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RESEARCH ARTICLE

Reduced Achilles tendon stiffness in aging associates with higher metabolic cost of walking

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Abstract

The mechanisms responsible for increased metabolic cost of walking in older adults are poorly understood. We recently proposed a theoretical premise by which age-related reductions in Achilles tendon stiffness (k_{AT}) can disrupt the neuromechanics of calf muscle force production and contribute to faster rates of oxygen consumption during walking. The purpose of this study was to objectively evaluate this premise. We quantified k_{AT} at a range of matched relative activations prescribed using electromyographic biofeedback and walking metabolic cost and ankle joint biomechanics in a group of 15 younger (age: 23 ± 4 yr) and 15 older (age: 72 ± 5 yr) adults. Older adults averaged 44% lower k_{AT} than younger adults at matched triceps surae activations during isokinetic dorsiflexion tasks on a dynamometer ($P = 0.046$). Older adults also walked with a 17% higher net metabolic power ($P = 0.017$) but indistinguishable peak Achilles tendon forces than younger adults. Thus, data implicate altered tendon length-tension relations with age more than differences in the operating region of those length-tension relations between younger and older adults. In addition, we discovered empirical evidence that lesser k_{AT}—likely due to the shorter muscle lengths and thus higher relative activations it imposes—was positively correlated with higher net metabolic power during walking ($r = -0.365$, $P = 0.048$). These results pave the way for interventions focused on restoring ankle muscle-tendon unit structural stiffness to improve walking energetics in aging.

NEW & NOTEWORTHY This study provides the first empirical evidence to our knowledge that age-related decreases in k_{AT} exact a potentially significant metabolic penalty during walking. These results pave the way for interventions focused on restoring ankle muscle-tendon unit structural stiffness to improve walking energetics in aging.

ankle; economy; muscle-tendon unit; plantarflexor; triceps surae

INTRODUCTION

When walking at the same speed, older adults (≥65 yr) consume metabolic energy much faster than younger adults (e.g., 18–35 yr) (1, 2), which can accelerate fatigue and reduce independence and quality of life (3). Unfortunately, the mechanisms responsible for the increasing metabolic cost in the aging process are poorly understood. Given their role in powering locomotion, muscle-tendon units (MTUs) spanning the ankle have been shown through experimental and computational modeling studies to play a role in governing metabolic cost (4, 5). In particular, neuromechanical interaction between triceps surae muscle function and Achilles tendon stiffness is critical for tuning positive power generation during push-off (6), which is in turn responsible for as much as half of the cost of walking (7, 8). This is significant, as there is now mounting evidence from in vivo measurements in humans showing reduced Achilles tendon stiffness (k_{AT}) with age (9, 10). Indeed, we recently proposed a theoretical mechanistic pathway by which age-related reductions in Achilles tendon stiffness can disrupt the neuromechanics of calf muscle behavior and contribute to faster rates of oxygen consumption during walking (11). This viewpoint would pave the way for interventions focused on restoring ankle MTU structural stiffness to improve walking energetics in aging. However, no study to date has moved beyond a theoretical proposal to provide direct empirical data in support of this association.

Basic physiological principles dictate that a muscle operating at shorter than optimal length will require greater excitations to generate a given amount of force. Conceptually, age-related reductions in k_{AT} would elicit more tendon stretch for a given load. Older and younger adults walk with similar ankle joint kinematics (12) and thus similar triceps

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surae muscle-tendon unit lengths (13). Thus, for a given activation required to generate the requisite force, say that needed to provide propulsion at a given walking speed, the more compliant Achilles tendon of older adults would compel shorter triceps surae muscle operating lengths. These predictions of shorter operating lengths are supported by computational simulations (14) and experimental comparisons between younger and older adults (11). Ultimately, it is this local structural bottleneck, arising from reduced k_{AT}, that leads to a neuromechanical cascade that we propose contributes at least in part to a higher metabolic cost of walking for older adults.

Net ankle joint function is thought to arise from a combination of activation-independent (i.e., Achilles tendon) and activation-dependent (i.e., muscle) components. Previous work from our laboratory indicates that ankle MTU stiffness is regulated via activation-dependent changes in triceps surae length-tension behavior (15, 16). Tendon length-tension relations are nonlinear at lower tissue strains, and the effective stiffness "seen" by muscle is force-dependent and thus can vary as a function of activation. Indeed, as muscle activation and, thus, force increase, stretch of the series tendon will reach a nominally stiffer local region of its force-displacement curve. Given the complexity of age-related differences in ankle MTU neuromechanics, it is possible that prior studies may have inadvertently compared k_{AT} between younger and older adults at different regions of their respective force-length curves. However, it is unknown how aging effects on Achilles tendon stiffness vary as a function of triceps surae activation. Understanding the landscape of these age-related differences in activation-mediated functional stiffness of the Achilles tendon is an important prerequisite to understanding their influence on walking energetics.

Therefore, the purpose of this study was twofold. First, we aimed to quantify age-related differences in local Achilles tendon stiffness across a range of matched muscle activations using electromyographic biofeedback. Second, we aimed to determine the relation between Achilles tendon stiffness at matched activations and the metabolic cost of walking across age in the same cohort. We hypothesized that: *1*) independent of age, Achilles tendon stiffness would increase with higher triceps surae activations, consistent with a shift from the nonlinear to linear region of the length tension curve; *2*) older adults would exhibit lesser Achilles tendon stiffness compared with young adults at matched activations; and *3*) lesser Achilles tendon stiffness would positively correlate with a higher metabolic cost of walking.

METHODS

Participants and Study Design

We recruited 15 younger adults (23 ± 4 yr, 8 F/7M, mass: 72.9 ± 14.2 kg, height: 1.7 ± 0.1 m) and 15 older adults (age: 72 ± 5 yr, 9 F/6M, mass: 74.6 ± 17.1 kg, height: 1.69 ± 0.10 m) who participated in a protocol approved by the University of North Carolina Biomedical Sciences Institutional Review Board after providing written informed consent (IRB No. 18-0797). Prior to participation, subjects were screened and excluded if they reported neurological disorders affecting the lower extremity, musculoskeletal injury to the lower extremity within the previous 6 mo or were currently taking medications that cause dizziness. Two experimental sessions were performed: one for isolated contractions and the determination of Achilles tendon stiffness and the other for determining net metabolic power during treadmill walking (Fig. 1). For all isometric and isokinetic tasks, participants were seated in a dynamometer (Biodex, Shirley, NY) at 85° hip flexion and 20° knee flexion. For the habitual walking task, participants walked on a Bertec split-belt treadmill at a fixed speed of 1.25 m/s.

Isolated Contractions: Protocol and Measurements

We placed surface recording electrodes (Delsys, Natick, MA) on participants' right soleus and lateral gastrocnemius after prepping the site by shaving and abrading the skin. Sensors were secured to the skin using an adhesive tape. For electromyographic (EMG) biofeedback, soleus and lateral gastrocnemius data sampled at 1,000 Hz were demeaned, full-wave rectified, and bandpass filtered (20–450 Hz). Soleus and lateral gastrocnemius data were averaged and defined as "triceps surae activation" throughout the rest of the article. Simultaneously, we recorded the three-dimensional (3-D) trajectories of 20 retroreflective markers placed on the right leg and clusters affixed to each of two ultrasound transducers using motion capture operating at 100 Hz (Motion Analysis, Santa Rose, CA). Participants first donned one 60-mm linear array transducer (LV7.5/60/128Z-2, Telemed Echo Blaster 128, Lithuania) secured to the right shank via a custom 3-D-printed housing and positioned to image the medial gastrocnemius muscle-tendon junction (MTJ) at 60 frames per second. Participants also donned a 38-mm transducer (L14-5W/38; Ultrasonix corp, Richmond, BC), operating at 70 frames per second, placed on the Achilles free tendon distal to the soleus muscle-tendon junction. Biodex position and torque data were recorded at 1000 Hz in synchrony with motion capture data. A voltage sync signal from each ultrasound machine identified the start and stop of their acquisitions.

Participants completed a series of plantarflexor maximum voluntary isometric contractions (MVICs) at six ankle dorsiflexion (DF) and plantarflexion (PF) joint angles (20° DF, 10° DF, 0°, 10° PF, 20° PF, and 30° PF). If a participant's maximal dorsiflexion range of motion (ROM) was >25°, a seventh joint angle was added that was equal to their maximum dorsiflexion ROM. We corrected the net ankle joint moment for gravitational and passive moments. Data from isometric contractions were used to *1*) determine the coefficients for participant-specific moment arm equations (all joint angles) and *2*) establish a reference maximum triceps surae activation for the isokinetic EMG biofeedback trials to follow (neutral joint angle).

Thereafter, we displayed triceps surae activation on a monitor positioned in front of the participant in real time with a target line corresponding to a percent of MVIC activation (Fig. 1). Participants performed eccentric isokinetic plantarflexor contractions at 20°/s for two activation conditions: 25% MVIC and 75% MVIC. Participants were instructed to match their instantaneous EMG (displayed as a dot on the screen) to a target line (a horizontal line across the screen). A third condition was performed during which the dynamometer moved

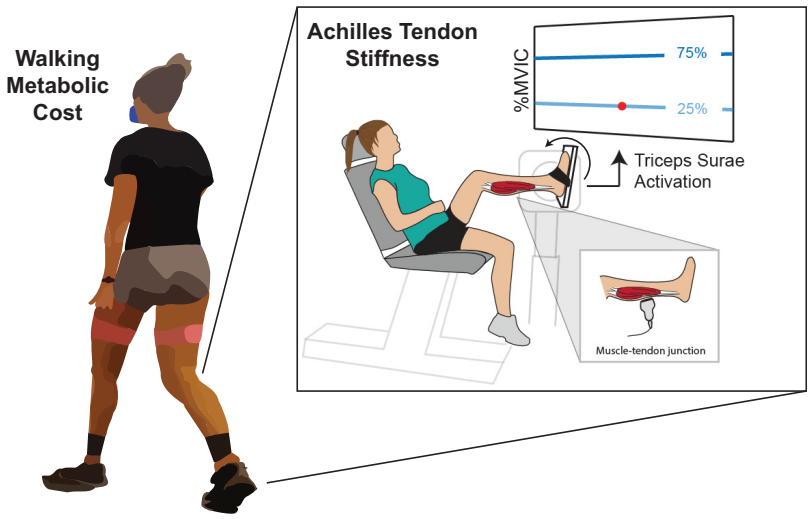

Figure 1. Methodological diagram showing the primary experimental paradigms and outcome measures used in this study. Subjects performed isokinetic ankle dorsiflexion tasks while responding to electromyographic biofeedback designed to matched different activation levels between younger and older participants. Motion capture-guided ultrasound imaging and dynamometry were combined to estimated Achilles tendon stiffness. We correlated those stiffness values with net metabolic power estimated from treadmill walking at a fixed speed of 1.25 m/s. MVIC, maximum voluntary isometric contraction.

the ankle joint through the prescribed range of motion without active subject resistance (referred to herein as passive rotation). Two trials were collected for each movement. Participants rested between trials and were allowed to practice the movement prior to data collection. All three of these conditions were randomized.

Isolated Contractions: Data Processing and Analysis

We located the position of the medial gastrocnemius MTJ in each frame of ultrasound video using an automated deep learning algorithm (17). We co-registered these positions with the position of the calcaneal marker as a surrogate for Achilles tendon insertion and calculated the Achilles tendon elongation relative to the start of each isokinetic contraction or passive rotation.

The Achilles free tendon ultrasound data and the corresponding motion capture data were then used to estimate participant-specific moment arms. For each ankle joint angle used during isometric testing, we estimated the Achilles tendon (AT) moment arm using previously published procedures as the average perpendicular distance between the tendon's line of action, registered manually in the ultrasound images, and the transmalleolar midpoint (18). We then fit a second-order curve to those points that we used to calculate AT moment arm as a function of ankle joint angle for each participant.

We estimated time series of AT force by dividing net ankle joint moments measured from the dynamometer by participant-specific AT moment arm. Finally, we calculated AT stiffness (i.e., k_{AT}) as the linear slope of the relation between AT force and AT elongation between 20% and 80% of each participant's dorsiflexion range of motion.

Treadmill Walking: Net Metabolic Power and Ankle Joint Biomechanics

During a 5-min standing trial and a 5-min habitual walking trial, we sampled breath-by-breath rates of oxygen consumption and carbon dioxide production using a COSMED K5 indirect calorimetry system (COSMED, Rome, Italy). For each, we computed the average rates of gas exchange over the final 2 min of each collection. We used the Brockway equation to estimate whole body net metabolic power from these average rates of oxygen consumption and carbon dioxide production (19). Finally, we subtracted standing values from walking metabolic power to calculate net metabolic power, which we normalized to participant body mass (W/kg). During the same 5-min habitual walking trial, we recorded 3-D ground reaction forces from a split-belt instrumented treadmill (1000 Hz, Bertec, Columbus, OH) and trajectories of a full body marker set of 53 markers (100 Hz, Motion Analysis, Santa Rose, CA). We used standard inverse kinematics and kinetics using previously published procedures (20) implemented in OpenSim (simtk.org) to estimate stride-averaged net ankle joint moment. Unlike the controlled measurements above that permit personalized estimates of the Achilles tendon moment arm, we have previously reported that the simultaneous and rapid changes in joint angle and muscle loading hallmark to the stance phase of walking (21) elicit complex effects on the Achilles tendon moment arm. Thus, we divided each subject's net ankle moment by a published Achilles tendon moment arm length of 44.7 mm (18) and retained only positive values to estimate peak plantarflexor, and thus Achilles tendon, force during walking (see discussion of limitations for important considerations).

Statistical Analysis

The primary outcome measures in this study were Achilles tendon stiffness, measured during passive rotation and during eccentric dorsiflexion tasks performed at 25% and 75% MVIC activation, and net metabolic power during walking. We assessed between-group differences in net metabolic power as well as peak plantarflexor force using an independent-samples t test. For k_{AT}, we performed a two-way mixed-effects ANOVA to test for a significant effect of age (between-subject effect; old vs. young) and activation (within-subjects factor; passive, 25%, 75%). Partial eta squared (η_p^2) provided the magnitude of the interaction and main effect sizes. We performed all analyses in SPSS and defined significance using an α level of 0.05 for all comparisons.

RESULTS

We did not find a significant interaction between triceps surae activation level and age for k_{AT} ($F_{2,56} = 1.41$, $P = 0.250$, $\eta_p^2 = 0.05$) (Fig. 2). However, a significant main effect of age ($F_{1,28} = 4.34$, $P = 0.046$, $\eta_p^2 = 0.13$) revealed that older adults exhibited, on average, 44% lesser k_{AT} than younger adults across activation conditions. In addition, a significant main effect of activation level ($F_{2,56} = 17.80$, $P < 0.001$, $\eta_p^2 = 0.39$) revealed that, across age-groups, k_{AT} increased roughly fourfold from passive rotation to 25% MVIC activation and again by +65% from 25% to 75% MVIC activation. We also found that older adults walked with 17% higher net metabolic power than younger adults (older vs. younger: 3.11 ± 0.36 W/kg vs. 2.66 ± 0.58 W/kg) ($P = 0.017$) but no significant difference in peak tendon force ($P = 0.470$). Post hoc analysis confirmed that ankle joint kinematics were indistinguishable between older and younger adults for peak ankle dorsiflexion ($P = 0.10$) and stance phase range of motion ($P = 0.33$). We found that during ankle plantarflexion MVICs at a neutral ankle angle of 0°, our older adults exhibited 28% smaller MVIC ankle moments (1.06 ± 0.40 N m/kg) than our younger adults (1.47 ± 0.37 N m/kg, $P < 0.001$). We found no correlations between k_{AT} during passive rotation or at 25% MVIC activation and net metabolic power during walking ($r \leq 0.07$, $P \geq 0.05$) (Fig. 3, *A* and *B*). Conversely, we found that k_{AT} measured at 75% MVIC activation significantly and positively correlated with net metabolic power during walking ($r = -0.365$, $P = 0.048$) (Fig. 3*C*). Finally, Fig. 4 illustrates representations of the tendon length-tension relations in younger and older adults combined with group-average net tendon forces to facilitate deeper discussion and interpretation in the next section.

DISCUSSION

The purposes of this study were to *1*) quantify age-related differences in local Achilles tendon stiffness across a range of matched muscle activations using electromyographic biofeedback and *2*) determine the relation between Achilles tendon stiffness at matched activations and the metabolic cost of walking across age. Consistent with our first hypothesis, younger and older adults exhibited Achilles tendon stiffness that increased with increasing triceps surae activation. This outcome reflects the nonlinear length-tension relation for tendon and demonstrates how the mechanics of a seemingly passive elastic tissue can depend on muscle activation-mediated force. Consistent with our second hypothesis, older adults exhibited, on average, 44% less Achilles tendon stiffness than younger adults at matched triceps surae activations. As we describe in more detail below, together with comparable peak tendon forces in walking, we offer an interpretation of these data to implicate altered tendon length-tension relations with age rather than differences in the operating region of those length-tension relations between younger and older adults. Finally, consistent with our third hypothesis and as the major contribution of this article, we discovered empirical evidence that lesser Achilles tendon stiffness exacts a metabolic penalty and is positively correlated with higher net metabolic power during walking.

Our results agree well with previously published literature. Our controlled-loading experiments generated activation-dependent (really, load-dependent) effects on Achilles tendon stiffness that are highly consistent with those published previously for ankle joint quasi-stiffness in younger and older adults (16). For example, we showed that ankle joint quasi-stiffness increased by a factor of 6- to 10-fold from passive rotation to isokinetic dorsiflexion at 75% MVIC activation,

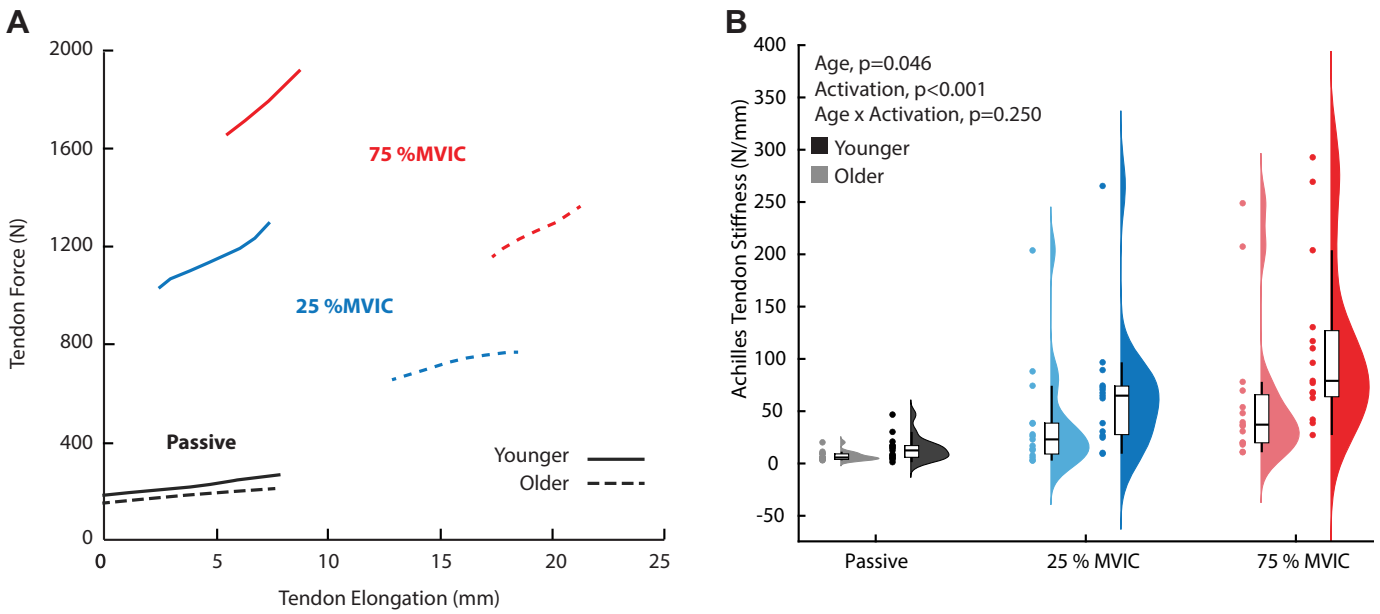

Figure 2. *A*: tendon force (N) vs. tendon elongation (mm) for younger (solid lines) and older adults (dashed lines) during isokinetic ankle dorsiflexion performed at rest (i.e., passive) and at 25% and 75% of peak activation during a maximum voluntary isometric contraction (MVIC). *B*: rain cloud plots showing Achilles tendon stiffness (N/mm) derived from the same isokinetic ankle dorsiflexion protocol as panel *A*.

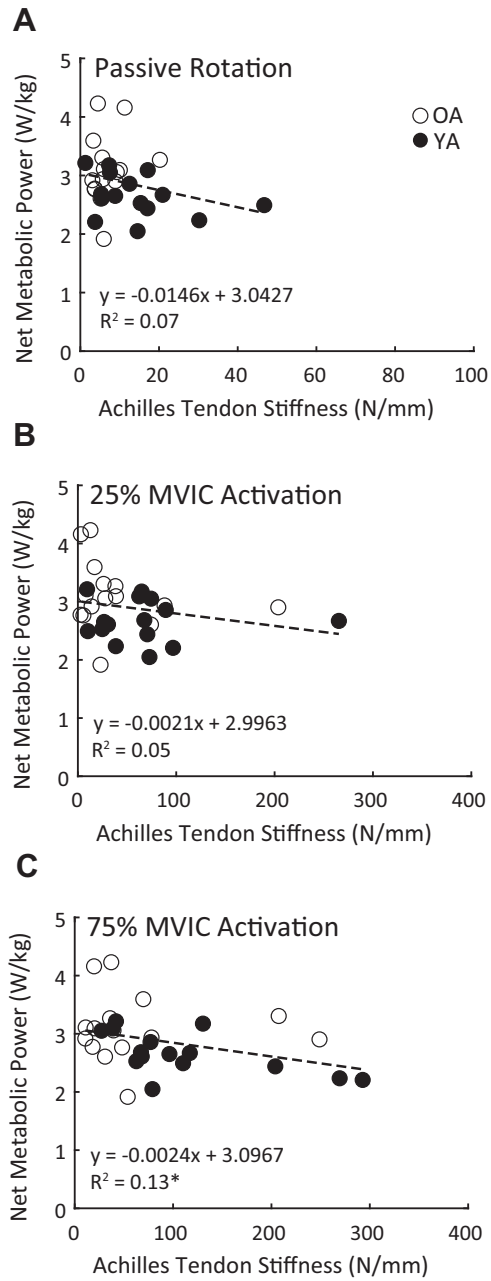

Figure 3. Correlations between Achilles tendon stiffness and net metabolic power during treadmill walking. Values shown represent Achilles tendon stiffness values derived during isokinetic ankle dorsiflexion performed at rest (*A*; i.e., passive) and at 25% (*B*) and 75% (*C*) of peak activation during a maximum voluntary isometric contraction (MVIC). Linear fit and statistical outcomes shown for the combined cohort of older and younger adults. *Correlation deemed statistically significant (i.e., $P < 0.05$).

whereas here k_{AT} increased herein by a factor of 8–9 over the same range of activations. These changes may at first be counterintuitive but reflect the nonlinear nature of tendon length-tension relations. In addition, our average between-group difference in Achilles tendon stiffness (i.e., −44% in older vs. younger adults) is consistent with the majority of in vivo human studies (9, 10, 22–27). Though, we acknowledge that animal studies sometimes arrive at different conclusions (28–30). We also note the discontinuities between conditions evident in Fig. 2. This may point to differences in relative load sharing between the plantarflexor muscles, suggesting that our results may be best interpreted in the context of the medial gastrocnemius and not necessarily extended to the soleus. Finally, our between-group differences in walking net metabolic power (i.e., +17% in older vs. younger adults) agree well with the range of previously published values, which typically average +15%–20% (31). From our data in Fig. 3 and Table 1, we can see a wide distribution among both age-groups and that the significant correlation between tendon stiffness and walking metabolic cost appears driven by the relation in younger adults. Thus, we emphasize the need for larger cohort studies designed to enroll exclusively older adults to determine the relevant factors that precipitate associations between tendon stiffness and walking metabolic cost.

There are at least two explanations for the observed age-related reduction in Achilles tendon stiffness across the range of matched activations prescribed using EMG biofeedback. The rightward shift evident in our overall data (i.e., indicating more tendon lengthening per unit increase in force) points to a reduction in k_{AT} as is classically defined by a shallower length-tension curve across the range of activations. We contend that this is typically how age-related reductions in Achilles tendon stiffness are interpreted in the available human literature (32). Indeed, we have used this interpretation as a mechanism for shorter triceps surae fascicle lengths in older adults during walking (33) and as evidence for a "structural bottleneck" that may have metabolic implications (11). Our data support these interpretations and implications. Conversely, our results contradict the other proposed effect of aging, namely, that older adults may operate their triceps surae during walking at a shallower region of their tendon length-tension relations than younger adults. This phenomenon is certainly true for older adults at a prescribed relative activation (Fig. 4). However, at least in our study, older adults walked with indistinguishable Achilles tendon forces as younger adults. Accordingly, although electromyography was not recorded during walking, we can reliably predict that these older adults are activating their calf muscles more than younger adults to generate these requisite walking forces—a behavior fully in line with our earlier theoretical work and thus a very plausible mechanistic explanation for our metabolic outcomes and novel correlations.

We have previously demonstrated that *1*) older and younger adults can modulate ankle joint quasi-stiffness via activation-dependent changes in triceps surae muscle length-tension behavior, and *2*) despite age-related reductions in ankle joint quasi-stiffness during controlled contractions, older adults maintain quasi-stiffness during walking via a local adaptive response of increasing triceps surae activation. This discovery motivated the need to deploy EMG biofeedback to match activation in comparisons of Achilles tendon stiffness between older and younger adults. However, our theoretical model in that previous article purported that, independent of age, ankle joint quasi-stiffness arises from activation-dependent (muscle) and activation-independent (tendon) components. Our results here reveal that the theoretical model motivating that earlier article was incorrect and neglected consideration that the nonlinear portion of the tendon's length-tension relation is relevant across a range of muscle activations. These results should compel efforts to revisit previous comparisons

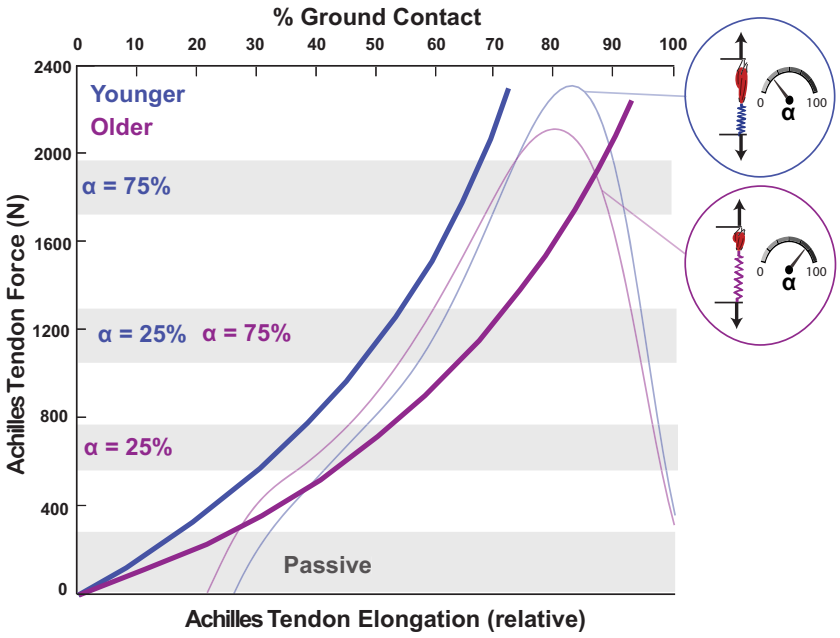

Figure 4. We offer here a conceptual interpretation of our stiffness data from Fig. 2 in the context of physiological tendon force levels estimated in older (purple) and younger (blue) adults during walking. Data implicate altered tendon length-tension relations with age rather than differences in the operating region of those length-tension relations between younger and older adults. Conceptually, the reduction in Achilles tendon stiffness in our older adults would compel shorter triceps surae muscle lengths and thus higher relative excitations (α) than younger adults to generate the requisite Achilles tendon forces necessary to walk at a given speed. We propose this mechanistic framework, supported by the empirical data in this article, as a likely explanation for associations between reduced Achilles tendon stiffness and higher metabolic cost of walking in our older adult participants.

of ankle-joint quasi-stiffness and its neuromechanical origins, to include the veracity of interpretations of between-condition and between-group comparisons.

From a clinical perspective, our results suggest that interventions designed to augment Achilles tendon stiffness may help to reduce walking metabolic cost for older adults. These results provide experimental credibility to similar recommendations made following the use of musculoskeletal simulations to predict the bioenergetic consequences of walking with reduced Achilles tendon stiffness (14, 20). As one example, conventional resistance training exercises (i.e., calf muscle strengthening) have been shown to effectively increase not only muscle strength, which we did find a deficit of in our older adult population, but also elicit tendon remodeling and increased stiffness. As an alternative example, if decreased tendon stiffness causes muscles to operate at shorter lengths, which requires greater requisite activation, passive elastic ankle exoskeletons may be beneficial due to their capacity to allow muscles to operate at longer lengths at lesser activation and thereby decrease metabolic cost (34, 35). The aforementioned interventions can directly augment Achilles tendon stiffness and thereby promote more economical triceps surae muscle contractions at longer lengths (36). However, one notable challenge to the clinical translation of our findings is the direct versus indirect consequences of age-related reductions in Achilles tendon stiffness on metabolic cost. For example, those with reduced k_{AT} may exhibit compensations at the hip, which could play a larger role in increasing metabolic cost. Thus, more work in this area is warranted, to consider precision joint-specific interventions—perhaps through the targeted use of both assistive and resistive wearable technologies.

There are several limitations of this work. One limitation is the lack of mechanistic walking data to more objectively link reduced k_{AT} with increased metabolic cost. We have previously outlined in detail the neuromechanical cascade we believe is responsible for this association (11), but more comprehensive-scale analyses relating changes in k_{AT} to individual muscle dynamics and/or lower limb joint mechanics during walking could help fill this gap (37) with more cause-effect precision. Another limitation is that we used EMG biofeedback to match activations between younger and older adults and not force. This was a purposeful methodological decision and should be used as motivation for further study. Our EMG biofeedback averaged lateral gastrocnemius and soleus activation, and potential differences in relative force contributions between these muscles were unaccounted for in our analysis and interpretation. We also acknowledge that the correlation between reduced k_{AT} and increased walking metabolic cost was significant but relatively weak. This is not surprising, as the mechanisms governing increased walking metabolic cost due to age are likely numerous and complex. As one example, Hortobágyi et al. (38) found that roughly one-third of the increase in metabolic cost could be explained by the economic consequences of antagonist muscle coactivation. We have no measure of dorsiflexor activation from our EMG biofeedback trials and assume negligible contributions from those muscles to the measured ankle joint moment. The same is true during walking for which, despite small but known contributions from other muscles (39), we assume that all of the net ankle moment during late stance is transmitted via the Achilles tendon. Thus, our tendon force outcomes may underestimate actual values, to

Table 1. *Group-specific correlation statistics*

	Passive Rotation		25% MVIC		75% MVIC	
k_{AT} vs. Net Metabolic Power	R^2	P	R^2	P	R^2	P
Younger adults	0.12	0.20	0.00	0.87	0.35	0.02*
Older adults	0.03	0.54	0.05	0.42	0.00	0.85
Combined	0.07	0.16	0.05	0.24	0.13	0.05*

*Significant correlation between Achilles tendon stiffness (k_{AT}) and net metabolic power ($P < 0.05$). MVIC, maximum voluntary isometric contraction.

include those used in the calculation of tendon stiffness. There may also be important interactions between age and co-activation during these isolated contractions that are worth exploring in future studies. This article simplifies the treatment of Achilles tendon architecture to a single series-elastic structure. More work in this area will be needed to determine the relevance of individual muscle-subtendon interaction (40) on the metabolic cost of operating the triceps surae during walking. Finally, we acknowledge a relatively small sample size, particularly considering the presumably complex etiology of higher metabolic costs in the aging process and the diversity of age-related mobility impairments.

In conclusion, we provide empirical evidence that lesser Achilles tendon stiffness in older versus younger adults exacts a significant metabolic penalty and is positively correlated with higher net metabolic power during walking. These results pave the way for interventions focused on restoring ankle muscle-tendon unit structural stiffness to improve walking energetics in aging.

DATA AVAILABILITY

Data will be made available upon reasonable request.

GRANTS

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DISCLAIMERS

This article was prepared while Rebecca L. Krupenevich was employed at the University of North Carolina at Chapel Hill. The opinions expressed in this article are the author's own and do not reflect the view of the National Institute on Aging, the National Institutes of Health, the Department of Health and Human Services, or the US government.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

R.L.K., G.S.S., and J.R.F. conceived and designed research; A.J.G. and R.L.K. performed experiments; A.J.G., R.L.K., and J.R.F. analyzed data; A.J.G., R.L.K., G.S.S., and J.R.F. interpreted results of experiments; A.J.G., G.S.S., and J.R.F. prepared figures; A.J.G. and J.R.F. drafted manuscript; A.J.G., R.L.K., J.A.B., G.S.S., and J.R.F. edited and revised manuscript; A.J.G., R.L.K., J.A.B., G.S.S., and J.R.F. approved final version of manuscript.

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