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WHICH MUSCLES AND TENDONS DO WORK DURING THE STANCE PHASE OF RUNNING?

[1]Matthew Millard, [1]Tim Dorn, [1]Ajay Seth and [1]Scott Delp
[1] Department of Bioengineering, Stanford University, USA; email: mjhmilla@stanford.edu

INTRODUCTION

The muscular work and changes of potential energy of the tendons of the human leg during the stance phase of running are unknown. While the muscular work and changes of tendon potential energy of the plantarflexors has been studied previously [1,2], it is difficult to place the plantarflexors in context without the contributions of the other muscles and tendons of the lower limb. A recent analysis found that the soleus does the most mechanical work of any musculotendon actuator [3] in the lower limb during the stance phase of running. This compelling result has motivated us to analyze the work contributions of the muscles and tendons of the leg to gain further insight into the energetics of human running.

The work done by a musculotendon actuator is the sum of the work done by the muscle less the potential energy stored in the tendon. The relative magnitude of the muscle's work contributions and the tendon's potential energy storage is largely determined by the stiffness of the tendon. At one extreme, where the tendon is rigid, the muscle does all the work of the musculotendon actuator. Conversely, it is possible for the tendon to do all of the work if the muscle contracts isometrically, acting like a mechanical clutch. In this case the actuator behaves like an ideal spring, and is able to store and release potential energy as it is lengthened and shortened.

While the relative contributions of the plantarflexor muscles and the Achilles tendon have been studied during human running [1,2], these contributions have not been placed in the context of the leg's other muscles and tendons. We hypothesize that the soleus muscle does the most work of any lower limb muscle during the stance phase of gait as suggested by several recent analyses [3,4]. The length of the Achilles tendon compels us to hypothesize that this tendon stores and releases more energy than any other tendon during the stance phase of running. We use a work analysis to test these hypotheses.

METHODS

We used the simulations of Hamner et al. [4] to compute the forces and contraction velocities of 43 Hill-type musculotendon actuators for each leg (Figure 1) of a single subject at four different running speeds: 2, 3, 4, and 5 m/s. The simulations were completed in OpenSim 3.0 [5] using a musculoskeletal model with 23 degrees-of-freedom and 92 musculotendon actuators. Activations were computed using

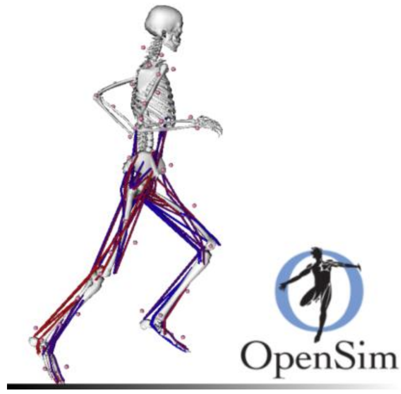

Figure 1: A musculoskeletal model of running [4] was used to calculate muscle work and tendon potential energy.

the Computed Muscle Control [6] algorithm. The muscles of the plantarflexors were treated as having their own independent section of Achilles tendon (denoted by superscript S, MG and LG for soleus, medial and lateral gastrocnemius respectively). Muscles were simulated using the damped-equilibrium muscle model [7] with a tendon compliance parameter set to 10% (strain at isometric muscle force) so that the Achilles tendon lengthened 18–22 mm during stance, which is consistent with experimental observations [1] of 22mm. A tendon compliance of 10% was used for all tendons to prevent a bias in the work analysis.

We computed the change in tendon potential energy during stance (ΔV) using the integral of its force-length curve (*V(t)*) during the simulations:

$$\Delta V = \max(V(t)) - \min(V(t)) \quad (1)$$

The work (*W(t)*) done by each muscle was computed by integrating the product of its force and shortening velocity:

$$W(t) = \int_{t0}^{t} f(t)v(t)\, dt \quad (2)$$

We computed the difference in work (ΔW) of each muscle during stance using Equation 2:

$$\Delta W = \max\big(W(t)\big) - \min\big(W(t)\big) \quad (3)$$

Energetically dominant muscles and tendons were identified by comparing the changes of tendon potential energy ΔV and muscular work ΔW. The Achilles^S tendon potential energy curves and soleus muscle work curves were also plotted to gain further insight into the dominance of the soleus musculotendon actuator in prior work.

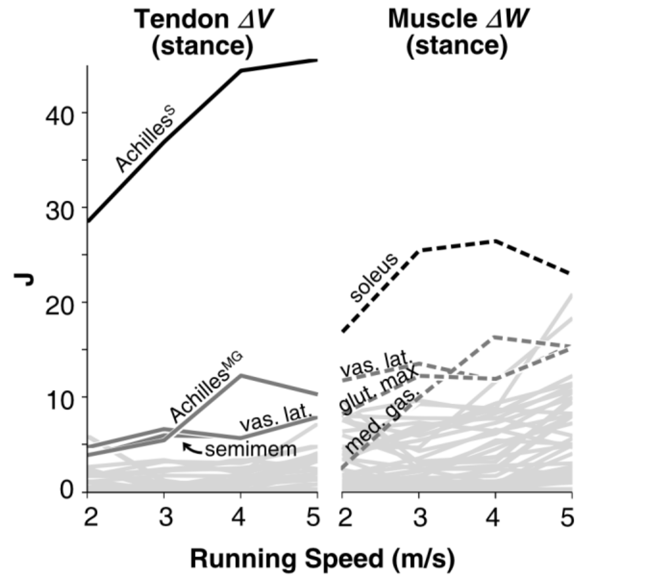

Figure 2: The left panel shows the potential energy stored and released, *ΔV*, by the tendons of the lower limb during stance. The right panel shows the change in work, *ΔW*, of the muscles of the lower limb during stance. Top contributors across all speeds are illustrated in black, major contributors in dark grey, and the rest in light grey.

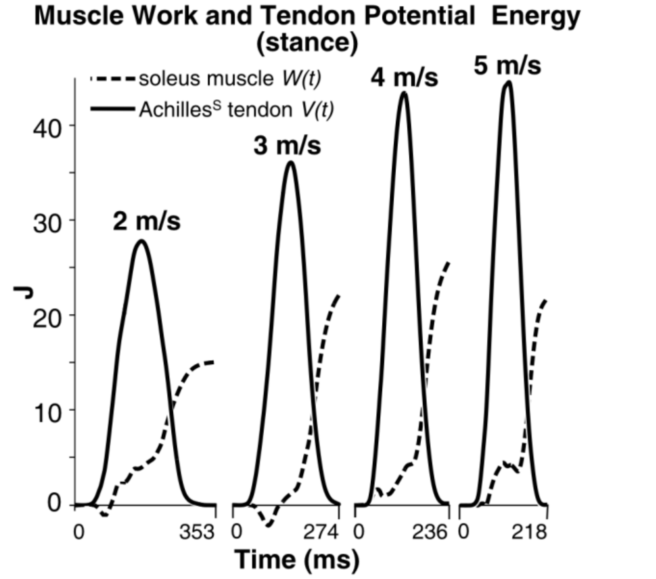

Figure 3: Work performed by the soleus muscle, *W(t)*, and Achilles tendon potential energy, *V(t)*, as a function of time across four running speeds (2-5m/s).

RESULTS AND DISCUSSION

Both the Achilles^S tendon and the soleus muscle are energetically impressive when compared to the other tendons and muscles of the lower limb (Figure 2). The Achilles^S tendon is exceptional: it stores and releases nearly 5 times the potential energy of the next closest tendons of the Achilles^{MG} and the vastus lateralis (left panel of Figure 2). While the soleus muscle does more work than any other muscle, the vastus lateralis, gluteus maximus, and medial gastrocnemius are close competitors (right panel of Figure 2). Dorn et al.'s simulation study [3] indicates that the work done by the hip muscles eventually exceeds the contribution of the soleus at running speeds beyond 5 m/s.

The soleus appears so dominant at the musculotendon actuator level [3] because of the large amount of energy stored and released by the Achilles^S tendon. The Achilles^S tendon stores and releases substantially more potential energy than the work that is done by the soleus muscle during the stance phase of all four running speeds studied (Figure 3), echoing similar findings during walking [8]. This imbalance indicates that, in addition to the soleus muscle, the actuator boundaries (e.g., calcaneus and tibia) are doing work on the Achilles tendon. We suggest that the hip and knee extensor muscles are driving the foot into the ground during stance, causing the foot to rotate at the ankle, and stretch the Achilles tendon.

CONCLUSIONS

Analyses of the musculotendon contributions to work [3] during the stance phase of running indicate that the soleus dominates the contributions of other musculotendon actuators. Our work analysis supports this finding, however it is the large amount of energy stored and released by the Achilles^S tendon during stance that makes the soleus musculotendon actuator appear so dominant. Additionally, we found that the Achilles^S tendon has by far the largest change in potential energy of any of the tendons simulated. Our results suggest that the Achilles^S tendon stores and releases twice as much potential energy than the work that is done by the soleus muscle alone. We speculate that the Achilles^S tendon is storing and releasing work contributions from the hip and knee extensor muscles during stance.

FUTURE WORK

Since the muscles and tendons of the plantarflexors appear to play such an important role in running it is imperative to develop a model that more faithfully represents their architecture. We modeled the soleus, medial and lateral gastrocnemius muscles as each having their own independent section of Achilles tendon, when in reality they all share one tendon.

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