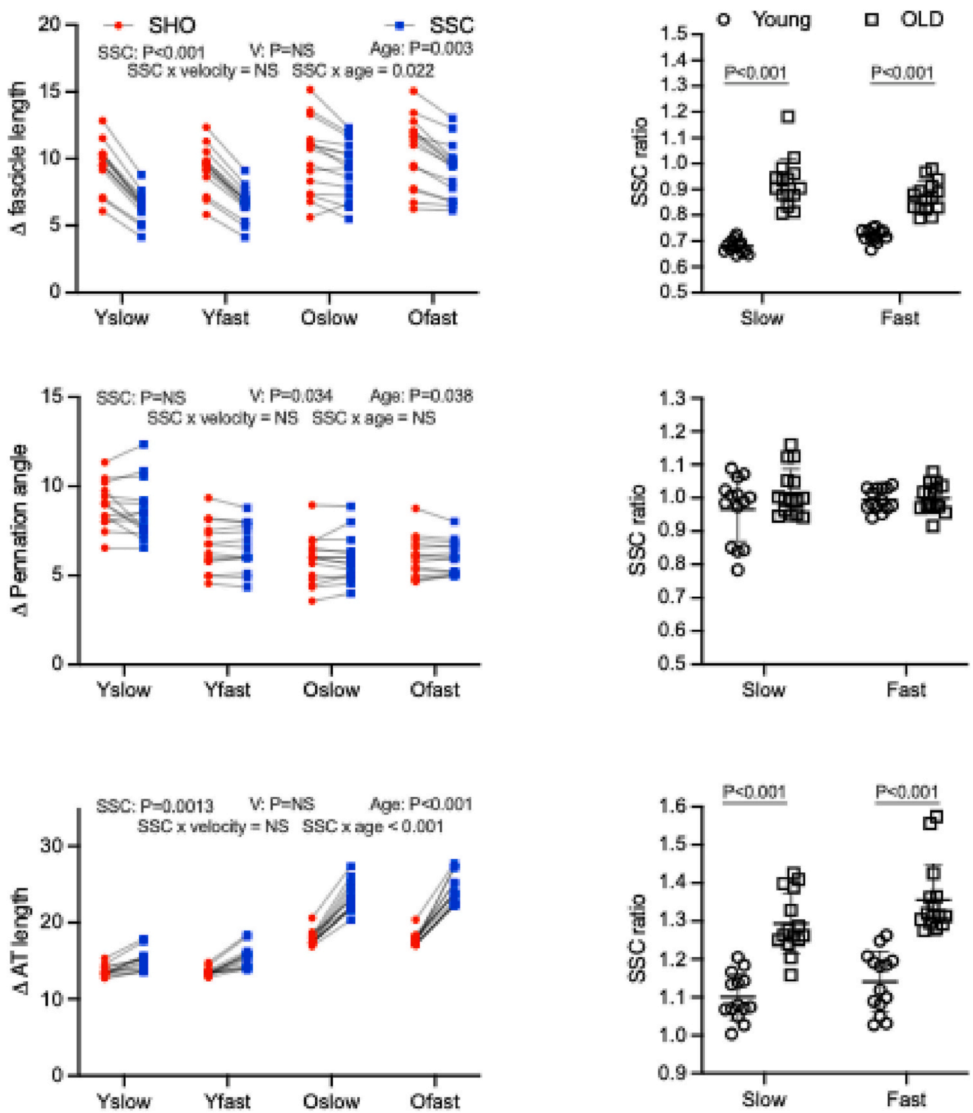

Fig. 5. Left panels refer to individual data reported by young (Y) and older (O) participants in all the investigated conditions. Red and blue dots represent the pure shortening phase and SSC contractions, respectively. Slow and Fast refer the angular velocities of 60 and 150°/s, respectively. SSC, V (velocity) and Age refer to the three-way repeated measure ANOVA results. Interactions between SSC and velocity and between SCC and age are also reported. Right panels refer to the SSC effect (ratio between the values obtained in the SSC condition over SHO condition). Significance bars and associated *P*-values refer to the comparison between young and older adults at each contraction velocity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

expenditure, it is reasonable to suggest that a decrease in fascicle work imposed by the SSC could contribute to reducing the energy cost of energy-saving locomotory tasks (e.g., walking and running (Monte et al., 2022; Monte and Zamparo, 2023; Roberts and Azizi, 2011)). This phenomenon, however, was not observed in the older adults, in whom the SSC did not affect fascicle work. This impairment in the SSC function warrants consideration as a potential contributor to the greater energetic cost of walking previously reported in older adults (Mian et al., 2007; Saibene and Minetti, 2003).

Interestingly, no significant changes in belly gearing were observed between SHO and SSC in either age cohort, showing that belly gearing could not explain the SSC effect. In agreement with the previous literature, the younger adults showed higher belly gearing than the older adults (Randhawa and Wakeling, 2013). However, while in the younger cohort belly gearing increased as a function of contraction velocity, in the older cohort it remained constant. Similar results were reported by Holt et al. (Holt et al., 2016) in a rat model, where young rats exhibited variable muscle belly gearing, whereas in older rats the gearing remained constant as a function of contraction speed. A variable belly gearing is the result of a complex interplay between active (i.e., muscle) and passive (e.g., connective tissues, intramuscular fat) components in the MTU, which affect the muscle's capacity to change its shape (Eng et al., 2018). As suggested by Holt et al. (Holt et al., 2016), one possible explanation is the greater intramuscular connective tissue infiltration in older adults, which in turn could decrease the muscle's capacity to change shape during contraction. However, this was not directly examined in the present study.

Pennation angle is one of the most important predictors of belly gearing, with larger pennation angle and fascicle rotation associated with greater belly gearing (Van Hooren et al., 2024; Monte, 2020). Older adults had smaller pennation angles than young participants (Narici et al., 2003), suggesting lower belly gearing, as reported by our data. Moreover, the changes in pennation angle between slow and fast contractions in the younger participants allowed them to adapt the belly gearing, while this was not the case for older adults (i.e., the same delta pennation between SHO and SCC implies similar values of belly gearing).

Another important uncoupling behaviour is related to the Achilles

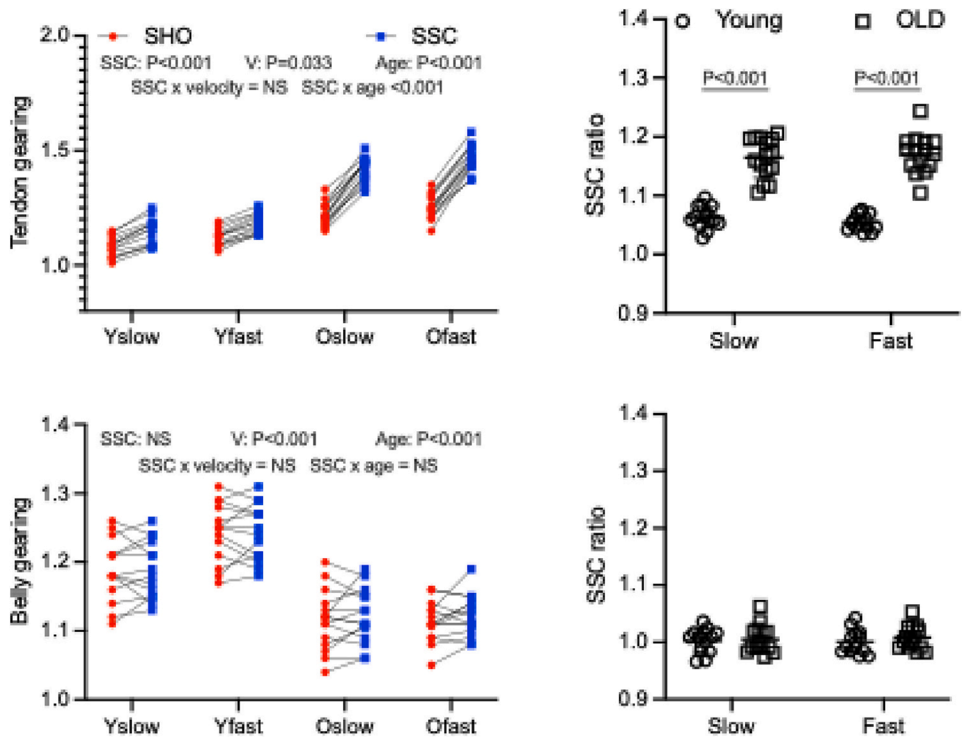

Fig. 6. Left panels refer to individual data reported by young (Y) and older (O) participants in all the investigated conditions. Red and blue dots represent the pure shortening phase and SSC contractions, respectively. Slow and Fast refer the angular velocities of 60 and 150°/s, respectively. SSC, V (velocity) and Age refer to the three-way repeated measure ANOVA results. Interactions between SSC and velocity and between SCC and age are also reported. Right panels refer to the SSC effect (ratio between the values obtained in the SSC condition over SHO condition). Significance bars and associated *P*-values refer to the comparison between young and older adults at each contraction velocity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

tendon. The energy return from the series elastic component of the MTU has been proposed as a major contributor to the enhanced forces during the shortening phase of SSCs compared with SHO (Cavagna et al., 1976; Cavagna et al., 1985). Our data showed that Achilles tendon length change and tendon gearing throughout the shortening phase were positively affected by the preceding stretch in both cohorts, thereby increasing the mechanical work released by the Achilles tendon during SSC. This suggests that SSC capacity at tendon level is comparable between the investigated populations. A larger force pulling on the tendon during the loading phase would result in a greater tendon length and reduced muscle belly and fascicle lengths (MacDougall et al., 2020; Maganaris et al., 1998; Alexander and Bennet-Clark, 1977). Our data reinforce this notion, showing that the Achilles tendon was associated with the largest changes in MTU during SSC in both cohorts, leaving the fascicle to near-isometrically. To note, the higher tendon gearing and Achilles tendon length changes in the older adults could be explained by the lower tendon stiffness. For a given contraction, the lower the stiffness the greater the fascicle and tendon length changes. Therefore, the decreases in Achilles tendon stiffness typically observed in older adults could affect SSC mechanisms in this population (Magnusson and Kjaer, 2019; Stenroth et al., 2016), leading to greater tendon length changes and compensate the decreases in force. This compensation could explain the similar values of elastic strain energy released by the Achilles tendon in the two cohorts.

From a mechanical perspective, greater tendon elongation during the lengthening phase enables greater energy storage and subsequent release during shortening, thereby supporting MTU work output despite reduced muscle force. However, this compensation likely comes with trade-offs, including altered fascicle operating conditions and reduced force transmission. Therefore, while tendon compliance may contribute to the comparable SSC performance in older adults, it also redistributes mechanical work within the MTU. Under the present experimental conditions, our findings indicate that older adults exhibited an SSC effect comparable to that of younger adults through a modified muscle-tendon interaction strategy. Younger individuals appeared to rely more on efficient redistribution of work, minimising fascicle contribution by utilising elastic energy effectively. In contrast, older adults relied more on tendon compliance and exhibited smaller changes in muscle architecture, resulting in altered fascicle behaviour and potentially greater energetic demand.

4.1. Methodological considerations

No Studies investigated the SSC-effect during the plantarflexor stretch-shortening cycle in humans using similar experimental conditions. Hence, we did not adopt an a priori sample size calculation. Even if this could be considered a methodological limitation, our data reported a strong effect size, suggesting the our data could represent the investigated populations.

GM force, work, and architectural behaviour were used as representative of the plantarflexor muscle-tendon unit. Although the GM is a major contributor to ankle plantarflexion and is commonly investigated in vivo because its superficial anatomical position facilitates scanning, its behaviour may not fully represent that of the entire triceps surae. Therefore, the present findings should be interpreted as primarily reflecting the behaviour of the GM muscle-tendon rather than that of the plantraflexor muscle group as a whole. Moreover, Achilles tendon length quantified in the present study extends from the gastrocnemius medialis myotendinous junction to the calcaneal insertion and therefore includes not only the free Achilles tendon but also the distal soleus aponeurosis. Consequently, the measured tendon length changes and mechanical work may partly reflect the mechanical behaviour of the soleus muscle–aponeurosis complex rather than exclusively the passive deformation related to the GM.

Muscle fascicle and tendon behaviour was assessed using two-dimensional ultrasonography. Consequently, all measurements relied on the assumption that the tracked fascicles and myotendinous junction accurately represented the behaviour of the whole muscle and tendon structures in 3D. Although 2D ultrasound scanning is currently the only viable method for recording muscle behaviour during high-speed human movement, this approach does not account for potential regional heterogeneity in fascicle behaviour, out-of-plane motion, or three-dimensional architectural changes occurring during dynamic contractions.

Muscle–tendon forces and mechanical work were estimated assuming that the GM contributes a fixed proportion of total plantarflexor force and that fascicle force can be calculated from tendon force and pennation angle. While these assumptions are commonly adopted in vivo and allow comparisons between conditions, they inevitably simplify the complex distribution of forces among synergistic muscles and may influence the absolute values reported. However, these assumptions were applied consistently across all experimental conditions and groups, making it unlikely that they affected the main between-condition comparisons.

In our study, we used electrically evoked contractions to isolate the mechanical determinants of the in vivo SSC effect in younger and older adults. Although this approach provides robust experimental control over muscle activation and is well suited to identifying differences in intrinsic age-related mechanisms, it markedly reduces the contributions of voluntary motor drive and stretch-reflex responses, both of which are important during natural SSC movements. Consequently, the present findings cannot be directly extrapolated to functional tasks such as walking or running, in which neural activation strategies are also likely to influence the SSC effect.

5. Conclusion

Our data suggest that no significant age-related difference in the magnitude of the SSC effect was detected under the present experimental conditions, despite substantial age-related alterations in the underlying muscle-tendon mechanics. Rather, ageing was associated with altered muscle-belly and tendon gearing, without a corresponding reduction in the magnitude of the SSC effect.

In older adults, the comparable SSC-induced force enhancement was accompanied by increased tendon compliance and altered fascicle behaviour, rather than by a more efficient redistribution of mechanical work as observed in younger adults. These findings provide new insights into age-related adaptations in the mechanical strategies used by the muscle-tendon unit during SSC contractions.

CRediT authorship contribution statement

Andrea Monte: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Constantinos N. Maganaris:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Formal analysis, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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