Gait & Posture 67 (2019) 194–200

Contents lists available at ScienceDirect

Gait & Posture

journal homepage: www.elsevier.com/locate/gaitpost

Plantarflexor metabolics are sensitive to resting ankle angle and optimal fiber length in computational simulations of gait

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ARTICLE INFO

Keywords:
Computational modeling
Gait
Muscle tendon unit
Resting ankle angle
Sensitivity analysis

ABSTRACT

Background: Plantarflexor structure is an important predictor of function in healthy, athletic, and some patient populations. Computational simulations are powerful tools capable of testing the isolated effects of muscle-tendon structure on gait function.

Research Question: The purpose of this study was to characterize the sensitivity of plantarflexor muscle function based on muscle-tendon unit (MTU) parameters. We hypothesized that plantarflexor metabolics and shortening dynamics would be sensitive to MTU parameters.

Methods: Stance phase of gait was simulated using a musculoskeletal model and computed muscle control algorithm. Optimal muscle fiber length, resting ankle angle, and tendon stiffness parameters were systematically changed to test these effects on plantarflexor metabolics, activation, and power. Dorsiflexor metabolics were also measured to determine the impact of the action of the antagonist muscle group.

Results and Significance: Plantarflexor metabolic demands were 1.5 and 2.7 times more sensitive to optimal fiber length and resting ankle angle, respectively, compared to the effect of tendon stiffness. Increased resting ankle plantarflexion induced a large passive plantarflexion moment during early stance, which required non-physiologic dorsiflexor contractions. Conversely, longer optimal fiber and more neutral resting ankle angles increased the shortening demands of the plantarflexors. These findings highlight the importance of carefully selecting MTU parameters when modeling gait with musculoskeletal models, especially in pathologic or high-performance athlete populations.

1. Introduction

Locomotor performance is associated with plantarflexor structure and function in both athletic and patient populations [1–4]. Longer muscle fascicles allow sprinters to generate more joint power [5], which, in part, explains performance differences between good and great sprinters [6]. Tendon stiffness, a function of both its slack length and material properties, dictates the shortening demands of the plantarflexor muscles and impacts movement efficiency [7–9]. While these muscle-tendon parameters seem to explain functional differences in patient and athletic cohorts, the isolated effects of these structural measurements are difficult to elucidate due to variability inherent to *in vivo* research models.

Musculoskeletal models are powerful tools used with clinical gait analysis to test specific questions regarding muscle and tendon structure and function in isolated computational experiments. In these models, joints are actuated by muscle-tendon units (MTU) that have been developed using cadaveric measurements of muscle and tendon structure [10]. While some models account for patient-specific differences in joint strength [11], many often rely on the default MTU parameters, including optimal fiber length and tendon slack length and stiffness to simulate gait. While these MTU parameters may be appropriate for some cohorts, special populations often have different muscle tendon structure [3,5]. Simulated gait mechanics are sensitive to MTU parameters [7,8,12]; for example, tendon slack lengths have the greatest effect on joint torques while tendon stiffness and optimal muscle fiber lengths appear to govern plantarflexor metabolic. However, the combined effects of these MTU parameters on simulated shortening dynamics and metabolic requirements of the plantarflexors during gait are not fully understood.

The purpose of this study was to perform a sensitivity analysis on plantarflexor MTU parameters during simulated gait. Specifically, we utilized a musculoskeletal model to test the effects of plantarflexor optimal fiber length, resting ankle angle (a surrogate measure of tendon length [13]), and Achilles tendon stiffness on the plantarflexor energetics and muscle shortening dynamics during the stance phase of

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https://doi.org/10.1016/j.gaitpost.2018.10.014
Received 22 May 2018; Received in revised form 9 October 2018; Accepted 11 October 2018
0966-6362/

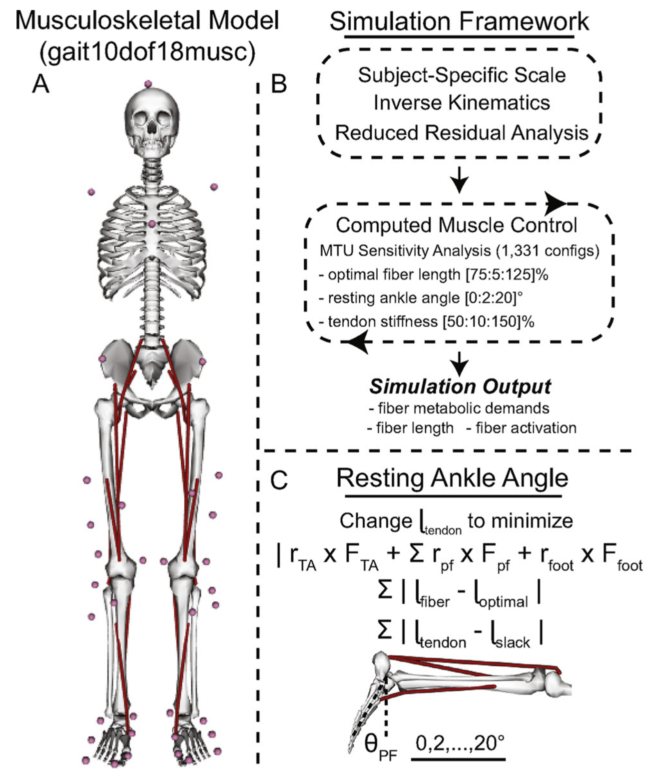

Fig. 1. Stance phase of gait was simulated using a musculoskeletal model constrained to move in the sagittal plane (*A*). A sensitivity analysis was performed on three muscle-tendon unit (*MTU*) parameters: optimal fiber length, resting ankle angle, and tendon stiffness (*B*). Muscle-tendon unit slack lengths were solved by calculating static equilibrium based on the three MTU parameters tested in this parameterization study.

walking. Based on prior computational and physical experiments, we hypothesized that plantarflexor metabolic demands would be sensitive to the three MTU parameters: (1) more plantarflexed resting ankle angles would decrease metabolic demands [3], (2) optimal fiber length would be negatively correlated with metabolic demands [7,14], and (3) tendon stiffness would be the strongest predictor of metabolic demands [14]. Shorter optimal fiber lengths and increased resting ankle angles should increase the amount of passive power generated by the MTU during stance, and thus reduce the plantarflexor metabolic demands.

2. Materials and methods

Human walking was simulated using open-source musculoskeletal modeling software (OpenSim, v3.3) and publically available gait data [15]. These gait data included marker trajectories for both a static pose as well as marker trajectories and ground reaction force data for a single walking trial. To reduce the complexity of human gait, we decided to utilize a computational model that moved only in the sagittal plane with simplified joints and a reduced set of muscles (Fig. 1). The sagittal plane model consisted of 8 segments that had 10°-of-freedom, defined by 7 sagittal-plane joints and actuated by 18 MTUs (gait10dof18musc, Opensim) and 3 pelvis degrees of freedom (X–Y translation and sagittal rotation). The ankle was modeled as a pin-joint that was flexed by a single dorsiflexor muscle, the tibialis anterior, and extended by two plantarflexor muscles, the soleus and gastrocnemius (which represents both the medial and lateral muscle bellies). Muscles were modelled as Hill-type muscle bundles that included a contractile muscle element in series with an elastic tendon-like element [16].

Stance phase during gait was simulated using a previously established framework [15] (Fig. 1). First, a generic model was scaled to match the anatomic proportions and body mass of the research subject. Second, joint kinematics were calculated to best fit the experimentally acquired motion data. using the Inverse Kinematics algorithm. Third, the Residual Reduction algorithm was performed to adjust the torso model mass and joint coordinate trajectories to ensure dynamic consistency of the simulation (average residual errors: anterior force 3.77 N, superior force 2.85 N, sagittal moment 3.38 Nm). Finally, the Computed Muscle Control (CMC) algorithm [17] calculated muscle excitations that generated model motion that matched the kinematics and externally applied forces while minimizing the sum of squared muscle activations. Reserve actuators provided additional joint torques to track the desired model kinematics (optimal load 1Nm).

A sensitivity analysis was performed to characterize the effects of perturbing MTU parameters on muscle metabolic demands and shortening dynamics (Fig. 1b). Specifically, we perturbed the default optimal muscle-fiber lengths, Achilles tendon stiffness values, and the resting ankle angle in order to test physiologically-relevant changes in tendon slack length (Fig. 1c). Optimal fiber lengths of the ankle plantarflexors (4.4 cm soleus and 5.5 cm gastrocnemii, [10]) were simultaneously scaled in 5% increments from 75% to 125% of the standard model lengths, which were compensated for by equivalent reductions in peak isometric force to simulate a constant muscle volume. Achilles tendon stiffness was modeled as the tendon strain at the maximum isometric force of each plantarflexor muscle. The default values of 4.9% strain at maximum isometric force were tested in 10% increments from 50% to 150% of default values [18–20]. Resting ankle angles were tested in 2° increments from 0° neutral to 20° plantarflexion (10° default), which represents physiologic ranges of healthy adults as well as those who suffered an Achilles tendon rupture [13]. These MTU parameter perturbations have been reported as physiologically relevant changes in patient populations [13,18] and trained athletes [6]. The dorsiflexor muscle optimal fiber length and stiffness were held constant at the model default, but the tendon slack lengths were changed in order to achieve ankle static equilibrium. In total, this parameterization study tested 1311 combinations of optimal plantarflexor fiber lengths, resting ankle angles, and Achilles tendon stiffness values.

Tendon slack lengths of the ankle muscles were modified for each MTU configuration in order to achieve a desired resting ankle angle (Fig. 1c). We performed the computational analog of instructing the patient to lay prone on a treatment table while the foot and ankle freely hangs at a 'resting angle'. First, the model was rotated 90° to simulate the subject resting in the prone position, and the optimal muscle fiber lengths and tendon stiffness values were adjusted. Second, the ankle was set to 18, −2, and 10° plantarflexion to calculate 'native' tendon slack lengths for the gastrocnemius, soleus, and tibialis anterior muscles, respectively [21,22]. Third, the ankle angle was set to the desired resting position between 0–20° of plantarflexion, and plantarflexor and dorsiflexor muscle activations were set to nominal amounts (1% and 3%, respectively). Finally, MTU slack lengths were adjusted to minimize a cost function Eq. (1) comprised of ankle joint torque, differences between optimal fiber lengths and simulated fiber lengths, and differences between the 'native' tendon lengths and previously determined tendon slack lengths and evaluated using a gradient-based optimization approach (fsolve, MATLAB, The Mathworks, Natick, MA). Native tendon slack lengths were used as initial guesses for all optimization calls and convergence occurred for all MTU parameter combinations.

$$minimize \begin{cases} \sum_{i=1}^{n\,pf} \left(\frac{isomax_{pfi}}{isomax_{pf}}\right) \times |\vec{r}_{TA} \times \vec{F}_{TA} + \vec{r}_{foot} \times \vec{F}_{foot} + \vec{r}_{pfi} \times \vec{F}_{pfi}| \\ \sum_{i=1}^{n\,musc} |\, l_{fiberi} - l_{optimali} \,| \\ \sum_{i=1}^{n\,musc} |\, l_{tendoni} - l_{native\_slacki} \,| \end{cases} \quad (1)$$

$$where \begin{cases} \vec{F}_{musc}(l_{tendon}) \\ l_{fiber}(l_{tendon}) \end{cases}$$

Where l_{tendon} – current tendon length, *r* – distance from force to ankle joint, F – force of MTU or foot segment, pf – plantarflexor muscles (gastrocnemius, soleus), TA – tibialis anterior, and $musc$ – all muscles (gastrocnemius, soleus, tibialis anterior), and F_{musc} and L_{fiber} were both functions of l_{tendon}.

Resting ankle angles were confirmed by performing forward simulations to calculate the true resting ankle angle as a function of the musculoskeletal parameters for each parameterized model. To confirm that the resting angle was not dependent on the starting position of the simulation, each model configuration was tested at initial positions that were offset from the desired resting ankle angle by 10° plantarflexion and 10° dorsiflexion. These simulations (N = 2662) always converged on the resting ankle angle (root mean square error: 0.29°).

Metabolic demands and shortening dynamics of the ankle muscles were evaluated during each simulation to quantify the effects of varying optimal plantarflexor fiber lengths, resting ankle angles, and tendon stiffness. Metabolic energy requirements of the gastrocnemius, soleus, and tibialis anterior muscles were estimated using a metabolic calculator developed by Umberger et al. [23]. Briefly, muscle metabolic requirements are expressed as the sum of the heat generated to activate and maintain muscle contraction, the heat generated during active shortening and lengthening, and the amount of mechanical work done. Thus, muscle activation, rate of fiber length change, and the force generated by the contractile element of the MTU are input variables into this algorithm. This algorithm was developed and validated using human data and found good agreement with the gastrocnemius, soleus, and tibialis anterior muscles during walking [23]. Muscle activations and active fiber powers were directly acquired from the musculoskeletal modeling software. Additionally, we calculated the metabolic costs of the combined hip muscles and knee muscles to determine if plantarflexor MTU parameters effected proximal muscle energetics.

The effects of MTU parameters on ankle muscle metabolics were quantified using a linear regression model (MATLAB, Mathworks, Natick, MA). Some simulations could not run to completion because of passive plantarflexion moments that were too large (150/1,331) to be countered by active dorsiflexor contractions and others (41/1,331) required greater than either 8 Nm of peak or 1 Nm of average reserve actuator torque to track the desired kinematics. We excluded these non-physiologic simulations from further analysis. We also performed multivariate linear regression to explain the effects of MTU parameters on dorsiflexor (tibialis anterior) metabolics. The effect sizes of each MTU parameter was reported as the change in metabolic energy consumption per kilogram of bodyweight for a 1% change in MTU parameters compared to the model default values. We decided to report each of these MTU parameter perturbations as a percent change from the default parameters and normalized by these physiologic ranges in order to demonstrate the relative sensitivity of this model to small changes in parameters.

3. Results

Optimal fiber length and resting ankle angles had effects of 1.5 and 2.7 times greater on plantarflexor metabolic demands than tendon stiffness, respectively (Table 1). Specifically, a 1% perturbation from the model default optimal fiber lengths, tendon slack lengths, and tendon compliances (Table 1) resulted in a 0.3%, −0.4%, and −0.1% increase in plantarflexor metabolic demands, respectively. Increased optimal fiber and decreased resting ankle plantarflexion angle imposed additional metabolic demands. Conversely, tendon stiffness demonstrated a slight parabolic effect on metabolics (Fig. 2); however, the effect of each of these MTU parameters was strongly explained by a linear regression model (R^2 = 0.752). Plantarflexor muscle activation patterns were most sensitive to changes in MTU parameters during late stance (Fig. 3A/C), particularly resting ankle angle (Fig. 3 top and middle row). Similarly, a less plantarflexed resting angle required greater plantarflexor shortening in order to maintain the necessary tendon tension (Fig. 3B/D).

Resting ankle angle had the strongest effect on dorsiflexor metabolic demands during stance phase of gait (Table 1). This demand was so great that 3% (41/1,331) of the simulations required large ankle, knee, or hip reserve actuator torques (average > 1Nm, peak > 8Nm) to track the desired kinematics (Fig. 4). These instances occurred exclusively when the resting ankle angle was plantarflexed (14–20°) and the optimal fiber lengths were reduced (≤95% model default). Decreased tendon stiffness mitigated the dorsiflexor demands with the resting ankle angle set between 14 and 16 °. The proximal muscles were not strongly affected by plantarflexor MTU perturbations, with the exception of the hamstring and biceps femoris muscles increased metabolic demands with a more plantarflexed resting ankle angle (Table 1).

Plantarflexor metabolic demands were minimized by reducing the optimal fiber length (−50% of physiologic range), increasing the resting ankle angle (30%), and reducing tendon stiffness (−50%). This metabolic minimum was explained by a short and stiff MTU that passively stored and returned energy during midstance (Fig. 5C), which reduced the amount of plantarflexor shortening and activation needed in late stance (Fig. 5A/B). MTU power was 76% greater (Fig. 5D) in this 'optimal' MTU configuration, which demonstrates that these large metabolic demands were non-physiologic and required increased dorsiflexor activations. Therefore, we excluded simulations that required more than 150% of the default dorsiflexor metabolic demands from further analysis. After excluding these simulations that produced non-physiologic metabolic demands (Table 1), plantarflexor metabolic demands were minimized when the optimal fibers were their shortest (−50%), increased resting ankle angle (20%), and a slightly more compliant tendon (−30%).

4. Discussion

In the present study, we highlighted the sensitive relationship between MTU parameters and muscle shortening dynamics and metabolic demands. Optimal fiber length and resting ankle angle had the strongest effects on plantarflexor shortening dynamics and metabolics (Figs. 2 and 3, Table 1). Surprisingly, tendon stiffness was less influential, despite the substantial relationships between stiffness and metabolics that has been reported by others [7,8]. In this model, we attempted to account for muscle remodeling that may be a response to functional demands [24] or injury [25,26] by changing tendon slack lengths in order to achieve static equilibrium in a range of resting ankle angles. Our results highlight the importance of plantarflexor MTU parameters on the metabolic cost of locomotion and should be considered carefully when simulating human motion.

Simulation results reported in this study compare favorably with previous computational investigations on the effects of MTU parameters on locomotor function. Resting ankle angle, a surrogate measure of tendon slack length [13] is the strongest predictor of metabolic demand as well as plantarflexor activation and shortening throughout stance (Fig. 3), which agrees with several other sensitivity studies [12,27–29]. Tendon stiffness had a slight parabolic effect of plantarflexor metabolics, with optimal muscle function occurring near the model default values, which matches the a previous report that leveraged the same inputs [8]. Plantarflexor metabolic demands were minimized when the optimal fiber lengths were reduced, which agrees with a prior report that found short muscle fibers in series with compliant tendons were optimal for walking [7]. Stiffer tendons reduced fiber shortening during the second half of stance (Fig. 3B/D), suggesting that strain energy can be more efficiently stored with less active muscle shortening.

Shorter optimal fiber lengths explain reduced metabolic demands (Fig. 2) and walking speed [14], which is in conflict with reports of longer muscle fibers being advantageous for faster motions like sprinting [5,30]. This difference between walking and running may not be that surprising given that walking is an energy efficient activity while sprinting is governed by how much work can be done to the ground. However, simple-submaximal activities such as rising on the

Table 1
Effect of 1% change of plantarflexor MTU parameters on muscle metabolics.

	%ΔPF	%ΔTA	%ΔGM	%ΔIL	%ΔRF	%ΔVA	%ΔHM	%ΔBF
Model results (N** = 1140**)								
Optimal fiber length	0.3*	< −0.1*	< 0.1*	< −0.1*	< −0.1*	< −0.1*	< 0.1*	−0.1*
Resting ankle angle	−0.4*	< 0.1*	< -0.1*	< 0.1*	< 0.1*	< 0.1*	0.2*	0.2*
Tendon stiffness	−0.1*	< 0.1*	< 0.01	< 0.1	< 0.1	< 0.1*	−0.1*	< −0.1*
Linear model fit (R^2)	0.752*	0.616*	0.049*	0.510*	0.191*	0.675*	0.704*	0.662*
Physiologic results (N** = 1021**)								
Optimal fiber length	0.2*	< −0.1*	< 0.1*	< −0.1*	< −0.1*	< −0.1*	< 0.1*	< −0.1*
Resting ankle angle	−0.3*	< 0.1*	< -0.1	< 0.1*	< 0.1*	< 0.1*	0.2*	0.3*
Tendon stiffness	−0.1*	< 0.1*	< −0.1	< 0.1*	< 0.1*	< 0.1*	< −0.1*	< −0.1*
Linear model fit (R^2)	0.764*	0.846*	0.030*	0.601*	0.149*	0.707*	0.866*	0.859*

PF – plantarflexors, DF – tibialis anterior, GM – gluteus maximus, IL – iliopsoas, RF – rectus femoris, VA – vastus, HM – hamstrings, BF – biceps femoris. Physiologic results exclude simulations with 1.5x greater DF metabolic demands.

* Significant predictors of metabolics ($P < 0.001$).

toes are correlated with tendon elongation, that can exceed 10% of the uninjured length, in patients who have suffered Achilles tendon ruptures [3]. Thus, there is a dichotomous need for shorter muscle fibers in order to walk efficiently and longer fibers to perform other tasks.

Based on our findings, simulation results are very sensitive to MTU parameters and must be carefully considered when utilizing musculoskeletal models to study muscle and tendon function. Deviations of MTU length as small as 2% from the default MTU length can result in simulations failing to run to completion or require non-physiologic amounts of reserve actuator or antagonist muscle activity (Fig. 4). These deviations in plantarflexor MTU parameters that increase passive tension affect the proximal muscles, most notably the knees that must expend greater metabolic energy to produce the desired kinematics. We decided to take one approach and 'tune' the MTU based on experimental measurements of tendon slack length [21,22]. Alternatively, subject-specific measurements of muscle function can be used to tune the model MTU parameters [31]. Regardless of the MTU tuning strategy, the current findings highlight the potential for non-physiologic simulation results with relatively small changes in resting ankle angles, and to a lesser extent optimal fiber length. However, the magnitude at which these effects are non-physiologic and cause for concern should be considered in the context of the specific research question and special population.

Several limitations should be considered when discussing the implications of this work. Model complexities were reduced to improve simulation speed, while reducing the uncertainty introduced by additional degrees of freedom and MTU actuators. We decided to utilize the Computed Muscle Control algorithm that minimized the sum of squared muscle activations [17,32]. This approach calculates muscle excitations that accurately track the desired kinematics; however, other approaches that permit alterations to joint kinematics may alter muscle metabolic demands. However, this approach is likely not suitable for simulating motion in individuals with injuries or disuse, which likely adopt different movement strategies. The plantarflexor muscles were modeled as two separate muscles with independent tendons rather than a combined tendon that represented the Achilles tendon. Further, the gastrocnemius was modelled as a single unit rather than having medial and lateral bellies, which have slightly different MTU structure [10]. We calculated muscle metabolic demands using an algorithm developed by Umberger et al. [23]. However, we did not test the effect of slow-fast twitch ratios, which differ between athletic populations [33] and simulated muscle metabolics can be prone to error [34]. Although the Achilles tendon is often recognized as a single connective tissue at the confluence of the plantarflexor muscles, recent evidence suggests that the discrete bundles that comprise the Achilles tendon function differently during walking [35]. Finally, we decided to utilize a well-documented and freely available data set so others can repeat these simulations; however, other activities and subject anthropometry could easily be implemented in future sensitivity analyses.

5. Conclusions

We performed a parameterization study to better understand the effects of MTU parameters on plantarflexor shortening dynamics and metabolic and during gait. The sensitivity of plantarflexors MTU parameters were tested due to effects of this muscle group on function in athletic [6], pathologic [3], and aging populations [2,14]. Our findings demonstrate that simulation results are very sensitive to optimal fiber and resting ankle angles, which should be carefully selected based on either experimental or optimization approaches. The relative lack of sensitivity to tendon stiffness, which conflicts with other reports, further highlights the importance of careful selection of MTU length

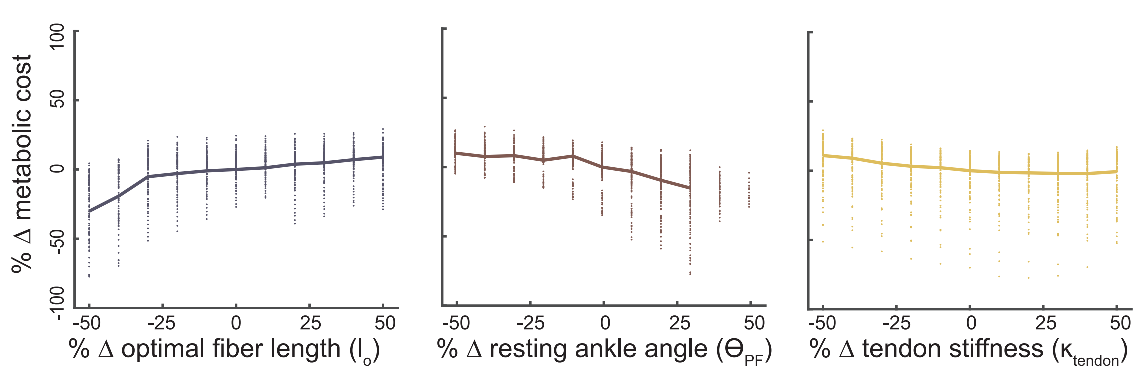

Fig. 2. Plantarflexor metabolic demands (Y-axis) were sensitive to small changes in muscle tendon unit (*MTU*) parameters (*X-axis*). Perturbations of the MTU parameters were normalized by the physiologic ranges of these parameters. Changes in plantarflexor metabolic demands were reported as percent changes from the default model results.

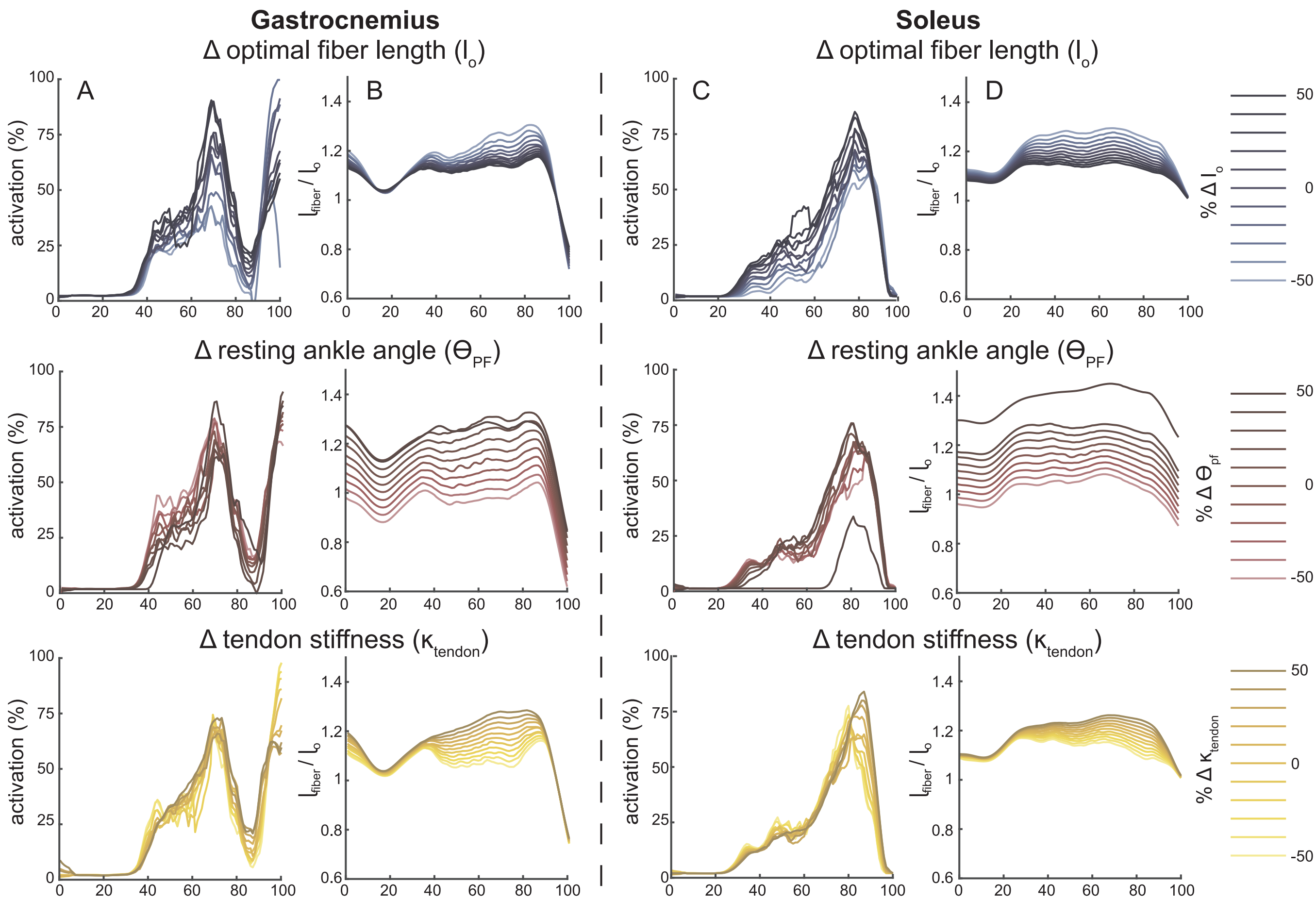

Fig. 3. Plantarflexor activations (*A,C*) and fiber lengths (*B,D*) during stance phase were more sensitive to changes in optimal fiber length (*top row, blue*) and tendon slack length (*middle row, red*) than tendon compliance (*bottom row, yellow*). Fiber length during stance phase was normalized by the optimal fiber length for that specific simulation (l_{fiber}/l_o). For clarity, these plots demonstrate the isolated effects of muscle tendon unit (*MTU*) parameters on activation and fiber length change by holding the other MTU parameters at their default values (Table 1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

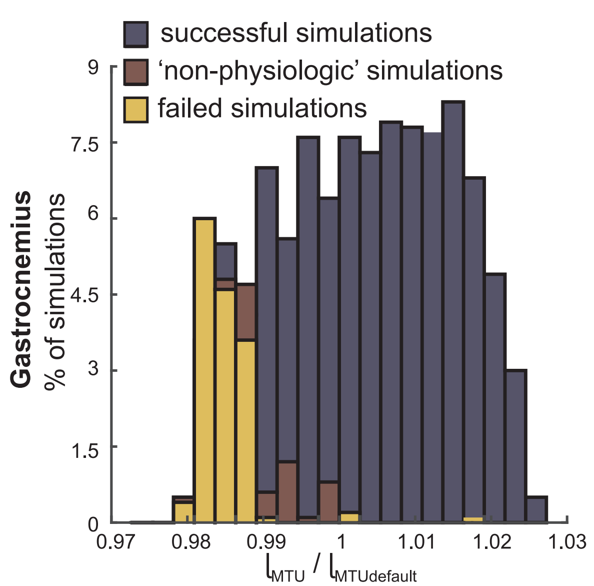

Fig. 4. Gastrocnemius muscle-tendon unit length, calculated as $lo \cdot cos\theta + lslack$ where θ is muscle pennation angle, appeared to be a strong determinant of whether a simulation ran successfully (*blue bars*), if 'non-physiologic' antagonist or reserve actuator torques were necessary (*red bars*), or if the simulation failed to complete (*yellow bars*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

parameters during simulation of human movement. Ongoing work is focused on improving MTU tuning algorithms aimed at modeling more physiologic muscle-tendon function.

Conflicts of interests

The authors have no disclosures that are related to this work.

Funding

No funding has been provided for this research.

Authors' contributions

JB and MH designed the experiment; JB performed the simulations and analyzed the data; JB and MH analyzed and interpreted the data; JB drafted the manuscript; JB and MH revised the intellectual content of the manuscript; JB and MH approved the final version of the manuscript; and JB and MH agreed to be accountable for all aspects of the study.

Acknowledgements

The Authors have no acknowledgements

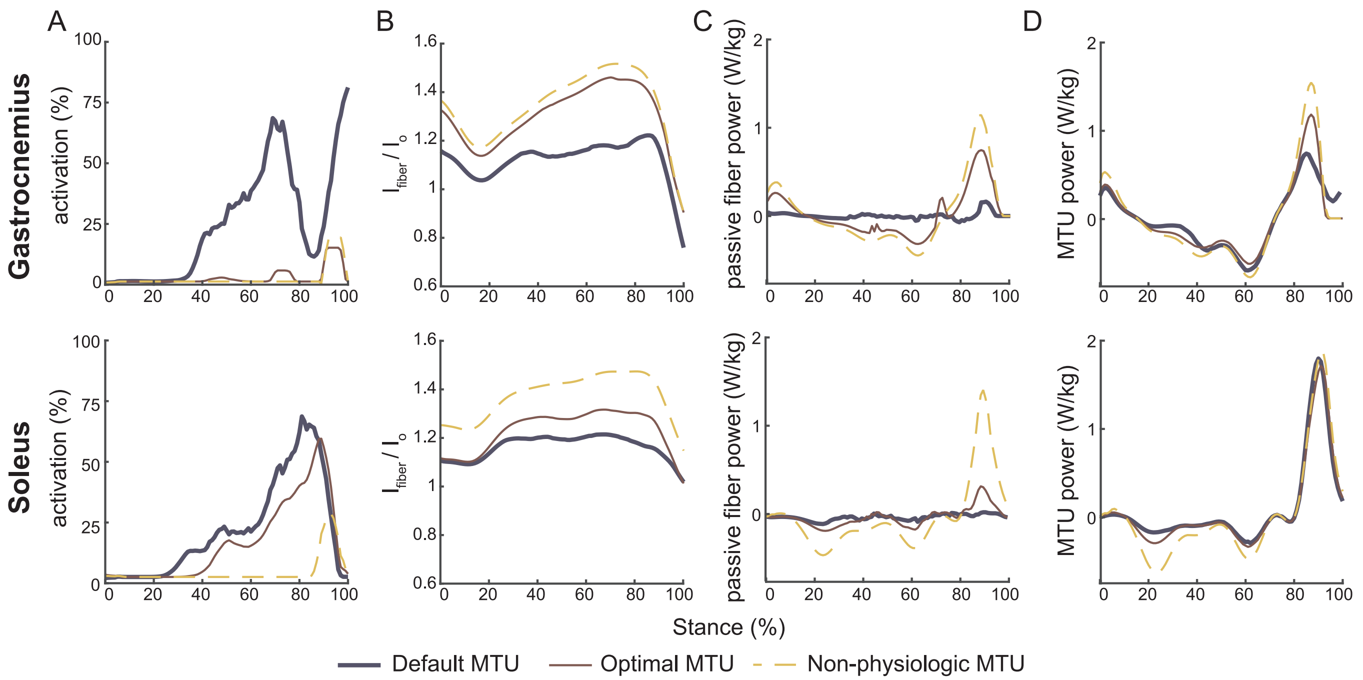

Fig. 5. Muscle activation (*A*), normalized fiber length (*B*), passive fiber power (*C*), and MTU power (*D*) differed between optimized plantarflexor shortening dynamics and the default MTU parameters (*thick blue line*). Non-physiologic MTU parameters (*dashed yellow line*) resulted in very short MTUs that required no activation to generate large amounts of passive fiber power. Optimized MTU parameters (*red line*), within physiologic conditions, reduced the gastrocnemius (*top*) activations but not the soleus (*bottom*) activation patterns. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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