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Short communication

The effects of Achilles tendon compliance on triceps surae mechanics and energetics in walking

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ABSTRACT

Achilles tendon (AT) compliance can affect the generation and transmission of triceps surae muscle forces, and thus has important biomechanical consequences for walking performance. However, the uniarticular soleus (SOL) and the biarticular (GAS) function differently during walking, with *in vivo* evidence suggesting that their associated fascicles and tendinous structures exhibit unique kinematics during walking. Given the strong association between muscle fiber length, velocity and force production, we conjectured that SOL and GAS mechanics and energetic behavior would respond differently to altered AT compliance. To test this, we characterized GAS and SOL muscle and tendon mechanics and energetics due to systematic changes in tendon compliance using musculoskeletal simulations of walking. Increased tendon compliance enlarged GAS and SOL tendon excursions, shortened fiber operation lengths and affected muscle excitation patterns. For both muscles, an optimal tendon compliance (tendon strains of approximately 5% with maximum isometric force) existed that minimized metabolic energy consumption. However, GAS muscle-tendon mechanics and energetics were significantly more sensitive to changes in tendon compliance than were those for SOL. In addition, GAS was not able to return stored tendon energy during push-off as effectively as SOL, particularly for larger values of tendon compliance. These fundamental differences between GAS and SOL sensitivity to altered tendon compliance seem to arise from the biarticular nature of GAS. These insights are potentially important for understanding the functional consequences of altered Achilles tendon compliance due to aging, injury, or disease.

1. Introduction

The triceps surae muscles (i.e., gastrocnemius and soleus) generate the majority of the mechanical power during push-off in walking and contribute significantly to vertical support and forward propulsion (Neptune et al., 2001). A simulated reduction in triceps surae strength negatively affects ankle power generation during push-off and, compared to weakness in other leg muscles, can preferentially elicit uncharacteristic gait patterns (Goldberg and Neptune, 2007). Hence, preserving gastrocnemius (GAS) and soleus (SOL) muscle function is considered clinically important. However, triceps surae muscle behavior is governed, in part, by series elasticity provided by the Achilles tendon (AT). Hence, changes in AT compliance, independent of triceps surae muscle strength, could have important biomechanical consequences that emerge during walking. A better understanding of the effects of AT compliance is necessary given the important changes in tendon mechanical behavior seen with age (Franz and Thelen, 2015; Slane and Thelen, 2015; Stenroth et al., 2012), injury (Geremia et al., 2015) and disease (Arya and Kulig, 2010; Child et al., 2010).

Prior studies reveal that simulating altered AT compliance substantially affects GAS mechanical work and metabolic energy consumption (Lichtwark and Wilson, 2008, 2007), as well as the magnitude and timing of ankle power generation (Zelik et al., 2014). Indeed, tuning between muscle activation, muscle fascicle behavior, and in series tendon elasticity is an important factor underlying muscle-tendon unit (MTU) performance. However, the effects of tendon compliance on SOL performance may differ from those on GAS (Uchida et al., 2016) due to differences in their function and kinematics. The uniarticular SOL and biarticular GAS

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contribute differently to vertical support and forward propulsion (Francis et al., 2013; Neptune et al., 2001; Stewart et al., 2007), and their associated tendinous structures exhibit different elongations (Franz et al., 2015). Therefore, GAS and SOL may also respond differently to the presence of altered tendon compliance in walking, with potential for unique changes in mechanical power generation and metabolic energy consumption.

We investigated how AT compliance differentially modulates GAS and SOL muscle-tendon mechanics and energetics during walking. Our approach involved systematically varying AT compliance in a musculoskeletal model of walking and estimating triceps surae mechanics and muscle-specific metabolic energy consumption. We tested the hypotheses that: (1) increasing AT compliance would increase tendon excursions, alter excitations and muscle fiber operating lengths, and increase muscle metabolic energy consumption, and (2) these changes would differ between GAS and SOL.

2. Materials and methods

We used available (simtk.org) kinematic and ground reaction force data from one healthy adult male (height: 1.8 m, mass: 75 kg) walking at 1.2 m/s on an instrumented treadmill (John et al., 2012). We implemented a simplified version of the Gait2392 model, with 12 segments and 10 degrees of freedom describing flexion-extension of the lumbar spine, hips, knees and ankles, pelvis tilt and vertical and anterior-posterior translation. Eighteen Hill-type muscles (Delp et al., 1990; Thelen, 2003) representing the ankle, knee and hip flexors and extensors, and one torque generator at the lumbar spine actuated the model. We modeled the Achilles tendon as two independent bundles: a gastrocnemius tendon and a soleus tendon. The musculoskeletal model was scaled using marker trajectories from a static pose and an inverse kinematic procedure found the generalized coordinates that best matched experimental marker trajectories during walking. A Residual Reduction Algorithm (RRA) adjusted the generalized coordinate trajectories and ensured dynamic consistency with measured external forces and modelling assumptions (Delp et al., 2007). Finally, a Computed Muscle Control algorithm (CMC) (Thelen and Anderson, 2006) derived GAS and SOL excitations that drove the musculoskeletal model (with $m = 18$ muscles and $n = 10$ generalized coordinates) to match available kinematic and ground reaction force data while minimizing the sum of squared muscle activation (a_i), in accordance with the performance criterion J (Eq. (1)).

We simulated altered AT compliance by increasing peak strain of the GAS and SOL AT bundles at maximum isometric muscle force (ε_0, range: 3.3–11.6%) while maintaining the nominal value (i.e., 3.3%) for all other tendons (Fig. 1). We assessed sensitivity of model predictions to CMC simulation settings. To do this, we repeated CMC six times for each AT compliance, slightly modifying the instant in the gait cycle at which simulation was initiated (2 conditions) and the CMC generalized coordinate tracking weights (w_j; 3 sets), which allowed each model generalized coordinate ($\ddot{q}_j$) to match the prescribed kinematics ($\ddot{q}_j^*$) within a specific error tolerance. Ensemble mean of the six simulations were computed for GAS and SOL excitations and fiber, tendon, and MTU excursions and powers. We focused our analyses on periods corresponding to GAS and SOL stretch-shortening (SS) cycles during stance and their respective stretching (ST) and shortening (SH) sub-phases.

$$J = \sum_{i=1}^{m} a_i^2 + \sum_{j=1}^{n} w_j(\ddot{q}_J^* - \ddot{q}_J)^2 \tag{1}$$

Positive, negative, and total work performed by GAS and SOL fiber, tendon, and MTU during the SS cycle and sub-phases were calculated by numerical integration of their respective power curves over the periods of interest. We also calculated the following quantities: the work performed on the tendon by external sources with respect to the MTU during the stretching phase (${}^{ST}W_T^{e-}$), i.e., tendon negative work (${}^{ST}W_T^-$) minus fiber positive work (${}^{ST}W_f^+$) during stretching; the work effectively performed by the tendon during the shortening phase (${}^{SH}W_T^{e+}$), i.e., tendon positive work (${}^{SH}W_T^+$) minus fiber negative work (${}^{SH}W_f^-$) during shortening.

GAS and SOL metabolic energy consumption were estimated using the OpenSim metabolic calculators, which predict mechanical work and thermal energy liberation according to the model from Umberger et al. (2003), which we normalized to body mass. Regression analysis estimates the values of ε_0 that minimized GAS and SOL metabolic energy consumption. The values obtained for GAS and SOL were compared using Z-Scores, considering a significance level of 5%.

3. Results

3.1. Muscle-tendon mechanics

Increasing AT compliance increased GAS and SOL tendon excursions (Fig. 2a) and caused their fibers to operate at shorter fiber lengths (Fig. 3). GAS tendon excursions were greater than SOL for all conditions, and this differential behavior became larger with increasing AT compliance (Fig. 2a). These changes were accompanied by larger GAS and SOL excitations during single support and smaller excitations during push-off (Figs. 2b and 3).

Several aspects of GAS and SOL tendon and fiber mechanics were affected differently by increasing AT compliance (Fig. 3). GAS fiber negative work during the stretching phase (${}^{ST}W_f^-$), decreased progressively with increasing AT compliance. In contrast, SOL ${}^{ST}W_f^-$ increased for $\varepsilon_0 > 5\%$ (Fig. 4b). Also during stretching, work performed on the tendon by the contractile element and by external sources with respect to the MTU increased with AT compliance for both GAS and SOL (Fig. 4a and c). Consequently, increasing AT compliance reduced positive GAS and SOL fiber work performed during the shortening phase (${}^{SH}W_f^+$, Fig. 4d). With increasing AT compliance, the percentage of energy stored in the tendon during stretching that was effectively reused during shortening decreased significantly only for GAS (Fig. 4e). Finally, only for GAS was ${}^{SH}W_T^{e+}$ less than the amount of work stored in the tendon

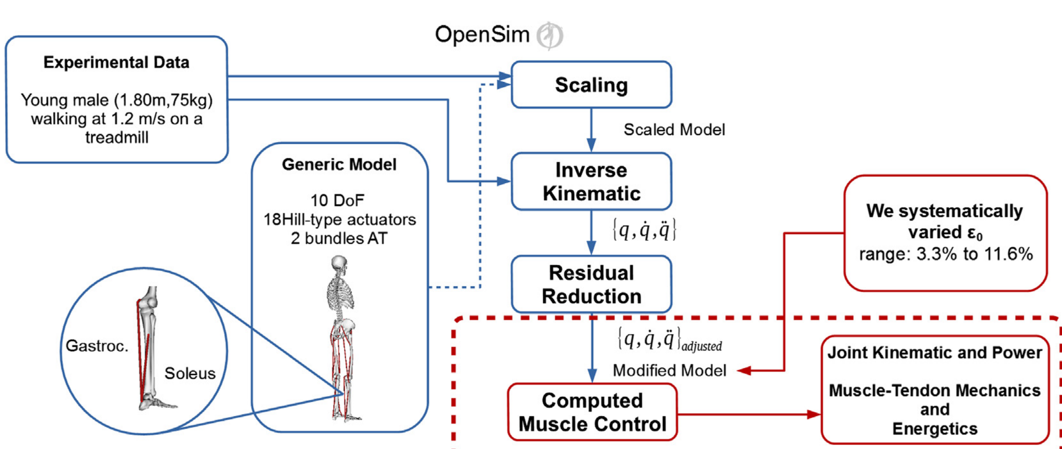

Fig. 1. Simulation workflow. In blue, the steps carried out before the data and model were made available for download via simtk.org; in red, the steps performed in order to modify the scaled model and run CMC algorithm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)