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Imaging and simulation of Achilles tendon dynamics: implications for walking performance in the elderly

Young Scientist Post-doctoral Award

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1. Abstract

The Achilles tendon (AT) is a complex structure, consisting of distinct fascicle bundles arising from each triceps surae muscle that may act as mechanically independent structures. Advances in tissue imaging are rapidly accelerating our understanding of the complexities of functional Achilles tendon behavior, with potentially important implications for musculoskeletal injury and performance. In this overview of our recent contributions to these efforts, we present the results of complementary experimental and computational approaches to investigate AT behavior during walking and its potential relevance to reduced triceps surae mechanical performance due to aging. Our experimental evidence reveals that older tendons exhibit smaller

differences in tissue deformations than young adults between regions of the AT presumed to arise from the gastrocnemius and soleus muscles. These observations are consistent with a reduced capacity for inter-fascicle sliding within the AT, which could have implications for the mechanical independence of the triceps surae muscles. More uniform AT deformations are also correlated with hallmark biomechanical features of elderly gait – namely, a loss of net ankle moment, power, and positive work during push-off. Simulating age-related reductions in the capacity for inter-fascicle sliding in the AT during walking predicts detriments in gastrocnemius muscle-tendon mechanical performance coupled with underlying shifts in fascicle kinematics during push-off. AT compliance, also suspected to vary due to age, systematically modulates those effects. By integrating *in vivo* imaging with computational modeling, we have gained theoretical insight into multi-scale biomechanical changes due to aging, hypotheses regarding their functional effects, and opportunities for experiments that validate or invalidate these assertions.

2. Introduction

The triceps surae muscles (i.e., gastrocnemius and soleus) generate 70-80% of the mechanical power needed for an effective push-off during walking (Farris et al. 2012, Zelik et al. 2015). However, despite similar stance phase activation profiles and a common insertion onto the Achilles tendon, the gastrocnemius and soleus muscles exhibit different fascicle kinematics during stance and have unique biomechanical effects on gait (Gottschall et al. 2003, Ishikawa et al. 2005, Miyoshi et al. 2006, McGowan et al. 2008, Francis et al. 2013). For example, while conclusions differ between studies, most attribute a larger role in forward propulsion and vertical support to the gastrocnemius and soleus, respectively (**Fig. 1**). Fascinatingly, the Achilles tendon (AT) may be uniquely designed to facilitate complex coordination between the triceps surae muscles; the AT consists of distinct bundles of tendon fascicles arising from the medial and lateral gastrocnemius and soleus that may act as mechanically independent structures (Szaro et al. 2009). Indeed, sliding between adjacent fascicle bundles in the AT may enable the gastrocnemius and soleus muscles to operate more independently, and perhaps facilitate contraction at lengths more effective for force production (Thorpe et al. 2012, Franz et al. 2015).

Within this anatomical framework, advances in tissue imaging are rapidly accelerating our understanding of the complexities of *in vivo* triceps surae muscle-tendon mechanics (Fukunaga et al. 2002, Lichtwark et al. 2005, Lichtwark et al. 2006, Magnusson et al. 2008, Farris et al. 2012), with important implications for coordination and performance. Our recent contributions to these efforts have focused on the *in vivo* characterization of localized AT deformations during walking and the relevance of those deformations to degradations in triceps surae mechanical performance due to aging (Franz et al. 2015, Franz et al. 2015). Compared to younger tendons, older tendons are thought to exhibit a reduced capacity for inter-fascicle sliding potentially arising from a proliferation of collagen cross-linking and inter-fascicle adhesions (Thorpe et al. 2013). Thus, if the AT is designed to facilitate relatively independent behavior between the gastrocnemius and soleus muscles during walking, old adults may be susceptible to a loss of that independence, with potentially detrimental effects on force and power production during push-off. Indeed, the net moment and power generated by the gastrocnemius and soleus during push-off decline precipitously in old age but the mechanisms underlying this biomechanical change are poorly understood (Winter et al. 1990, DeVita et al. 2000, Franz et al. 2014).

In this overview of our recent work, we present our experimental findings and introduce a complementary *in silico* approach as we seek to investigate aging effects on triceps surae muscle-tendon coordination during walking. Throughout, we frame our discussion first in the context of functional anatomy and second with regard to multi-scale biomechanical changes due to aging. Our ongoing work is founded on two working hypotheses. First, we hypothesize that the anatomical arrangement of the triceps surae facilitates relatively independent gastrocnemius and soleus muscle-tendon behavior in walking. Second, we hypothesize that this independent behavior is altered by aging in a way that negatively affects triceps surae muscle-tendon coordination and thus net ankle joint kinetics during push-off. Finally, we describe opportunities for future experiments to validate or invalidate the theoretical framework and hypotheses arising from the interpretation of our findings thus far.

3. Characterizing *in vivo* Achilles tendon tissue deformations

Cine ultrasound imaging has provided tremendous insights into triceps surae behavior during locomotion. However, traditional ultrasound imaging tracks distinct landmarks such as a muscle-tendon junction, and thus can only estimate average behavior (e.g., elongation) over the length of the Achilles tendon (Fukunaga et al. 2002, Lichtwark et al. 2005, Lichtwark et al. 2006). To overcome this limitation, we have adopted a novel 2D ultrasound speckle-tracking algorithm to directly image localized Achilles tendon tissue motion *in vivo*. We have previously elaborated on the technical details of the approach, its validity, and its use during functional and dynamic activities (Chernak et al. 2012, Slane et al. 2014, Franz et al. 2015). In our ongoing experimental work, we use this technique to characterize differences in tendon tissue deformations (i.e., displacements and elongations) during walking between regions of the Achilles free tendon thought to arise from the gastrocnemius and soleus muscles (Franz et al. 2015) and how this *in vivo* behavior changes with aging (Franz et al. 2015).

3.1. In vivo ultrasound imaging

In these experiments, subjects walk barefoot on a force-sensing treadmill (Bertec Corporation, Columbus, OH) while wearing an orthotic securing a 10 MHz, 38 mm linear array transducer (L14-5 W/38, Ultrasonix Corporation, Richmond, BC) over their right Achilles free tendon, on average centered 6 cm superior to the calcaneal insertion (**Fig. 1**). In brief, we use this transducer to collect radiofrequency (RF) data at 155 frames/s from a longitudinal cross-section of the tendon through a 2 cm depth. We then create a reference B-mode image of the relatively unloaded Achilles tendon immediately after toe-off and manually place of grid of nodes (1 mm × 0.5 mm initial spacing) on the image of the visible tendon. We then apply a 2D speckle-tracking algorithm, which calculates frame-to-frame nodal displacements from the maximum of 2D normalized cross-correlations between RF data in rectangular kernels (2 mm x 1 mm) centered at the nodal positions and those in rectangular search windows in the subsequent frame. Kernel trajectories are accumulated by integrating frame-to-frame displacements over all frames within a cine collection. When analyzing a gait cycle, we generate cyclic nodal displacement trajectories as a weighted average of forward and backward tracking results, a process used to minimize the accumulation of bias errors (Pelc 1995). Finally, we average nodal displacements originating from two equally-sized depths of the Achilles tendon, superficial and deep, approximating the tendon tissue arising from the gastrocnemius and soleus, respectively (**Fig. 1**).

There are two major challenges to this imaging approach. First, 2D ultrasound images do not allow for tracking out-of-plane tissue motion, which may arise both due to the helical structure of tendon and the anatomical arrangement of fascicle bundles within the Achilles tendon. The prospective use of three-dimensional ultrasound in musculoskeletal image tracking represents an exciting opportunity to overcome this challenge. Nevertheless, our speckle-tracking approach has reliably estimated tissue motion within axially loaded tendons free to exhibit transverse rotation (Slane et al. 2014). Second, we regularly observe very strong normalized cross-correlations between successive frames, even during dynamic activities such as walking (r > 0.95). However, impact transients, such as that arising from heel-strike when walking at faster speeds, tend to temporarily de-correlate frame-to-frame estimates of nodal displacements, which can temporarily reduce the accuracy of motion estimates. We have thus far avoided frame-to-frame decorrelations by studying treadmill walking at speeds of 1.25 m/s and slower. Although not a focus of the present work, overcoming this limitation could enable *in vivo* characterization of localized Achilles tendon tissue deformations during activities more prone to tendon injury such as running, jumping, or other sports-related activities.

3.2. Integrated motion capture and analysis

Using ultrasound imaging alone, we calculate relative displacements between AT regions attributed to the gastrocnemius and soleus as an indicator of inter-fascicle sliding. However, inspired by prior studies (Lichtwark et al. 2005, Lichtwark et al. 2006), our work also uses synchronized motion capture operating at 200 Hz to record the motion of the ultrasound transducer as well as the trajectories of 17 anatomical markers on the pelvis and right and left legs and an additional 14 tracking markers affixed using rigid clusters. These data enable us to project the 2D AT tissue displacements into 3D laboratory coordinates, thereby co-registering the ultrasound images with down-sampled anatomical marker trajectories. Using these data, we estimate AT tissue elongation (i.e., stretch[1]) as the change in length between the ultrasound-based nodal displacements and the calcaneal insertion, estimated using the posterior calcaneus marker.

[1] We use the term stretch in this instance as a synonym for tendon tissue elongation relative to toe-off. However, this reference length may not represent the actual slack length of the Achilles tendon. Thus, we use the term elongation throughout the manuscript.

Our work seeks to test the hypothesis that a reduced capacity for sliding between fascicles in the aging Achilles tendon alters in vivo behavior, thereby affecting gastrocnemius and soleus muscle-tendon biomechanical performance in old adults. Thus, as outlined in our recent publication (Franz et al. 2015), we use inverse dynamics to estimate net ankle joint moment, power, and positive mechanical work during push-off and correlate these outcomes with superficial-deep variations in Achilles tendon deformations. In the following section, we briefly summarize our experimental evidence to date in support of this hypothesis.

4. Aging and triceps surae muscle-tendon coordination: experimental evidence

4.1. In vivo Achilles tendon deformations

In our experiments, the AT of young adults exhibited behavior indicative of inter-fascicle sliding during walking, evidenced by deformations that differ significantly between superficial and deep regions of the tendon presumed to arise from the gastrocnemius and soleus muscles, respectively (**Fig. 1B**). Moreover, depth-dependent variation in tendon motion in young adults became progressively larger with faster walking speed, averaging 27% during the stance phase of walking at 1.25 m/s (**Fig. 2A**). In contrast, old adults failed to exhibit this progressive increase in relative motion between superficial and deep AT regions. Consistent with an age-related reduction in the capacity for inter-fascicle sliding, old adults exhibited 41% smaller superficial-deep variations in AT tissue deformations when walking at 1.25 m/s (**Fig. 2A**).

4.2. Relation to triceps surae biomechanical performance

Our ongoing work further suggests that the reduction in relative motion between the superficial and deep regions of the AT is associated with unfavorable changes in gastrocnemius and soleus muscle-tendon coordination in old adults. This is highly relevant, as reduced mechanical performance of the plantarflexor muscles during walking (e.g., **Fig. 2B**) may precede the age-related slowing of walking speed, which in turn compromises health and independence. Our experiments have revealed that smaller superficial-deep variations in AT tissue deformations are most strongly correlated with reduced peak ankle moment (R^2=0.40, p<0.01), but also correlated with peak ankle power (R^2=0.15, p<0.01) and positive work (R^2=0.19, p=0.01) during push-off (**Fig. 2C**).

4.3. Interpretation and implications

Our experimental observations in young adults reveal that fascicle bundles within the human AT exhibit markedly different *in vivo* behavior during walking, which may reflect their role as mechanically independent structures. We also find a potentially important association between altered triceps surae muscle-tendon coordination, evidenced by more uniform AT deformations, and diminished net ankle joint kinetics in walking due to aging. One possible explanation for these significant correlations is that a reduced capacity for sliding in old Achilles tendons unfavorably couples gastrocnemius and soleus muscle-tendon behavior, which could in turn negatively affect muscle force production. However, obvious challenges preclude the use of human subject testing to investigate inter-fascicle sliding as an independent variable to gain mechanistic insight into its biomechanical consequences. Thus, in the following section, we sought to tailor a computational proxy to investigate the implications of altered AT behavior on triceps surae muscle output.

5. Aging and triceps surae muscle-tendon coordination: computational predictions

5.1. Musculoskeletal model development

Current musculoskeletal models simplify triceps surae architecture by representing the gastrocnemius and soleus as independent muscle-tendon actuators (Arnold et al. 2010). This may be an appropriate assumption if their respective tendinous structures freely slide relative to one another. However, this assumption may not hold with aging, as inter-fascicle adhesions form and reduce the capacity for sliding between adjacent tendon fascicles (Thorpe et al. 2013). Tendon also undergoes microstructural changes with aging that are believed to increase its compliance (Onambele et al. 2006), consistent with ultrasound imaging studies of the Achilles tendon in walking (Mian et al. 2007, Panizzolo et al. 2013). Tendon compliance systematically influences muscle fiber kinematics and kinetics (Lichtwark et al. 2008), and could thereby modulate the effects of inter-fascicle adhesions in the aging Achilles tendon. Here, we developed simple computational models of the plantarflexor muscle-tendons (**Fig. 3**) to investigate the independent and combinatory effects of inter-fascicle adhesions and tendon compliance on triceps surae muscle fiber kinematics and the performance of mechanical work in walking.

Ten young adults (age: 25.4 ± 2.8 years, mass: 65.1 ± 11.6 kg, height: 1.71 ± 0.11 m) walked at their preferred speed (1.34 ± 0.14 m/s) down a 10 m walkway. On average, subjects walked overground at a speed of 1.34 ± 0.14 m/s, slightly faster than the prescribed treadmill speed of 1.25 m/s used in our imaging studies. A motion capture system operating at 200 Hz recorded the three-dimensional trajectories of markers placed on the pelvis and lower extremities. For each subject, we estimated gastrocnemius and soleus muscle-tendon unit (MTU) lengths over one stance phase from scaled, seven-segment, 18 degree-of-freedom musculoskeletal models (Arnold et al. 2010). MTU lengths then served as boundary conditions in models composed of (*i*) independent and (*ii*) coupled gastrocnemius and soleus Hill-type muscle-tendon actuators (Zajac 1989) implemented in Simulink (Mathworks, Natick, MA) (**Fig.**

3). Muscle-tendon actuators incorporated excitation-activation dynamics and force-length and force-velocity actuation dynamics (Zajac 1989). We calculated changes in pennation angle during the stance phase using changes in muscle length by neglecting muscle shape changes (Azizi et al. 2008), thereby assuming invariant muscle anatomical width. Muscle and tendon properties (i.e., maximum isometric force, optimal fiber length, pennation angle, and tendon slack length) were prescribed for each subject according to Arnold et al. (2010). In models composed of independent muscle-tendons, we used constrained optimization (fmincon, Mathworks, Inc., Natick, MA) to derive muscle excitation profiles that maximized stance phase MTU positive work per unit activation. These excitations were prescribed for models composed of coupled muscle-tendons, described as follows.

We modeled inter-fascicle adhesions (i.e., MTU coupling) by incorporating a section of the distal AT common to the gastrocnemius and soleus muscles and shortening the distinct gastrocnemius and soleus tendons accordingly. To simulate varying degrees of inter-fascicle adhesion, we incorporated two shared AT lengths (i.e., 10 cm and 20 cm). For simulations with coupled muscle-tendon dynamics, we calculated lengths of the shared Achilles tendon and the distinct gastrocnemius and soleus tendons that satisfied:

$$l_{S,MTU} = l_{AT} + l_{S,tendon} + l_{S,fiber} \cos \alpha_S \quad (1)$$

$$l_{G,MTU} = l_{AT} + l_{G,tendon} + l_{G,fiber} \cos \alpha_G \quad (2)$$

$$F_{AT} = F_{S,tendon} + F_{G,tendon} \quad (3)$$

In Eqs. (1) – (3), l_{AT} refers to the shared Achilles tendon length, and $l_{S,MTU}$ and $l_{G,MTU}$ refer to the lengths of the prescribed soleus and gastrocnemius muscle-tendon units, $l_{S,tendon}$ and $l_{G,tendon}$ to the lengths of the distinct soleus and gastrocnemius tendons, and $l_{S,fiber}$ and $l_{G,fiber}$

to the lengths of the soleus and gastrocnemius muscle fibers, respectively. Also, F_{AT} ,$F_{S,tendon}$, and $F_{G,tendon}$ refer to the forces in the shared Achilles tendon and the distinct soleus and gastrocnemius tendons, respectively, and α is the pennation angle. Finally, we repeated all simulations using a range of tendon compliances, from 3 to 12% strain at maximum isometric force (ε_o), representing that commonly evaluated in the literature (Arnold et al. 2013).

For each simulation, we extracted the following outcome measures: fiber and tendon length, fiber velocity, MTU force, power, and positive mechanical work. A two-way repeated measures ANOVA tested for significant main effects of and interactions between adhesions (i.e., MTU coupling) and compliance on each outcome measure using an alpha level of 0.05.

5.2. Triceps surae muscle-tendon kinematics

Simulating inter-fascicle adhesions altered muscle-tendon kinematics, with opposing changes evident in the gastrocnemius and soleus that became more pronounced with greater MTU coupling (**Fig. 4**). Compared to independent MTUs driven by the same excitations, MTU coupling elicited up to an average of 5% longer peak fiber lengths (i.e., further from optimal) and 6% faster peak shortening velocities in the gastrocnemius (main effect, p's < 0.01). These changes contrasted those in the soleus, for which adhesions elicited 9% shorter peak fiber lengths (i.e., closer to optimal) and 3% slower peak shortening velocities (main effects, p's < 0.01). Although gastrocnemius and soleus fiber lengths at the instant of peak force were relatively insensitive to MTU coupling (i.e., <1% change), fiber velocities at peak force were greatly affected (**Fig. 5A**). At the instant of peak force, simulating adhesions simultaneously elicited on average up to 13% faster gastrocnemius shortening velocities and 7% slower soleus shortening velocities (main effects, p's<0.01).

5.3. Triceps surae muscle-tendon kinetics

Simulating adhesions also elicited significant and similarly opposing changes in gastrocnemius and soleus muscle-tendon kinetics. When coupled to the soleus MTU, peak gastrocnemius MTU force and power averaged up to 8% and 9% smaller, respectively, compared to actuators acting independently (main effects, p's < 0.01) (**Fig. 4**). In contrast, simulating adhesions increased peak soleus MTU force and power by an average of up to 4% and 3%, respectively (main effect, p's < 0.01). Accordingly, these changes elicited, on average, up to a 13% decrease in gastrocnemius positive work coupled with a 5% increase in soleus positive work during stance (main effect, p<0.01) (**Fig. 4**). While significant (p<0.01), reductions in total triceps surae power and positive work for coupled vs. independent MTUs were modest (i.e., < 1%).

5.4. Modulation by altered tendon compliance

Tendon compliance systematically altered muscle-tendon performance, wherein an average optimum elasticity (ε_o=8.3%) maximized both gastrocnemius and soleus MTU positive work per unit activation (main effect, p's < 0.01) (**Fig. 4**). Tendon compliance also modulated the effects of inter-fascicle adhesions, with significantly larger changes in muscle-tendon behavior arising with increasing tendon compliance (**Figs. 4-5A**). Significant interactions revealed that the reductions in gastrocnemius MTU peak force, peak power, and positive work due to MTU coupling were on average up to six times larger at the highest tendon compliance (i.e., ε_o=12%) compared to those at the lowest (i.e., ε_o=3%) (p's < 0.01). The corresponding enhancements in soleus MTU peak force, peak power, and positive work also increased significantly for the same change in tendon compliance (interaction, p's < 0.01).

5.5. Interpretation and implications

We used simple musculoskeletal models to gain mechanistic insight into the experimentally observed relation between more uniform Achilles tendon deformations and reduced plantarflexor performance during the push-off phase of walking in old compared to young adults. We interpret model outcomes as coarse predictions of the functional consequences of inter-fascicle adhesions in the aging Achilles tendon, which may act to couple gastrocnemius and soleus muscle-tendon behavior during movement. Foremost, we found that simulating age-associated adhesions in the Achilles tendon redistributed force, mechanical power, and positive work from the gastrocnemius to the soleus in a manner consistent with changes in muscle fiber kinematics. Moreover, our findings at the instant of peak force during late stance suggest that altered fiber velocities contributed significantly more than altered fiber operating lengths to these changes in muscle-tendon kinetics. This latter finding is consistent with an exploratory series of simulations in which we removed the force-length characteristics of muscle and found a similar redistribution of mechanical performance from the gastrocnemius to the soleus (**Fig. 5B**).

Due to considerable but offsetting changes in gastrocnemius and soleus kinematics and kinetics, we observed only modest effects of coupled versus independent MTUs on total triceps surae power and positive work. However, the gastrocnemius and soleus are known to perform different biomechanical functions in walking, with the prevailing theory that the gastrocnemius contributes more to forward propulsion than the soleus (Gottschall et al. 2003, Miyoshi et al. 2006, Francis et al. 2013). In this context, despite little change in net triceps surae mechanical output, it is functionally significant that the relative mechanical deficits experienced by the gastrocnemius were considerably larger than the mechanical enhancements experienced by the soleus. For example, compared to acting as an independent actuator, the faster shortening velocities of the gastrocnemius were accompanied by up to a 16% reduction in positive mechanical work during push-off when coupled to the soleus MTU. The apparent redistribution of that positive work to the soleus represented only a 6% enhancement, resulting largely from slower shortening velocities during push-off. Thus, a reduced capacity for inter-fascicle sliding in the aging Achilles tendon (Thorpe et al. 2013) may preferentially influence the triceps surae's ability to generate forward propulsion during walking, an important function of the gastrocnemius muscle and well-documented biomechanical difference between old and young adults (Winter et al. 1990, DeVita et al. 2000, Franz et al. 2014).

Coupling of the gastrocnemius and soleus MTUs via inter-fascicle adhesions is but one of many plausible and potentially interdependent musculoskeletal mechanisms underlying the age-related reduction in plantarflexor performance in walking. Indeed, we observed the most substantial changes in muscle-tendon kinematics and kinetics when co-simulating a reduced capacity for inter-fascicle sliding and an increase in tendon compliance. Prior studies have used models to investigate the independent effects of tendon compliance on triceps surae behavior, and our simulation results are in good agreement with these observations (Lichtwark et al. 2008, Arnold et al. 2013). Moreover, the optimal tendon compliance identified by our simulations (i.e., ε_o=8.3%), while higher than some modeling studies (Lichtwark et al. 2008), are near that recently found to best match experimental estimates of net ankle moment and power (i.e., 10%) (Arnold et al. 2013). Increased compliance and inter-fascicle adhesions are both purported features of the aging Achilles tendon (Mian et al. 2007, Panizzolo et al. 2013, Thorpe et al. 2013) and may also vary with musculoskeletal injury or disease. We show here that these factors have independent and combinatory effects that significantly alter model predictions of triceps surae behavior. Thus, our observations may have broad implications for simulating the effects of aging, injury, or disease, for which modeling efforts generally simplify triceps surae architecture by representing the gastrocnemius and soleus as independent muscle-tendon actuators (Arnold et al. 2010).

6. Summary and conclusions

Our ongoing work seeks to investigate: (*i)* the extent to which triceps surae anatomy facilitates relatively independent gastrocnemius and soleus muscle-tendon behavior in walking, and (*ii*) whether this independent behavior is altered by aging in a way that negatively affects triceps surae muscle-tendon coordination and thus net ankle joint kinetics during push-off. We have summarized the results of complementary experimental and computational approaches investigating aging effects on triceps surae muscle-tendon coordination during walking. Together, our findings suggest that relative independence between fascicle bundles comprising the human AT may be important for the effective transmission of gastrocnemius and soleus muscle forces in walking. The theoretical insight into multi-scale biomechanical changes due to aging and hypotheses regarding their functional effects developed thus far now provide important opportunities for experiments that validate or invalidate our assertions. For example, the strategic use of electrical muscle stimulation in synchrony with *in vivo* imaging may isolate changes in the relative independence of the gastrocnemius and soleus MTUs due to aging. Our computational predictions also provide a reference for important future *in vivo* imaging work investigating aging effects on individual triceps surae muscle fascicle kinematics in walking. Ultimately, future comparative experiments combining *ex vivo* and *in vivo* techniques with multi-scale imaging and image-based modeling may provide the most direct evidence to test these hypotheses.

By continuing to integrate *in vivo* imaging with computational modeling, we hope to improve our understanding of age-related changes in triceps surae muscle-tendon coordination and its relevance to independent mobility in our aging population. Investigating the prevalence and functional relevance of inter-fascicle adhesions in the aging AT may have translational potential to inform preventative or restorative therapies to better maintain mechanical performance of the plantarflexor muscles in old adults. Comparative work may consider the introduction of lubricin to aging tendon, a glycoprotein recently found to facilitate tendon fascicle sliding by reducing inter-fascicular friction (Kohrs et al. 2011). More conservative approaches may include the potential for activities such as running to prevent the onset of inter-fascicle adhesions or physical therapy to promote independent actuation of the gastrocnemius and soleus muscles.

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Conflict of Interest Statement:

The authors have no conflicts of interest to disclose.

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Figure Captions

Figure 1. (A) We used a custom orthotic and a two-dimensional ultrasound speckle-tracking algorithm to estimate tendon tissue displacements in superficial and deep regions of the Achilles tendon during treadmill walking at 0.75, 1.00, and 1.25 m/s (copied with permission from Franz et al. 2015). (B) Young adult average (standard error) ankle moment during the stance phase of walking at 1.25 m/s plotted over the stance phase. During the push-off phase of walking, contributions from the gastrocnemius and soleus muscles to accelerating the center of mass are shown, adapted with permission from Liu et al. (2006). Although conclusions differ between studies, most studies attribute larger roles in forward propulsion and vertical support to the gastrocnemius and soleus, respectively, consistent with their induced acceleration vectors shown here. Finally, accompanying their biomechanical differences, regions of the AT presumed to arise from the gastrocnemius (i.e., superficial) and soleus (i.e., deep) muscles exhibit significantly different peak elongations. Asterisk (*) indicates $p<0.05$.

Figure 2. Old and young adult average (standard error) peak (A) AT tissue displacement (B) and ankle moment, and (C) the association between these outcome measures across the range of walking speeds tested. Our experimental findings reveal that: (i) old adults exhibit significantly more uniform (defined as difference between deep and superficial portions of the free AT) deformations than young adults, and (ii) more uniform AT deformations are associated with reduced net ankle moment, power, and positive mechanical work during push-off.

Figure 3. Computational model development to simulate the effects of inter-fascicle adhesions and altered tendon compliance. Muscle-tendon unit (MTU) lengths derived from scaled, seven segment, 18 degree-of-freedom musculoskeletal models [2], which then served as boundary conditions in models composed of independent and coupled gastrocnemius and soleus Hill-type muscle-tendon actuators. Muscle excitations for each muscle were derived via constrained optimization to maximize an objective function defined as the positive MTU work per unit activation.

Figure 4. Model-predicted effects of inter-fascicle adhesions and tendon compliance on gastrocnemius and soleus muscle-tendon (A) kinematics and (B) kinetics. Results are shown across the range of simulated tendon compliances, from 3% to 12% strain at maximum isometric force (ε_o). For data plotted over the stance phase, gray shading indicates the period over which the gastrocnemius or soleus muscle is active, determined using the constrained optimization approach outlined in Section 5.1. a and b indicate significant effects of adhesions at 3% and 12% strain, respectively ($p<0.05$). HS: heel-strike, TO: toe-off.

Figure 5. (A) Model-predicted effects of inter-fascicle adhesions and tendon compliance on gastrocnemius and soleus force-velocity characteristics at the instant of peak muscle-tendon unit force. Results are shown across the range of simulated tendon compliances, from 3% to 12%

strain at maximum isometric force (ε_o). (B) Results for simulations including both the force-length (FL) and force-velocity (FV) characteristics of muscle compared to simulations excluding the force-length characteristics for a representative subject at a nominal tendon strain of 8%. Our findings suggest that altered fiber velocities contribute significantly more than altered fiber operating lengths to changes in muscle-tendon kinetics due to simulating adhesions.