Title: Musculoskeletal modeling deconstructs the paradoxical effects of elastic ankle exoskeletons on plantar-flexor mechanics & energetics during hopping

Authors: Dominic James Farris\textsuperscript{1,2*}, Jennifer Lee Hicks\textsuperscript{3}, Scott L. Delp\textsuperscript{3,4}, Gregory S. Sawicki\textsuperscript{2}

\textsuperscript{1}School of Human Movement Studies, University of Queensland, Australia
\textsuperscript{2}Joint Department of Biomedical Engineering, University of North Carolina-Chapel Hill & North Carolina State University, USA
\textsuperscript{3}Department of Bioengineering, Stanford University, USA
\textsuperscript{4}Department of Mechanical Engineering, Stanford University, USA
*Corresponding author - d.farris@uq.edu.au

Keywords: Assistive Robotics, Dynamics Simulation, Energetics, Locomotion. Metabolic Energy, Muscle Mechanics

Running Title: Modeling hopping in ankle exoskeletons
MUSCULOSKELETAL MODELING DECONSTRUCTS THE PARADOXICAL EFFECTS OF ELASTIC ANKLE EXOSKELETONS ON PLANTAR-FLEXOR MECHANICS & ENERGETICS DURING HOPPING

ABSTRACT

Experiments have shown that elastic ankle exoskeletons can be used to reduce ankle joint and plantar-flexor muscle loading when hopping in place and, in turn, reduce metabolic energy consumption. However, recent experimental work has shown that such exoskeletons cause less favourable soleus (SO) muscle-tendon mechanics than is observed during normal hopping which might limit the capacity of the exoskeleton to reduce energy consumption. To directly link plantar-flexor mechanics and energy consumption when hopping in exoskeletons, we used a musculoskeletal model of the human leg and a model of muscle energetics in simulations of muscle-tendon dynamics during hopping with and without elastic ankle exoskeletons. Simulations were driven by experimental electromyograms, joint kinematics and exoskeleton torque taken from previously published data. The data were from seven males who hopped at 2.5 Hz with and without elastic ankle exoskeletons. The energetics model showed that total rate of metabolic energy consumption by ankle muscles was not significantly reduced by an ankle exoskeleton. This was despite large reductions in plantar-flexor force production (40-50%). The lack of larger metabolic reductions with exoskeletons was attributed to increases in plantar-flexor muscle fiber velocities and a shift to less favourable muscle fiber lengths during active force production. This limited the capacity for plantar-flexors to reduce activation and energy consumption when hopping with exoskeleton assistance.

INTRODUCTION

Recent advances in exoskeletons or wearable robotic technology designed to assist human locomotion frequently include passive spring-loaded elements to conservatively store and return energy (Ferris et al., 2006; Grabowski and Herr, 2009; Wiggins et al., 2011; Bregman et al., 2012; Farris and Sawicki, 2012a). The springs take inspiration from the actions of series elastic components (SEC) in muscle-tendon units (MTU) of the leg (Cavagna, 1977; Alexander, 1988; Fukunaga et al., 2001; Lichtwark and Wilson, 2006). During locomotion energy is stored in the SEC’s of anti-gravity muscles during the first half of stance as the body center of mass (COM) either passes over (walking) or compresses (running) the support leg. This energy can then be returned later in stance to help propel the COM into the next step. This spring-like action of the
leg has inspired wearable technologies or exoskeletons that attach externally to the leg and aim to provide parallel assistance to the underlying muscles. This is usually with the aims of lowering metabolic energy consumption, unloading biological tissues and/or providing mechanical power that muscles cannot. Grabowski and Herr (2009) showed that the metabolic cost of hopping in place could be reduced by an exoskeleton that employed a leaf-spring in parallel with the whole leg. The participants in their study reduced the contribution of biological tissues to leg stiffness and effectively shared the load with the exoskeleton. The plantar-flexor muscle group makes excellent use of elastic mechanisms, storing and returning energy in the compliant Achilles tendon during walking and running (Ishikawa et al., 2005; Lichtwark et al., 2007; Farris and Sawicki, 2012b). This has inspired the design of ankle exoskeletons that store and return energy in a spring placed in parallel with the plantar-flexors, attached to the body via an ankle-foot orthosis (Ferris et al., 2006; Wiggins et al., 2011; Farris and Sawicki, 2012a). These exoskeletons are intended to reduce the mechanical demand on the plantar-flexors and consequently, reduce the metabolic cost of human movement. Previous work has shown that participants hopping in such devices reduce the activation to their plantar flexor muscles and, in turn, the contribution of these muscles to ankle joint stiffness (Ferris et al., 2006).

In a recent experimental study we showed that such exoskeletons reduced the whole-body net metabolic cost of bilateral hopping (Farris and Sawicki, 2012a). This reduction in net metabolic cost was associated with significant reductions in ankle joint work and moments (Farris and Sawicki, 2012a). In a further study, to examine mechanics of the MTU, we also employed ultrasound imaging of soleus muscle fascicles (Farris et al., 2013). These data revealed that the exoskeletons did not reduce soleus fascicle work despite reducing muscle force and electromyographic activity. This was owed to increased soleus fascicle length change when hopping in exoskeletons. From this we postulated that observed reductions in metabolic cost with exoskeletons were partially a result of reduced soleus muscle forces and the mechanical work done by fascicles was less important energetically. However, our capacity to draw such conclusions was limited because our metabolic measure was whole-body net metabolic power, encompassing energy consumed by all the muscles involved in the movement, not just soleus. More directly linking individual muscle mechanics and energetics would provide better insight into how spring-loaded exoskeletons affect underlying muscle function and energy consumption. This is an important step in understanding how exoskeletal devices provide assistance to the biological system.
Ultrasound imaging of fascicles for all the relevant muscles is impracticable because of the
requirement for multiple synchronised ultrasound transducers and an exoskeleton to be attached
to the leg. It is also not plausible to directly measure individual muscle forces in human subjects. A
viable alternative for obtaining individual muscle mechanics was to use a musculoskeletal model
based on some experimental inputs [e.g. Delp et al. (1990); Zajac et al. (2003); Arnold and Delp
(2011)]. With knowledge of individual muscle mechanics, the metabolic energy consumed by
individual muscles may be estimated with an energetics model [e.g. Lichtwark and Wilson (2005a);
Umberger and Rubenson (2011)].

In this study we sought to better understand how spring-loaded ankle exoskeletons affect plantar-
flexor muscle mechanics and energetics. To achieve this we employed two models: 1) A
musculoskeletal model to predict muscle-tendon dynamics during bilateral hopping with and
without spring-loaded ankle exoskeletons and 2) An energetics model to predict the metabolic
energy consumed by the muscles in the musculoskeletal model. Previously published experimental
data including electromyograms (soleus, medial and lateral gastrocnemius and tibialis anterior),
kinematics and external forces (Farris and Sawicki, 2012a; Farris et al., 2013) were used to drive
simulations of muscle-tendon dynamics for seven models, each scaled to individual experimental
participant’s anthropometrics. Simulations of hopping with and without ankle exoskeletons were
generated. These simulations output muscle-tendon dynamics for the Medial Gastrocnemius
(MG), Lateral Gastrocnemius (LG), Soleus (SO) and Tibialis Anterior (TA) which were passed to a
previously published model of muscle energetics (Lichtwark and Wilson, 2005a) to compute
individual muscle metabolic energy consumption. We hypothesised from experimental data (Farris
et al., 2013) that plantar-flexor muscle forces would be reduced by exoskeletons but contractile
work done by these muscles would be unchanged. We reasoned that plantar-flexor energy
consumption would be less with exoskeletons owing to lower muscle forces and reduced muscle
activation outweighing any competing effects of increased contractile element length change or
velocity on muscle energy consumption.

RESULTS

Musculoskeletal Model Evaluation
Performance of the musculoskeletal model was primarily evaluated by comparing net ankle joint
moments and powers generated by the muscles in the simulation of muscle-tendon dynamics
against those calculated from an inverse dynamics solution. Fig. 1 shows the time course of
instantaneous moments and powers from both solutions. For a more detailed comparison, Table 2
compares the timings and magnitudes of peak moments and powers. Generally mean values for
timings and magnitudes from the simulations of muscle-tendon dynamics were within one
standard deviation of the mean values from the corresponding inverse solutions. The exception to
this was that peak moments from the simulations of hopping with exoskeletons fell below this
range. However, there were no statistically significant (paired t-test, $\alpha = 0.05$) differences
observed between simulations of muscle-tendon dynamics and inverse solutions, for any of the
timing or magnitude metrics.

We also compared muscle mechanics data output by the musculoskeletal simulations with
previous experimental data (Farris and Sawicki, 2012a; Farris et al., 2013). Experimental EMG
signals were used as inputs to the model of activation dynamics. Consequently, the activations
produced by this part of the model were essentially constrained to follow closely the experimental
EMG data. Therefore in the simulations, wearing exoskeletons reduced SO average activation but
did not change MG and LG activation, as was shown with the experimental EMG (Farris and
Sawicki, 2012a). Simulated SO fiber length change patterns agreed with experimental SO fascicle
length change data, both showing initial lengthening upon ground contact followed by shortening
and both showing a significantly greater length change with exoskeletons (Fig. 1e-f). The
magnitudes of fiber shortening during ground contact were also comparable between
experimental (NE $\sim$3-4 mm, SE $\sim$5-6 mm) and simulation (NE $\sim$ 4-5 mm, SE $\sim$ 7-8 mm) results,
although slightly greater in the simulations. However, whereas the model results showed a
reduced average SO fiber length (-7 mm) with exoskeletons (Table 1), the experimental data did
not (Farris et al., 2013).

Muscle Energetics

**Energetics** - Results from the simulations of muscle-tendon dynamics and energetics model
showed that total rate of metabolic energy consumption for all muscles was not significantly
reduced for hopping with exoskeletons (0.68 $\pm$ 0.07 vs. 0.57 $\pm$ 0.04 vs. J $\cdot$ kg$^{-1}$ $\cdot$ hop$^{-1}$), despite a trend
for a small reduction (Table 1). Examination of individual muscles revealed that MG was the only
muscle to exhibit a significant reduction in rate of metabolic energy consumption (Table 1).
Although LG and SO trended toward a reduced metabolic cost with exoskeletons, no statistically
significant difference was found and TA’s energy consumption was slightly but non-significantly
greater with exoskeletons.

Muscle Mechanics
Medial Gastrocnemius - Simulation results showed that MG forces appeared generally lower throughout the hop cycle (Fig. 2e) and there was a significant reduction in peak and average MG forces when exoskeletons were used (Fig. 3a, Table 1). Also, the use of spring-loaded exoskeletons resulted in significantly shorter average MG fiber length output by the model (Figs. 2i & 3a, Table 1) and a shift in MG operating length down the ascending limb of its force-length relationship (Fig. 4a). Furthermore, simulated average MG fiber velocity significantly increased when exoskeletons were used (Fig. 3a, Table 1). $F_{\text{ind}}$ is the index of force producing capability of a muscle and represents the ratio of the force being produced relative to the maximum force the muscle could produce given its active state (Equation 1 - Materials & Methods). Related to the above mechanical changes, $F_{\text{ind}}$ for MG was significantly reduced when exoskeletons were worn (Fig. 3a, Table 1). Rate of positive mechanical work done by MG fibers was unchanged with exoskeletons, but the rate of negative work increased (Table 1). Time series group average data for MG activation (Fig. 2a) shows that for the majority of ground contact (20-70% hop cycle), MG activation followed a similar trend and was of similar magnitude with and without exoskeletons. As a result, there was no difference in MG peak or average activations between these conditions (Fig. 3a, Table 1).

Lateral Gastrocnemius - LG activation, fiber force, fiber length, and fiber velocity output from the simulations are plotted throughout the hop cycle in Fig. 2(b, f, j & n). There were significant reductions in LG peak and average forces with exoskeletons (Fig. 3b, Table 1). No differences in average fiber length or velocity were observed with exoskeleton use for LG although LG's $F_{\text{ind}}$ was reduced with exoskeletons (Fig. 3b, Table 1). Positive mechanical fiber work were unchanged with exoskeletons for LG although there was a decrease in negative fiber and MTU rate of work that resulted in more positive net work of the fiber and MTU per hop (Fig. 3b, Table 1). Average and peak LG activations were unchanged for hopping with exoskeletons versus without (Fig. 3b, Table 1).

Soleus - Similar to other plantar-flexors, simulation results showed that SO demonstrated a significant reduction of average and peak forces when exoskeletons were used. Notably the simulations revealed that there was a threefold increase in average fiber shortening velocity for SO with exoskeletons and SO operated at a significantly shorter average length in that condition (Fig. 3c, Table 1). This caused a rightward shift along SO's force-velocity relationship (Fig. 5c) and a shift down the ascending limb of its force-length relationship when exoskeletons were used (Fig. 4c). The net result of these mechanical changes was a significantly lower $F_{\text{ind}}$ for SO for hopping in
However, there was a significant decrease in negative rate of work for SO fibers and MTU with exoskeletons and this caused greater positive net work per hop (Table 1). SO average activation was significantly less with exoskeletons (-21%) although peak activation was unchanged (Fig. 3c, Table 1).

**Tibialis Anterior** - Time series plots of simulated TA activation (Fig. 2d) and force (Fig. 2h) showed similar trends and magnitudes in both conditions during ground contact. This was evidenced further by the lack of difference in average or peak activations and forces for TA between hopping with exoskeletons and without (Fig. 3d, Table 1). In fact, there were no significant differences in mechanical variables between conditions for TA (Fig. 3d, Table 1).

**DISCUSSION**

In this study we sought to mechanistically link changes in mechanics of ankle muscles to changes in muscle energy consumption when humans hop with and without elastic ankle exoskeletons that assist plantar-flexion. Our first hypothesis was that plantar-flexor muscle forces would be reduced by the use of spring-loaded ankle exoskeletons. There was strong support for this hypothesis as peak and average forces were significantly less for all plantar-flexors (MG, LG and TA) when hopping was assisted with exoskeletons. Our second hypothesis was that contractile work of the plantar-flexor muscles would not change with exoskeletons. This hypothesis was also supported, as there was no change in positive fiber work for any of the plantar-flexors when hopping in exoskeletons due to a paradoxical trade-off between force production and fiber shortening. Finally, we hypothesised that ankle exoskeletons would reduce the rate of metabolic energy consumption by plantar-flexors due to reduced forces and activations. This hypothesis was not supported as the combined rate of energy consumption and all individual muscle activations were not statistically significantly reduced with exoskeletons.

**Linking Muscle Mechanics and Energetics**

$F_{ind}$ was our measure of how favourable the state of a muscle was for producing force given its fiber length and velocity. $F_{ind}$ can be any value between 0 and 1 and the closer it is to 1, the less activation is required to produce a given force and the greater the maximum force that can be produced is. With exoskeletons, $F_{ind}$ was significantly less than without for all the plantar-flexor muscles for the period of ±25% hop cycle time either side of the time of maximum force. This indicated that even though the forces required of the plantar-flexors were reduced, their contractile elements were not in as favourable a state for producing force. This finding was further
confirmed by inspection of plantar-flexor muscle velocities and lengths (Figs. 3, 4 and 5; Table 1). In Fig. 2m-o it can be seen that during periods of greatest force production, plantar-flexors reached higher shortening velocities with exoskeletons than without. This resulted in significantly higher average shortening velocities for MG and SO and a significantly higher peak shortening velocity for SO (Figs. 3a-c & 5c; Table 1). Faster shortening velocities reduce the force generating capacity of muscle (Fenn and Marsh, 1935). Thus, the increased average velocities for MG and SO with exoskeletons were contributing to the lower $F_{\text{ind}}$ values observed for those muscles.

The length-tension relationship of skeletal muscle (Gordon et al., 1966) describes that at lengths above and below an optimum length ($L_0$), the muscle's force producing capability is impaired. As can be seen in Fig. 2, all the plantar-flexors consistently operated at fiber lengths less than $L_0$ and average fiber lengths were shorter for MG and SO with exoskeletons (Fig. 3a-c, Table 1). This shifted MG and SO fiber operating lengths down the ascending limb of the force-length relationship (Fig. 4a,c) where contractile elements have lower force-producing capacities. This shift also contributed to the lower $F_{\text{ind}}$ values observed for MG and SO when hopping in exoskeletons. Although LG did not exhibit any significant changes in peak or average fiber lengths and velocities, it did demonstrate a reduced $F_{\text{ind}}$ when exoskeletons were used, likely due to a cumulative effect of small changes in LG length and velocity.

Despite average forces for MG, LG and SO muscles being 42%, 37% and 56% lower with exoskeletons (Fig. 3, Table 1), the expected concomitant reductions in muscle activation were offset by poor contractile conditions that required higher activation per unit force (i.e. reduced $F_{\text{ind}}$). In fact, of the plantar-flexors, only SO had significantly lower average activation (Fig. 3, Table 1) and this was only reduced by 21% despite SO average force being 56% less. Furthermore, positive muscle fiber work was not significantly altered for any of the plantar-flexors by exoskeletons (Table 1). The amount of fiber work is dependent on the amount of shortening of a fiber and the force produced during that shortening. Because fiber force was reduced with exoskeletons but fiber shortening velocity (and therefore shortening) increased with exoskeletons, positive fiber work was unchanged. Thus, a trade-off between force and shortening velocity seems to occur for plantar-flexor muscles when hopping with and without assistance from a parallel spring. These findings agree well with our previous experiment that indicated SO force was reduced by exoskeletons but not SO fiber positive mechanical work (Farris et al., 2013). As can be seen from Table 1, negative rate of work was significantly less when hopping in exoskeletons for LG and SO, but not MG which exhibited more negative work per hop for the MTU and the fibers.
An inspection of fiber length and force data in Figure 2 reveals that this is likely due to reductions in force and activation of LG and SO when fibers are lengthening.

The changes we observed in muscle fascicle mechanics can be used to understand the factors that drive changes in underlying metabolic energy consumptions of individual ankle muscles during spring-assisted hopping. The model of muscle energetics produces rates of energy consumption based on inputs of mechanical fiber work, fiber forces, muscle activations and fiber velocities. Increases in any of these variables will generally increase rates of energy consumption (although not proportionally). Therefore, we can see that the computed reductions in average and peak plantar-flexor forces with exoskeletons would serve to reduce rates of energy consumption by these muscles. Fiber positive mechanical work was unchanged between conditions and thus, had little influence on relative rates of energy consumption with and without exoskeletons. However, net rate of fiber work was more positive for LG and SO with exoskeletons and this will have served to increase metabolic rate for these muscles and might be why metabolic rate was not significantly reduced for these muscles, in contrast to MG whose metabolic rate decreased and net fiber work remained unchanged. This effect would have been somewhat mitigated by a concomitant reduction in rate of negative work for the fibers of LG and SO with exoskeletons.

Average activation was only reduced by exoskeletons for SO. The final factor that determined energy consumption was fiber velocity and this significantly increased with exoskeletons for MG and SO and did not change for LG (Fig. 3, Table 1). Thus, combined plantar-flexor fiber velocities would have served to increase rates of energy consumption. In the case of SO, velocity increased threefold with exoskeletons and thus, may have acted to increase energy consumption sufficiently to override any reductions resulting from reduced SO activation. For LG, no changes were observed in activation or velocity and as these terms dominate energy consumption in the energetics model (Equations 4 and 5) it is unsurprising that LG energy consumption was unchanged with exoskeletons. MG did have a lower rate of energy consumption with exoskeletons and this was primarily due to the effect of reduced force levels outweighing the effect of an increase in fiber velocity which was somewhat less than the increase observed for SO (Fig. 3). However, SO is by far the largest of the plantar-flexors and therefore has the potential to dominate energy consumption by this muscle group. Therefore, the lack of change in SO energy consumption with exoskeletons washed out the reduction from MG when all muscles were combined. Of course TA also contributed to total energy consumption but showed no change in any mechanical or energetic variables (Fig. 3d, Table 1) and as such, contributed consistently across conditions.
The model prediction of no significant reduction in total rate of energy consumption seems at odds with our previous experimental measures of whole body net metabolic power that did show a reduction when hopping in ankle exoskeletons (Farris and Sawicki, 2012a; Farris et al., 2013). A close inspection of the energetic model outputs shows that total rate of energy consumption of all ankle muscles was 0.68 and 0.57 J·kg\(^{-1}\)·Hop\(^{-1}\) for without and with exoskeletons, respectively. This gives a difference of 0.11 J·kg\(^{-1}\)·Hop\(^{-1}\) for the musculature of one ankle. In the previous experimental study, whole body net metabolic power was reduced by 0.9 W·kg\(^{-1}\) with exoskeletons compared to without exoskeletons. Half of this reduction was attributed to reductions in knee power output (Farris et al., 2013) leaving 0.45 W·kg\(^{-1}\) attributable to changes in ankle muscle mechanics in both legs. Halving this value again gives us a net reduction of 0.225 W·kg\(^{-1}\) for one ankle's musculature. Dividing this value by 2.5 (hopping frequency) returns a value of 0.09 J·kg\(^{-1}\)·Hop\(^{-1}\) that compares well with the prediction of the metabolic model. First, we note that in both analyses this is a small difference and only accounts for about half the experimentally observed reduction in whole body net metabolic power (Farris et al., 2013). Our previous inverse dynamic analysis suggested that the remaining metabolic reductions were likely a result of reduced mechanical power output at the knee joint when exoskeletons were worn (Farris and Sawicki, 2012a; Farris et al., 2013). This presents an interesting scenario where an exoskeleton that directly assists at one joint may affect mechanical changes at other joints that impact upon the overall mechanical and metabolic demands of locomotion. Secondly, we note that the similarity of experimental and modeled energetic values gives us good confidence in our energetic model predictions, even though the simulation results showed no significant difference between conditions. It may be that our statistical power was insufficient to detect a statistically significant reduction when the reduction is of a relatively small magnitude. We therefore suggest that ankle exoskeletons may not totally fail to reduce metabolic energy consumption of ankle muscles but rather the paradoxical trends in muscle mechanics limit the reduction to being quite small and, in our case, not statistically significant.

**Model Evaluation**

To evaluate our simulations of muscle-tendon dynamics, we employed the same approach as Arnold et al. (2013) and compared ankle joint kinetics to those computed by inverse dynamic solutions using the same experimental data. As shown in Fig. 1 and Table 2, ankle moments and powers showed good temporal agreement between inverse solutions and simulations and generally a non-significant shortfall in magnitudes. One might expect the simulations to under
predict muscle forces and thus, moments and powers. This is owing to the fact that muscle $F_{\text{max}}$
was not scaled to individual participants. The model parameter values for muscle properties came
from cadavers with a mean age of $83 \pm 9$ years including a mixture of male and female specimens
(Ward et al., 2009). The experimental group used for the current study consisted of young (mean
age = $28 \pm 7$ years), physically active males who likely had larger/stronger muscles than the
cadaver specimens. Thus, it was not surprising that magnitudes of ankle moments and powers
were quantitatively less in the muscle-tendon dynamics simulations. However, the temporal
agreement was good and the magnitudes were generally within one standard deviation of each
other, giving us good confidence in the simulations of muscle-tendon dynamics.

This confidence was furthered because similar trends in SO muscle mechanics between conditions
were predicted by the model as were observed in recent experimental data collected using
ultrasound imaging to measure SO fascicle length changes when hopping in ankle exoskeletons
(Farris et al., 2013). The fascicle length changes represent lumped length changes of the muscle
contractile elements, as does fiber length in the musculoskeletal model. Therefore the terms
fascicle and fiber will be considered interchangeable in this discussion even though they may have
distinct anatomical definitions. Both simulated and experimental data showed that fiber length
changes increased significantly with exoskeletons (Fig. 1E-F). This similarity was most important
for providing confidence that our model was appropriate for our research question, which was
related to the effects of exoskeletons. However, there were some discrepancies in the length
change patterns of simulated and experimental fascicle lengths. The gross length change pattern
for simulations and experimental data was lengthening followed by shortening over ground
contact and then a return to the starting length during the aerial phase. However, the period of
fiber shortening began somewhat earlier in the simulations (Fig. 1E-H) and length changes were
generally larger in the simulations. Exact quantitative agreement between the simulated and
experimental fiber lengths might be unrealistic to obtain given that the exact properties of
participant’s muscles were not known and the model is a simplification of reality. Muscle dynamics
were relatively insensitive to changes in muscle parameters (supplementary information, Figs. S1-
S3) and as noted earlier, the simulated effects of exoskeletons were comparable to experimental
findings in terms of muscle dynamics and metabolic data. A noteworthy discrepancy between the
experimental and simulation datasets was that the simulations showed that exoskeletons reduced
SO average fiber length whilst experimental data showed no change in average fascicle length
[Table 1 in Farris et al. (2013)]. The whole SO MTU length was reduced with exoskeletons because
the ankle was more plantar-flexed throughout the hops in this condition. The experimental data

11
showed this length change to occur entirely by shortening of series elastic structures (i.e. the Achilles tendon) allowing the SO fascicles to be at the same average length with and without exoskeletons. However, the simulations showed that both the SO tendon and fibers were at shorter average lengths when exoskeletons were worn. A plausible explanation for this discrepancy is that the SO tendon compliance set in the musculoskeletal model was too great. A less compliant tendon would have been stretched less by the forces applied by SO and thus, the muscle fiber length would have shortened less or not at all. An overly compliant tendon might also explain why SO fiber length changes were slightly greater in the simulation results than in the experimental data. Tendon compliance values for the plantar-flexors ($T_{strain}$ in Table 3) were determined such that when acting in parallel the combined stiffness of the MG, LG and SO tendons would match an experimentally determined value for Achilles tendon stiffness of 180 N-mm$^{-1}$ (Lichtwarck and Wilson, 2005b). This is a simplification of the real anatomy where the three muscles insert through a common tendon of this stiffness. Achilles tendon compliance may also vary greatly between individuals (Lichtwarck and Wilson, 2005b) and be inversely proportional to muscle strength (Muraoka et al., 2005). Given that the participants in the experimental data collection were young physically active males, it is possible that this group’s average tendon compliance would be less than for previously published data from participant groups with potentially lesser muscle strength. However, repeating the simulations with a 10% stiffer tendon in each muscle, for one of the scaled models, produced only marginally shorter fiber lengths during hopping and minimal changes in other outcome measures (supplementary information, Fig S1). Therefore we believe our findings to be relatively insensitive to tendon compliance and that any effect would be systematic across experimental conditions.

Generally the musculoskeletal model performed well and we believe it capable of accurately predicting the effects of ankle exoskeletons on ankle muscle mechanics during hopping. This is despite some limitations of the muscle model which include not incorporating: variable gearing of pennate muscles (Azizi et al., 2008), force depression after shortening and stretch induced force enhancement (Julian and Morgan, 1979), changes in the force-velocity and force-length relations that occur with submaximal activation (Rack and Westbury, 1969), three-dimensional structure or non-homogenous structure (Huijing, 1998). Each of these factors could affect muscle force predictions. Azizi et al. (2008) showed that pennate muscle such as the triceps surae might rotate their fibers more during low force-high velocity contractions and keep them more aligned with the muscle line of action during high force-low velocity contractions (variable gearing). The exoskeletons reduced muscle forces which would place the muscles more towards the low force-
high velocity end of this spectrum and thus, a model incorporating variable gearing would likely predict greater fascicle rotation in the exoskeleton condition which would only serve to further reduce force along the line of action of the MTU by making the fibers more oblique to it. Residual force enhancement would suggest that after a stretch, muscle fibers are able to produce more force at a given length. There was generally less stretch of muscle fibers of the plantar flexors with exoskeletons and thus the difference in forces between the two conditions might have been greater had force enhancement been included in the muscle model. The skeletal muscle force-length relation shifts to the right (longer optimal length) at submaximal activations and this is not accounted for in the muscle model. Because of the dynamic interaction between length, force and activation it is difficult to predict what the effects of accounting for this might be. Generally lower activations and shorter lengths of fibers were observed with exoskeletons, which would suggest that the difference in forces between the conditions might have been greater than observed owing to a more rightward shift of optimal length and shorter predicted lengths of fibers with exoskeletons. The energetics model has been carefully validated against experimental data previously (Lichtwarck and Wilson, 2005a). This and the good agreement with experimental metabolic data from this study (discussed in detail above) gave us confidence in our energetic predictions also.

CONCLUSIONS

Using a musculoskeletal model we have shown that spring-loaded ankle exoskeletons can negatively influence plantar-flexor muscle mechanics during bilateral hopping. Negative effects were: 1) Increased muscle fiber shortening velocity and 2) A shift in average operating length down the ascending limb of the force-length relationship. As a result, mechanical work done by muscle fibers was not reduced by exoskeletons and these devices caused only limited reductions in plantar-flexor muscle activations. Consequently, our energetics model predicted that only medial gastrocnemius consumed less energy with exoskeletons and ankle muscle energy consumption was not significantly reduced by spring-loaded ankle exoskeletons. This indicates that experimentally observed reductions in whole body net metabolic cost are heavily influenced by the effects of ankle exoskeletons at other joints as well as those on ankle musculature.

MATERIALS & METHODS

Experimental Data
The musculoskeletal modeling required experimental data as input to the simulations of muscle-tendon dynamics. The data included kinematic, ground reaction force (GRF) and surface electromyography (EMG) recordings. This data was taken from the results of a previously published study (Farris and Sawicki, 2012a) which describes the data collection procedures and the ankle exoskeleton design in detail. Briefly, seven male participants (mean ± sd, age = 28 ± 7, height = 1.8 ± 0.06 m, mass = 80 ± 10 kg) hopped bilaterally in two conditions: without exoskeletons and with spring-loaded ankle exoskeletons to assist plantar-flexion. The exoskeletons consisted of a carbon fibre foot section embedded in a running shoe and a carbon fibre cuff around the shank which were connected by aluminium bars via a freely rotating joint aligned with the malleoli. When spring-loaded, a spring was attached to a bracket on the posterior aspect of the cuff and a bolt on the heel of the foot segment. The rotational stiffness provided about the ankle joint by the spring was calculated as 91 N-m-rad\(^{-1}\). The spring was at its resting length when the ankle was at an angle of 129° (foot segment relative to shank segment, 90° = foot perpendicular to the shank).

Participants hopped at 2.5 Hz in time with a metronome. Reflective markers were placed over the right leg and pelvis (see ref. [2] for details of placements) and their trajectories captured and labeled using an eight-camera Vicon motion analysis system and Vicon Nexus software (Vicon, UK). The same system synchronously recorded GRF data from the left and right legs that were measured using each half of a split-belt instrumented treadmill (Bertec, OH, USA). Also logged synchronously were surface EMG signals from the medial gastrocnemius, lateral gastrocnemius, soleus and tibialis anterior muscles. Raw EMG signals were processed in Matlab (The Mathworks, MA, USA) with a band-pass filter (20-300 Hz) and a moving average root mean square calculation made over successive windows of 20 ms. Processed signals were then normalised to the average peak (in each hop, from a series of 10 hops) of the processed signal from the condition where that muscle's signal had the greatest peaks (i.e. with exoskeletons for MG, LG and SO; without exoskeletons for TA).

Musculoskeletal Model

The generic musculoskeletal model (Fig. 6A) was adapted from the model of the pelvis and lower limb published by Arnold et al. (Arnold et al., 2010) that has been used to produce dynamical simulations of human walking and running (Arnold and Delp, 2011; Arnold et al., 2013) and analyse lower limb muscle function during locomotion (Arnold and Delp, 2011; Arnold et al., 2013). Here, we were only interested in the mechanics of a subset of the 35 muscles included in
the original model: medial gastrocnemius (MG), lateral gastrocnemius (LG), soleus (SO) and tibialis anterior (TA). Because we prescribed joint angles during the simulations of muscle-tendon dynamics (see Musculoskeletal Simulations), it was unnecessary to model the other lower limb muscles. Therefore, we removed all muscles except those listed above from the model. Consequently, there were no muscles in the model attached to the pelvis and so the pelvis segment was removed. The rigid bodies in the model included thigh (femur and patellar), shank (tibia and fibula) and foot (talus, calcaneus metatarsals and phalanges) segments. The geometry of the segments was from the digitisation of the bones of an adult male (Delp et al., 1990). Articulation between segments was possible at the knee and ankle joints. The ankle was a revolute joint between the tibia and talus with one degree of freedom (plantar-flexion/dorsi-flexion) (Inman, 1976; Arnold and Delp, 2011). The knee joint also had one rotational degree of freedom (flexion/extension) with translations and rotations between the femur, patellar and tibia being described by the equations from Walker et al. (Walker et al., 1988) and Delp (Delp, 1990). A joint between the thigh and the lab coordinate system was created with six degrees of freedom to allow the leg to translate and rotate relative to the lab.

Each muscle’s path was modeled by line segments between origin and insertion that included wrapping surfaces and via points to account for parts of those paths where the muscle wraps over bones or other muscles or is constrained by retinacula (Arnold et al., 2010). Each muscle was modeled as a Hill-type muscle with a single fiber in series with a series elastic element (subsequently referred to as tendon). Muscle parameters are described in Table 3. Architectural muscle parameters were optimal fiber length ($L_0$), pennation at optimal fiber length ($\alpha_0$) and tendon slack length ($T_s$). $L_0$ and $\alpha_0$ were taken from a study of 21 cadavers (Ward et al., 2009) and $T_s$ values were defined as by Arnold et al. (Arnold et al., 2013) who used the joint positions and fiber lengths from Ward et al. (Ward et al., 2009) to set $T_s$. The maximum isometric force ($F_{max}$) of each of the plantar-flexors was taken from Arnold et al. (Arnold et al., 2010) who calculated $F_{max}$ from the physiological cross-sectional areas reported by Ward et al. (Ward et al., 2009) and a specific tension for muscle of 61 N/cm$^2$. The $F_{max}$ of TA was increased from the value in Arnold et al. (Arnold et al., 2010) to that reported by Raasch et al. (Raasch et al., 1997) so as to include the force producing capabilities of other dorsi-flexors (Table 3). This was done to produce realistic ankle joint moments and powers during periods of co-contraction of plantar-flexors and dorsi-flexors. Architectural muscle parameters were used to scale normalised curves relating active force, passive force and tendon force to muscle kinematics [e.g. (Zajac and Gordon, 1989; Millard et al., 2013)]. Scaled curves provided multipliers to, in combination with activation level,
determine muscle fiber and tendon force from normalised fiber length, shortening velocity and tendon strain (Zajac and Gordon, 1989). The normalised curves for active force-length and force-velocity were modeled with natural cubic splines (Zajac and Gordon, 1989; Arnold et al., 2013). Maximum shortening velocity was set to 10 \( \text{L}_0/\text{s} \) for all muscles. Passive force-length and tendon force-strain were represented by exponential functions (Thelen, 2003; Arnold et al., 2013). Detailed equations for this process are described in Arnold et al. (Arnold et al., 2013). Tendon force-strain relationship is dictated by the tendon strain at \( F_{\text{max}} \). Often this strain value has been set to 0.03 for all muscles. However, the muscles surrounding the human ankle joint typically have long compliant tendons that experience larger strains. Arnold et al. (Arnold et al., 2013) found that strain at \( F_{\text{max}} \) for ankle muscles needed to be increased to 0.10 to yield reasonable ankle kinetics in their simulations of muscle-tendon dynamics. Here we set the strain at \( F_{\text{max}} \) values for the plantar-flexors to values that when combined (in parallel), would produce Achilles tendon stiffness similar to that reported in experimental studies (Lichtwark and Wilson, 2005b; Farris et al., 2012). TA tendon strain at \( F_{\text{max}} \) was also set such that its stiffness was similar to experimental data (Maganaris, 2002). These values were all close to 0.10 (Table 3). The sensitivity of muscle dynamics and metabolic energy consumption to the values of tendon stiffness, \( F_{\text{max}}, V_{\text{max}} \) was tested by re-running simulations having altered these parameters by \( \pm 10\% \) of the values in Table 3. The results of these simulations are shown in the supplementary information (Figs. S1-S3 and Table S1).

### Musculoskeletal Simulations

OpenSim software (v3.0) (Bobbert, 2014) was used to generate simulations of muscle dynamics during hopping at 2.5 Hz with and without spring-loaded ankle exoskeletons for the seven participants described above. For each participant’s data a series of 10 consecutive hops was analysed in each condition. First, the generic musculoskeletal model was scaled to match individual participant anthropometrics. This was done using distances between motion capture markers positioned on segment endpoints during quiet standing. Muscle \( L_0 \) and \( T_s \) were scaled with MTU lengths such that the ratio \( L_0/T_s \) remained the same as in the generic model. Next, previously collected motion capture data (Farris and Sawicki, 2012a) were used in conjunction with the scaled musculoskeletal models to determine model joint angles via an inverse kinematic solution to best fit the experimental data. This generated knee and ankle joint angles as well as translations and rotations of the thigh in the lab. Next, the inverse kinematic solution was combined with GRF data in an inverse dynamics analysis to determine ankle plantar-dorsi flexion net moments and the power generated by those moments. These moments and powers would be
compared to the net moments and powers generated by the muscles in the model during the
simulations of muscle-tendon dynamics to evaluate the simulations. The inverse kinematics and
dynamics data were computed with the current models and are therefore not identical to the
previously published joint mechanics data in Farris and Sawicki (2012a).

As can be seen from Fig. 6B, the experimental inputs to the simulations were: joint kinematics,
exoskeleton torques and muscle electromyograms. The latter two of these were taken from Farris
and Sawicki (2012a). The inverse kinematic solutions described above were used to prescribe
coordinates (translational and rotational) for the model joints in simulations of muscle-tendon
dynamics, run with the scaled musculoskeletal models (Fig. 6B) and effectively determined
muscle-tendon unit lengths. To simulate the contribution of the exoskeletons, experimentally
determined moments produced by the exoskeleton about the ankle joint (Farris and Sawicki,
2012a) were applied as equal and opposite moments on the shank and foot segments of the
model. An overview of how experimental data was integrated into the models is shown in Fig. 6B.

Processed surface EMG signals (see Experimental Data) were considered as muscle excitations and
passed to an activation dynamics model to determine muscle activations. This model was a non-
linear first order differential equation as used by Thelen (2003) which includes different time
constants for activation ($\tau_{act}$) and deactivation ($\tau_{deact}$). We adjusted these time constants to match
experimental muscle-specific data (Winters and Stark, 1988) (Table 3). Bounds were set on the
activation signals such that they could not exceed 1 or fall below 0.01. Muscle activations and
kinematic data served as inputs to the model of contraction dynamics described above. Outputs
from the simulations included muscle fiber and tendon forces and muscle fiber and tendon
kinematics. As a metric of each muscle’s force producing potential we calculated an index of force
producing ability ($F_{ind}$). This index is described by Arnold et al. (Arnold et al., 2013) and is
calculated as:

$$F_{ind} = \frac{F_T}{Act \cdot F_{max}}$$  \hspace{1cm} (1)

Where, $F_{ind}$ is the index of force producing capability, $F_T$ is the active force generated along the line
of the tendon, Act is activation and $F_{max}$ is the muscle’s maximum isometric force. $F_T$ depends on
the normalised length and velocity of the muscle fiber and its pennation angle (Arnold et al.,
2013).

Energetics Model
Having determined muscle fiber forces and kinematics, and using the same values for individual muscle parameters as in the musculoskeletal model, we employed a previously published and validated model of muscle energetics (Lichtwark and Wilson, 2005a) to predict individual muscle metabolic energy consumption. This model calculates the energy consumed by the contractile element of a muscle as the sum of mechanical work and heat production. Work is defined as being positive when the muscle fiber produces force while shortening (positive fiber velocities) and negative when the fiber produces force while lengthening (negative fiber velocities). To determine muscle fiber net mechanical work, fiber force was multiplied with fiber velocity to compute fiber power that was subsequently integrated with respect to time over a trial. Detailed descriptions of the equations used to calculate heat production are given in the supplementary information of Lichtwark and Wilson (2007). Briefly, there were two main heat terms to compute - maintenance heat rate and shortening heat rate. Maintenance heat rate was determined as:

\[
\frac{dH_m}{dt} = \gamma \left( \frac{V_{max}}{g^2} \right) \quad \text{for } V_{ce} > 0 \tag{2}
\]

\[
\frac{dH_m}{dt} = 0.3 \left( \gamma \left( \frac{V_{max}}{g^2} \right) \right) + 0.7 \left( \gamma \left( \frac{V_{max}}{g^2} \right) \cdot e^{-7V_{max}(P-1)} \right) \quad \text{for } V_{ce} < 0 \tag{3}
\]

Shortening heat rate was determined as:

\[
\frac{dH_s}{dt} = \left( \frac{V_{CE}}{g} \right) \quad \text{for } V_{CE} > 0 \tag{4}
\]

\[
\frac{dH_s}{dt} = -0.5P \cdot V_{CE} \quad \text{for } V_{CE} < 0 \tag{5}
\]

Total heat (H) was the sum of maintenance and shortening heat scaled by activation (Act) and the fraction of bound cross-bridges (X):

\[
X = P(l) \cdot Act \tag{6}
\]

\[
\frac{dH}{dt} = 0.3Act \left( \frac{dH_m}{dt} \right) + 0.7X \left( \frac{dH_m}{dt} \right) + X \left( \frac{dH_s}{dt} \right) \tag{7}
\]

Where, \( V_{CE} \) is contractile component velocity relative to \( V_{max} \); \( H_m \) is maintenance heat; \( \gamma \) is a constant (1.5) multiplier of stable heat rate to account for its labile component; \( V_{max} \) is the
maximum shortening rate of the muscle's contractile element (10 \( L_0 \text{s}^{-1} \)); G is a constant (4.0) that determines the curvature of the muscle's force-velocity curve; P is the force produced relative to the maximum active force that can be produced at the current contractile element velocity (from the force-velocity curve); \( P(l) \) is the maximum force that can be produced at a given contractile element length relative to \( F_{\text{max}} \).

Total heat was integrated over a trial with respect to time and summed with net mechanical work to give total energy consumed by each muscle. The energy consumed by all muscles was summed to give total energy consumption of the ankle muscles. All values for energy consumption were divided by body mass and the number of hops to give a rate of energy consumption in \( \text{J kg}^{-1} \cdot \text{hop}^{-1} \).

**Data Reduction and Statistics**

Time series data for muscle mechanics were split up into individual hops based on vertical ground reaction force data and normalised to 101 evenly spaced points over each hop cycle. Averages of all hops for each subject were then computed and used to calculate group averages and standard deviations that were plotted against normalised hop time (e.g. Fig. 2). Peak muscle forces, activations, lengths and velocities were calculated in each hop and averaged across all hops within a subject and then across subjects. Average muscle forces, activations, lengths and velocities were computed for a period spanning ± 25% of the hop cycle, either side of the occurrence of peak muscle force (for that muscle). \( F_{\text{ind}} \) was calculated from these values of average force and activation. Muscle mechanics data were normalised to either maximal activation (activation), \( F_{\text{max}} \) (forces) or \( L_0 \) (lengths and velocities) for that muscle. All data presented are group means and standard deviations unless otherwise stated. To test for differences in outcome variables between hopping with and without exoskeletons, paired t-tests were used and an alpha level less than 0.05 as the criteria for statistical significance.

**Acknowledgements**

The authors would like to acknowledge Dr Glen Lichtwark (The University of Queensland, Australia) for his assistance in implementing the model of muscle energetics.

**Competing Interests**

The authors declare no competing financial interests.

**Author Contributions**
D.J.F., G.S.S. and J.L.H. contributed to the conception of this project. D.J.F., G.S.S. S.L.D & J.L.H. contributed to the design and interpretation of the musculo-skeletal simulations, as well as drafting and revision of the article. D.J.F. executed the musculoskeletal simulations and metabolic modelling.

**Funding**

This work was supported by the Visiting Scholars Program of The National Center for Simulation in Rehabilitation Research (NCSRR). The NCSRR is a National Center for Medical Rehabilitation Research supported by NIH research infrastructure grant R24 HD065690.

This study was in part funded by US Israel Binational Science Foundation Start Up Grant 2011152 awarded to G. S. Sawicki.

**REFERENCES**


FIGURE CAPTIONS

Figure. 1. Data used in the evaluation of the musculoskeletal model. A comparison of the net ankle moments (A-B) and powers (C-D) calculated from the moments produced by the muscle forces in the simulations of muscle-tendon dynamics (solid lines) and the net moments and powers calculated using an inverse dynamics approach (dashed lines). Panels E-H compare SO fiber length changes and corresponding velocities from the simulations with previously published (Farris and Sawicki, 2013) SO fascicle length changes and velocities measured experimentally from ultrasound imaging. The no exoskeleton condition data are on the left panels (A, C & E) and the spring-loaded exoskeleton data the right panels (B, D & F). Data are the average of all seven scaled models ± standard deviation (shaded regions) normalised to hop time as a percentage of the hop cycle starting from landing. The vertical dotted lines indicate takeoff.

Figure. 2. Group mean (± s.d.) plots of modelled muscle activation (A-D), normalised fibre force (E-H), normalised fibre length (I-L), normalised fibre velocity (M-P) and fiber power (Q-T) for the medial gastrocnemius (A, E, I, M,O), lateral gastrocnemius (B, F, J, N, R), soleus (C, G, K, O, S) and tibialis anterior (D, H, L, P, T). Positive values for velocities correspond to shortening of muscle fibers. Solid lines represent the condition without exoskeletons (NE) and dashed lines the condition with spring-loaded exoskeleton (SE). Data are normalised to hop cycle time (0-100%), 0% representing landing and the dotted vertical lines indicating takeoff.

Figure. 3. Group mean (± sd) average fiber force (F), average activation (Act), average velocity (V), average length (L), index of force producing ability (F_ind) and rate of metabolic energy consumption (E_met) for MG (a), LG (b), SO (c) and TA (d). Values are normalised to the value in
the condition without exoskeletons. Without exoskeletons (NE) is represented by black bars and with spring-loaded exoskeletons (SE) by white bars. Arrows with * indicate a significant change in that variable from NE to SE ($P < 0.05$).

Figure. 4. The generic muscle model force-length relationship with the average operating lengths for each muscle [MG-(a), LG-(b), SO-(c) and TA-(d)] shown for without exoskeletons (NE) and with spring-loaded exoskeletons (SE) with filled and empty circles, respectively. Arrows with * highlight a significant ($P < 0.05$) left-shift down the ascending limb of the force-length relationship from NE to SE for MG (a) and SO (c).

Figure. 5. The generic muscle model force-velocity relationship with the peak velocities for each muscle [MG-(A), LG-(B), SO-(C) and TA-(D)] without exoskeletons (NE) and with spring-loaded exoskeletons (SE) conditions with filled and empty circles, respectively. The arrow with a * highlights a significant ($P < 0.05$) right-shift along the force-velocity relationship from NE to SE for SO (c).

Figure. 6 a) The musculoskeletal model adapted from Arnold et al. (2010). The exoskeleton torque from the experimental data was applied as equal and opposite torques acting on the shank and foot. The ground reaction force (GRF, blue arrow) and markers used to determine the joint angles for the ankle and knee (pink spheres) are also shown. b) Schematic giving an overview of the integration of experimental EMG and kinematic (joint angle) data into the modeling process. Processed EMG signals were considered as excitations and fed into a first order model of activation dynamics to produce activations. Experimentally determined joint angles were input to the musculoskeletal model to compute MTU lengths. Activations and MTU lengths were combined in an equilibrium model of contraction dynamics to calculate muscle fiber force ($F_m$), fiber length ($L_m$) and fiber velocity ($V_m$). $F_m$, $L_m$, $V_m$ and activations served as inputs to the energetics model to compute rates of metabolic energy consumption ($\dot{E}_{met}$).

SUPPLEMENTARY FIGURE CAPTIONS

Figure S1. Sensitivity of muscle dynamics to tendon compliance. The original simulations (black solid line) were recomputed with tendon compliance of all simulated muscles set ten percent greater (red dashed line) or ten percent less (blue dotted line) for one of the scaled musculoskeletal models.
Figure S2. Sensitivity of muscle dynamics to $v_{\text{max}}$. The original simulations (black solid line) were recomputed with $v_{\text{max}}$ of all simulated muscles set ten percent greater (red dashed line) or ten percent less (blue dotted line) for one of the scaled musculoskeletal models.

Figure S3. Sensitivity of muscle dynamics to maximum isometric force ($F_{\text{max}}$). The original simulations (black solid line) were recomputed with $F_{\text{max}}$ of all simulated muscles set ten percent greater (red dashed line) or ten percent less (blue dotted line) for one of the scaled musculoskeletal models.

### TABLES

#### Table 1. Group mean (±sd) metrics of muscle mechanics for hopping with (SE) and without (NE) spring-loaded exoskeletons output by the simulations of muscle-tendon dynamics

<table>
<thead>
<tr>
<th></th>
<th>M. Gastrocnemius</th>
<th>L. Gastrocnemius</th>
<th>Soleus</th>
<th>Tibialis Anterior</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>NE</td>
<td>SE</td>
<td>NE</td>
<td>SE</td>
</tr>
<tr>
<td>Normalised Peak Activation</td>
<td>0.79 ± 0.08</td>
<td>0.86 ± 0.09</td>
<td>0.94 ± 0.11</td>
<td>0.81 ± 0.09</td>
</tr>
<tr>
<td>Normalised Average Activation*</td>
<td>0.14</td>
<td>0.13</td>
<td>0.16</td>
<td>0.11</td>
</tr>
<tr>
<td>Peak fascicle shortening velocity* (L0/s)</td>
<td>0.61 ± 0.60</td>
<td>0.60 ± 0.53</td>
<td>0.56 ± 0.44</td>
<td>0.44 ± 0.39</td>
</tr>
<tr>
<td>Average fascicle velocity* (L0/s)</td>
<td>0.14</td>
<td>0.11</td>
<td>0.14</td>
<td>0.11</td>
</tr>
<tr>
<td>Average Fascicle Length* (L0/L0)</td>
<td>0.16</td>
<td>0.09*</td>
<td>0.16</td>
<td>0.08</td>
</tr>
<tr>
<td>Peak Force ($F/F_{\text{max}}$)</td>
<td>0.64 ± 0.48</td>
<td>0.59 ± 0.38</td>
<td>0.73 ± 0.44</td>
<td>0.54 ± 0.68</td>
</tr>
<tr>
<td>Average Force* ($F/F_{\text{max}}$)</td>
<td>0.16</td>
<td>0.05*</td>
<td>0.14</td>
<td>0.06*</td>
</tr>
<tr>
<td>Index of force producing ability ($F_{\text{lim}}$)</td>
<td>0.74 ± 0.46</td>
<td>0.63 ± 0.45</td>
<td>0.89 ± 0.50</td>
<td>0.79 ± 0.77</td>
</tr>
<tr>
<td>Positive fiber work (J kg$^{-1}$ hop$^{-1}$)</td>
<td>0.06 ± 0.040</td>
<td>0.03 ± 0.053</td>
<td>0.032 ± 0.036</td>
<td>0.04 ± 0.048</td>
</tr>
<tr>
<td>Negative fiber work (J kg$^{-1}$ hop$^{-1}$)</td>
<td>0.02 ± 0.01</td>
<td>0.01 ± 0.01</td>
<td>0.013 ± 0.03</td>
<td>0.02 ± 0.04</td>
</tr>
<tr>
<td>Net fiber work (J kg$^{-1}$ hop$^{-1}$)</td>
<td>0.015 ± 0.015</td>
<td>0.015 ± 0.032</td>
<td>0.004 ± 0.026</td>
<td>-0.056 ± 0.078</td>
</tr>
<tr>
<td>Positive MTU work (J kg$^{-1}$ hop$^{-1}$)</td>
<td>0.02 ± 0.02</td>
<td>0.01 ± 0.01</td>
<td>0.06 ± 0.06</td>
<td>0.04 ± 0.04</td>
</tr>
<tr>
<td>Negative MTU work (J kg$^{-1}$ hop$^{-1}$)</td>
<td>0.004 ± 0.015</td>
<td>0.015 ± 0.015</td>
<td>0.004 ± 0.026</td>
<td>-0.052 ± 0.019</td>
</tr>
<tr>
<td>Net MTU work (J kg$^{-1}$ hop$^{-1}$)</td>
<td>0.02 ± 0.01</td>
<td>0.00 ± 0.01</td>
<td>0.04 ± 0.04*</td>
<td>0.05 ± 0.01</td>
</tr>
<tr>
<td>Ratio of fascicle to MTU positive work</td>
<td>0.65 ± 0.53</td>
<td>1.76 ± 1.76</td>
<td>0.12 ± 0.22</td>
<td>0.46 ± 0.52</td>
</tr>
<tr>
<td>Energy Consumption (J kg$^{-1}$ hop$^{-1}$)</td>
<td>0.03 ± 0.01</td>
<td>0.01 ± 0.01</td>
<td>0.03 ± 0.02</td>
<td>0.04 ± 0.03</td>
</tr>
</tbody>
</table>

* These variables were calculated for a period of ±25% the hop cycle either side of peak fascicle force
* Denotes statistically significant difference between with and without exoskeletons ($P < 0.05$)
** Denotes statistically significant difference between with and without exoskeletons ($P < 0.01$)

#### Table 2. Comparison of forward and inverse solutions for ankle kinetics

<table>
<thead>
<tr>
<th></th>
<th>No Exo</th>
<th>Exo</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Forward</td>
<td>Inverse</td>
</tr>
<tr>
<td>Peak ankle moment (Nm/kg)</td>
<td>-1.48 ± 0.41</td>
<td>-1.74 ± 0.40</td>
</tr>
<tr>
<td>Time of peak moment (% hop cycle)</td>
<td>32 ± 7</td>
<td>34 ± 4</td>
</tr>
<tr>
<td>Peak ankle power (W/kg)</td>
<td>4.2 ± 1.8</td>
<td>4.4 ± 1.4</td>
</tr>
<tr>
<td>Time of peak power (% hop cycle)</td>
<td>49 ± 7</td>
<td>47 ± 7</td>
</tr>
</tbody>
</table>
Table 3. Muscle properties of the generic model

<table>
<thead>
<tr>
<th>Source</th>
<th>M. Gastrocnemius</th>
<th>L. Gastrocnemius</th>
<th>Soleus</th>
<th>Tibialis Ant.</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>F_{max} (N)</td>
<td>1308</td>
<td>606</td>
<td>3586</td>
<td>1375*</td>
<td>Arnold et al. (2010)</td>
</tr>
<tr>
<td>V_{max} (L_0/s)</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
<td>*Raasch et al. (1997)</td>
</tr>
<tr>
<td>L_0 (m)</td>
<td>0.051</td>
<td>0.059</td>
<td>0.044</td>
<td>0.049</td>
<td>Zajac &amp; Gorton (1989)</td>
</tr>
<tr>
<td>T_{ext} (m)</td>
<td>0.40</td>
<td>0.38</td>
<td>0.28</td>
<td>0.31</td>
<td>Arnold et al. (2010)</td>
</tr>
<tr>
<td>T_{act} (%)</td>
<td>10</td>
<td>10</td>
<td>11</td>
<td>9</td>
<td>Calculated</td>
</tr>
<tr>
<td>T_{max} (%)</td>
<td>0.011</td>
<td>0.009</td>
<td>0.031</td>
<td>0.015</td>
<td>Winters &amp; Stark (1988)</td>
</tr>
<tr>
<td>T_{max} (%)</td>
<td>0.045</td>
<td>0.038</td>
<td>0.111</td>
<td>0.055</td>
<td>Winters &amp; Stark (1988)</td>
</tr>
</tbody>
</table>

*F_{max} of Tibialis Anterior was adjusted to include the force producing capability of all dorsiflexors as per Raasch et al. (1997)