Elastic ankle exoskeletons reduce soleus muscle force but not work in human hopping

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Farris DJ, Robertson BD, Sawicki GS. Elastic ankle exoskeletons reduce soleus muscle force but not work in human hopping. J Appl Physiol 115: 579–585, 2013. First published June 20, 2013; doi:10.1152/japplphysiol.00253.2013.—Inspired by elastic energy storage and return in tendons of human leg muscle-tendon units (MTU), exoskeletons often place a spring in parallel with an MTU to assist the MTU. However, this might perturb the normally efficient MTU mechanics and actually increase active muscle mechanical work. This study tested the effects of elastic parallel assistance on MTU mechanics. Participants hopped with and without spring-loaded ankle exoskeletons that assisted plantar flexion. An inverse dynamics analysis, combined with in vivo ultrasound imaging of soleus fascicles and surface electromyography, was used to determine muscle-tendon mechanics and activations. Whole body net metabolic power was obtained from indirect calorimetry. When hopping with spring-loaded exoskeletons, soleus activation was reduced (30–70%) and so was the magnitude of soleus force (peak force reduced by 30%) and the average rate of soleus force generation (by 50%). Although forces were lower, average positive fascicle power remained unchanged, owing to increased fascicle excursion (+4–5 mm); Net metabolic power was reduced with exoskeleton assistance (19%). These findings highlighted that parallel assistance to a muscle with appreciable series elasticity may have some negative consequences, and that the metabolic cost associated with generating force may be more pronounced than the cost of doing work for these muscles.

ultrasound; fascicle; tendon; metabolic power; plantar flexors

ASSISTIVE EXOSKELETONS OR wearable robots have the potential to restore locomotor function in individuals with musculoskeletal disorders and augment locomotor function for healthy persons. The desired outcome of wearing an exoskeleton is typically to reduce the demands placed on the musculoskeletal system during locomotion (17). This might be with the intention of 1) lowering the metabolic cost of transport (7, 15, 25, 38); 2) reducing musculoskeletal injury risk; and/or 3) providing mechanical power output that the biological tissues cannot (3).

One of the main challenges of designing exoskeletons is to minimize their mass but still have them be capable of powering locomotion. One possible solution for this is to remove powered actuators and replace them with passive springs that are lightweight but can store and return energy to help power locomotion (7, 15, 17, 25, 40). This approach takes advantage of the natural springlike mechanics of the human leg during locomotion (35). A simple spring-mass model can be used to replicate the motion of the body center of mass during locomotion (5), highlighting the potential for storage and return of energy within elastic tissues in the legs during stance. In particular, elastic tissues in series with muscles (e.g., tendons) can be used to store energy from, and return energy to, the center of mass (2, 9).

Taking inspiration from this biological mechanism, passive exoskeletons using springs in parallel with the muscles of the legs have been developed (7, 11, 15, 17, 25, 40). Grabowski and Herr (25) showed that an exoskeleton with springs spanning all three joints (ankle, knee, and hip) of the leg could be used to reduce the metabolic cost of two-legged hopping in place. These authors demonstrated that, when hopping in the exoskeletons, individuals reduced their biological (muscular) contribution to leg stiffness to maintain normal overall stiffness (biological plus exoskeleton) and center of mass mechanics. Similar effects have been observed specifically at the ankle joint for humans hopping in ankle-foot orthoses that were spring loaded to assist plantar flexion (11, 15, 17). In these studies, plantar flexor electromyographic (EMG) activity was reduced when hopping with the device. This was shown to reduce the biological contribution to ankle stiffness (17) and, at certain hopping frequencies, net metabolic power during hopping (15).

Based on the aforementioned studies of joint and center of mass level mechanics, one might conclude that these spring-loaded exoskeletons are successful in achieving their goals of reducing mechanical and metabolic demands on the musculoskeletal system. However, to date, nobody has studied the effects of providing parallel assistance to a muscle-tendon unit (MTU) on the mechanics of the MTU itself. This may be of particular importance for MTUs such as those comprising the ankle plantar flexors that have relatively short, pennate fascicles in series with a longer, compliant series elastic element (SEE) composed of aponeurosis and external tendon (21). This morphology allows length changes of the muscle fascicles to be decoupled from ankle joint rotation because angular excursion at the joint can be provided by stretch and recoil of the SEE (19, 37). One of the benefits of this decoupling of muscle length change from joint excursion is that muscle fibers are potentially able to produce force with minimal changes in length and at relatively slow velocities (37). This should reduce the required muscle activation and metabolic energy consumption for a given level of force production (16).

Ultrasound imaging studies of human plantar flexor MTU mechanics have actually shown that, during the stance phase of walking, running, and hopping, muscle fascicles contract relatively slowly, and length changes are primarily occurring in the SEE (14, 20, 22, 29, 30). This allows the SEE to store and return energy, minimizing the work that must be done by active muscle that has the primary function of producing force isometrically (or with minimal length change) to stretch the SEE. Therefore, it seems that, in a healthy individual, muscle-tendon
interaction within MTUs that have a compliant SEE is well tuned to provide work output at the joint level with high efficiency (31, 32).

However, assuming that the SEE has a reasonably constant stiffness and that ankle joint kinematics remain constant, the tuned interaction of muscle and tendon must require a particular force profile to be applied to the SEE by the muscle. As stated above, assistive ankle exoskeletons reduce plantar flexor muscle activation (15, 17), leading to reduced muscular contributions to joint stiffness (17). Presumably this indicates that the muscles are producing lesser forces and thus may not be able to stretch the SEE to the same extent as when unassisted. Therefore, it could be that providing parallel assistance to a MTU with a compliant SEE interferes with the MTU’s efficient mechanics. This might mean that there are some negative effects of providing such assistance, as well as the previously stated benefits.

The aim of this study was to test, in vivo, whether providing exoskeletal assistance in parallel to a MTU with a compliant SEE during a cyclic movement interferes with the normally efficient muscle-tendon interaction that occurs. It was hypothesized that, when assistance is provided in parallel to the human plantar flexors, soleus (SO) would reduce its activation and force production levels, resulting in decreased stretch of the SEE and a compensatory increase in length change of the muscle fascicles. Furthermore, it was expected that the predicted increase in SO fascicle length change would increase SO fascicle mechanical work, despite the decreased load on the muscle.

METHODS

Participants. Seven male participants (mean ± SD, age = 28 ± 7 yr, height = 1.8 ± 0.06 m, mass = 80 ± 10 kg) gave written, informed consent to participate in this study. All participants were in good health and had no recent history of lower limb musculoskeletal injury. All procedures were approved by an institutional review board and complied with the guidelines for research involving human participants, as set out in the Declaration of Helsinki.

Experimental protocol. Bilateral hopping is a bouncing gait with similar spring-mass mechanics to running but simpler kinematics. The plantar flexors undergo a stretch-shortening motion, meaning a simple spring-loaded ankle exoskeleton can be used to provide parallel assistance to the plantar flexors. Therefore, each participant was required to perform bilateral hopping in place with the beat of a metronome operating at 2.5 Hz. This frequency was chosen because a previous study using the same motion found that this was the frequency around which metabolic cost was minimized when hopping in spring-loaded exoskeletons (25). The hopping task was performed for 4 min to allow the participants to reach a metabolic steady state and was completed under three experimental conditions: 1) with no exoskeleton (NE); 2) with bilateral ankle exoskeletons but no spring (NS); 3) with spring-loaded exoskeletons to assist plantar flexion (S).

The exoskeletons. The devices have been previously described elsewhere (15), and a sketch of the exoskeletons used is shown in Fig. 1. The exoskeleton consisted of a carbon fiber cuff around the upper shank, which was connected to a carbon fiber foot section via two aluminum bars, which had a freely rotating joint aligned with the participants’ malleoli. The foot section was embedded in a training shoe, through the sole, and around the heel. An extension spring could be attached to a bracket on the posterior aspect of the cuff and a bolt on the heel of the foot segment via a number of metal links. The number of links was adjusted for each participant such that the resting length of the spring coincided with an ankle angle of 127°, which has been determined as the typical angle at ground contact in hopping (17). This same approach was used by Ferris et al. (17) for a similar exoskeleton. A compression load cell (Omega drugs) was placed on the inferior side of the bolt at the heel of the foot segment and attached to the links in series with the spring. This was used to measure the forces in the spring. The stiffness of the spring in tension was 5 kN/m, and its moment arm about the joints was 0.135 m. This gave a rotational stiffness of 1.59 Nm/° (91 Nm/rad), which is ~40% of ankle stiffness during unassisted hopping at preferred frequency (17).

External kinematics and kinetics. An eight-camera motion analysis system (Vicon, Oxford, UK) was used to capture the three-dimensional (3D) positions of 22 reflective markers attached to the pelvis and right leg. Raw marker positions were filtered using a second-order low-pass Butterworth filter with a cutoff of 10 Hz. A static standing trial was captured, and the positions of markers on segment end points were used to calibrate a four-segment (pelvis, thigh, shank, and foot) model for each subject using established inertial parameters (12). Clusters of three or four markers on rigid plates were attached to the pelvis, thigh, and shank segments to track segment motion during hopping. For the foot, a cluster of three markers was attached directly to the shoe. Joint angles for the hip, knee, and ankle were computed in 3D as the orientation of the distal segment with reference to the proximal segment.

3D ground reaction forces applied to the left and right legs were computed during vertical hopping using a split belt instrumented treadmill (Bertec, OH) with the belts turned off. Participants hopped such that each foot was on a separate half of the treadmill, and thus the two 3D force vectors could be attributed separately to the left and right legs. Raw analog force platform signals were filtered using a low-pass Butterworth digital filter with the cutoff set to 35 Hz. Inverse dynamic analyses (41) were then used to compute net joint moments at the hip, knee, and ankle. Kinematics and kinetics were calculated for the right leg only, and it was assumed that the left leg behaved symmetrically. Inverse dynamics procedures were performed with Visual 3D software (C-motion, Germantown, MD). For the S condition, the contribution of the exoskeleton to the net ankle joint moment had to be determined. The force in the spring was computed from the load cell output voltage (from its factory calibration data) and multiplied by the moment arm of the spring about the ankle joint. This gave the plantar flexion moment provided by the exoskeleton, and this was subtracted from the total ankle moment to give the moment provided by biological tissues.
Determination of SO muscle parameters. SO muscle fascicle length during hopping was measured from B-mode ultrasound images (27) (Fig. 1). A linear ultrasound transducer (LV7.5/60/96ZT, Telene) operating at 8.0 MHz was placed over the midbelly of the SO and aligned so that SO fascicles could be visualized from deep to superficial aponeuroses (Fig. 1). The reliability and accuracy of ultrasound measurements of fascicle length are reported elsewhere (1, 18, 36). Images were sampled at 50 Hz, and a pulse from the ultrasound system that was high (3–5 V) during recording and low (0 V) before and after was used to trigger collection of all other data synchronously. To obtain fascicle length from each image, a custom MATLAB (The Mathworks, Natick, MA) program was used to digitize the points of attachment of a fascicle on the superficial and deep aponeuroses, and the length was calculated as the distance between these two points. Pennation angle was defined as the angle between the digitized fascicle and the deep aponeurosis (Fig. 1). The instantaneous length of the whole SO MTU was calculated from ankle joint flexion-extension angle using the equations of Hawkins and Hull (26). To obtain a value for the length of the SEE, the length of the fascicle was multiplied by the cosine of pennation angle and subtracted from the MTU length (Ref. 21; Fig. 1). Initial fascicle length (L0) was taken as the length of the fascicle at landing. Following landing, fascicles lengthened then shortened. Fascicle lengthening (ΔLpr) was calculated relative to L0 by subtracting L0 from the peak length during stance. Fascicle shortening (ΔLf) was calculated as the length at take-off minus the peak length during stance. Overall length change was the sum of the absolute values of ΔLpr and ΔLf.

SO muscle kinetics. Procedures for determining SO kinetic data were similar to those employed by Farris and Sawicki (14) previously for the gastrocnemius. Direct measurement of muscle force was not possible, and so it was estimated from inverse dynamics and SO muscle parameters. Forces transmitted by the Achilles tendon to the calcaneus were calculated as the biologically generated ankle moment divided by the moment arm of the Achilles tendon about the ankle joint (14, 30). This moment arm was calculated as the first derivative of SO MTU length with respect to ankle angle (6, 32). To reduce this force solely to that contributed by SO, it was multiplied by the relative physiological cross-sectional area (PCSA) of SO within the plantar flexors (0.54 from Ref. 23). Next, SO force was divided by the cosine of SO pennation angle to calculate the force generated along the line of the fascicle (Fso). The average rate of Fso production (Fso) was calculated by differentiating Fso with respect to time, integrating the period when the derivative was positive during a hop, and dividing the integral by the time taken for an entire hop. This value was calculated for multiple hops (8–10) and averaged.

The velocities of the SO fascicles, MTU, and SEE were calculated as the first derivative of their lengths with respect to time. The power output of the fascicles, SEE, and MTU were then calculated as the product of their respective forces and velocities. Positive work done by fascicles, SEE, and SO was estimated by integration of positive product of their respective forces and velocities. Positive work done output of the fascicles, SEE, and MTU were then calculated as the first derivative of their lengths with respect to time. The power for multiple hops (8–10) and averaged. These values were then smoothed by calculating the root-mean-squared (RMS) value of the signals over a rolling window of 20 ms. The RMS of each muscle’s signal was also calculated over the period of ground contact and the aerial phase of each hop as a metric of total activity over these two phases of the hop. Processed EMG signals for each muscle were normalized to the average of the local (within each hop) maxima of the signal recorded in that muscle in the NS condition.

Metabolic power. Rates of oxygen consumption and carbon dioxide production during hopping trials were recorded using a portable metabolic system (Oxycon Mobile, Viasys Healthcare). Before hopping, measurements were made during 5 min of quiet standing, and values from the last 2 min were averaged and used to calculate rates of metabolic energy consumption while standing. For the hopping trials, data from the last two of the 4 min were averaged for the calculation of metabolic rate. Visual inspection of rates of oxygen consumption with time (averaged over 30-s intervals) confirmed that participants were at steady state during this period, and the respiratory exchange ratio was never greater than one. Rates of oxygen consumption and carbon dioxide production were converted to metabolic powers using standard equations detailed by Brockway (8). Net metabolic powers during hopping were calculated by subtracting metabolic power during standing from metabolic power during hopping, and these values were normalized to individual body mass (W/kg). Metabolic data were presented as the normalized net value, unless otherwise stated.

Statistical analyses. All time series data for individual participants were reduced to the mean of at least 10 hops for each experimental condition. Unless otherwise stated, the values presented in this paper are the means ± SE for the whole participant group. To test for statistical differences in dependent variables between conditions, a one-way ANOVA with repeated measures was employed using SPSS software (IBM). The independent variable for the ANOVA was spring condition (3 levels: NE, NS, S). F-ratios for main effects were considered significant for P < 0.05. If a significant main effect was found, paired t-tests were used to make pairwise comparisons between spring conditions.

RESULTS

Hop heights and duty factors (proportion of a hop cycle spent in contact with the ground) were not significantly different between conditions (Table 1), indicating that the overall mechanical demand of the hopping task on the lower limbs was not different between conditions (15). RMS EMG for SO during the aerial phase and ground contact, peak Fso, and Faso were all significantly (P < 0.01) less for the S condition than for NS and NE conditions (Table 1, Fig. 2). These reductions occurred concurrently with a significant increase in both SO fascicle total excursion (lengthening + shortening) and ΔLpr for S compared with NS (P = 0.01) and NE (P = 0.048) during the stance phase (Table 1, Fig. 3A). There was no difference in length changes (relative to 0% hop time) of the SEE or MTU between conditions (Fig. 3, B and C). However, both the MTU and the SEE were at significantly (P < 0.00) shorter lengths on average throughout the hop cycle in the S condition (Table 1). This was associated with the ankle joint being more plantar flexed on average over a hop cycle for S (Table 1). A full description of joint kinematics and kinetics has been previously published (15).

Fascicle length change increased, and Fso decreased in S (Figs. 3A, 2B). This trade-off meant that Ppr was unchanged between conditions (Fig. 4). However, both Ppr and Pmtu were significantly less for S than for NS and NE (Fig. 4). The
Table 1. Group mean MTU metrics

<table>
<thead>
<tr>
<th></th>
<th>NE</th>
<th>NS</th>
<th>S</th>
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<tbody>
<tr>
<td>H, mm</td>
<td>20 ± 8</td>
<td>13 ± 6</td>
<td>15 ± 9</td>
</tr>
<tr>
<td>Duty factor</td>
<td>0.72 ± 0.07</td>
<td>0.75 ± 0.06</td>
<td>0.69 ± 0.07</td>
</tr>
<tr>
<td>(L_{SA} ), mm</td>
<td>254 ± 9*</td>
<td>246 ± 8*</td>
<td>237 ± 7</td>
</tr>
<tr>
<td>(L_{FAS} ), mm</td>
<td>39 ± 3</td>
<td>41 ± 4</td>
<td>38 ± 4</td>
</tr>
<tr>
<td>(L_{MTU} ), mm</td>
<td>291 ± 8*</td>
<td>285 ± 8*</td>
<td>273 ± 6</td>
</tr>
<tr>
<td>(\Delta L_{FAS} ), mm</td>
<td>2 ± 1</td>
<td>4 ± 1</td>
<td>4 ± 1</td>
</tr>
<tr>
<td>(\Delta L_{FAS} ), mm</td>
<td>3 ± 1*</td>
<td>3 ± 1*</td>
<td>5 ± 1</td>
</tr>
<tr>
<td>(\Delta L_{TOT} ), mm</td>
<td>5 ± 1*</td>
<td>7 ± 1*</td>
<td>9 ± 1</td>
</tr>
<tr>
<td>Peak FSO, N</td>
<td>1,623 ± 14*</td>
<td>1,667 ± 19*</td>
<td>1,166 ± 19*</td>
</tr>
<tr>
<td>(\theta_{\text{ank}} ), °</td>
<td>104 ± 1*</td>
<td>113 ± 2*</td>
<td>128 ± 2</td>
</tr>
<tr>
<td>(T_{\text{ank}} ) ground</td>
<td>1.07 ± 0.18*</td>
<td>1.00 ± 0.00*</td>
<td>1.42 ± 0.13</td>
</tr>
<tr>
<td>(T_{\text{ank}} ) aerial</td>
<td>1.07 ± 0.20*</td>
<td>1.00 ± 0.00*</td>
<td>2.84 ± 0.67</td>
</tr>
<tr>
<td>SO( \text{g} ) round</td>
<td>1.00 ± 0.06*</td>
<td>1.00 ± 0.00*</td>
<td>0.73 ± 0.06</td>
</tr>
<tr>
<td>SO( \text{a} ) round</td>
<td>0.72 ± 0.10*</td>
<td>1.00 ± 0.00*</td>
<td>0.29 ± 0.10</td>
</tr>
<tr>
<td>MG( \text{g} ) round</td>
<td>1.05 ± 0.04</td>
<td>1.00 ± 0.00</td>
<td>1.05 ± 0.06</td>
</tr>
<tr>
<td>MG( \text{a} ) round</td>
<td>1.02 ± 0.08*</td>
<td>1.00 ± 0.00</td>
<td>0.40 ± 0.08</td>
</tr>
<tr>
<td>LG( \text{g} ) round</td>
<td>1.09 ± 0.02</td>
<td>1.00 ± 0.00</td>
<td>0.95 ± 0.20</td>
</tr>
<tr>
<td>LG( \text{a} ) round</td>
<td>1.22 ± 0.20*</td>
<td>1.00 ± 0.00*</td>
<td>0.49 ± 0.20</td>
</tr>
</tbody>
</table>

Values are means ± SE. NE, with no exoskeleton; NS, with bilateral ankle exoskeletons but no spring; S, with spring-loaded exoskeletons to assist plantar flexion; H, hop height; \(L_{SA} \), \(L_{FAS} \), \(L_{MTU} \), average lengths of the series elastic element (SEE), fascicle (FAS), and muscle-tendon unit (MTU), respectively; \(\Delta L_{FAS} \) and \(\Delta L_{FAS} \): lengthening and shortening, respectively, of fascicle during ground contact; \(\Delta L_{TOT} \), change in total length; \(FSO \), soleus (SO) force; \(\theta_{\text{ank}} \), mean ankle angle during ground contact; \(T_{\text{ank}} \), tibialis anterior; MG, medial gastrocnemius; LG, lateral gastrocnemius; rms ground and rms aerial: root mean square electromyographic values from the stance and aerial phases, respectively, for each muscle. *Statistically significant (\(P < 0.05\)) difference from the S condition.

The net result of these findings was that the ratio of \(\bar{P}_{\text{FAS}}^+ \) to \(\bar{P}_{\text{SEE}}^+ \) went down in S, indicating that a smaller proportion of \(P_{\text{MTU}} \) was being provided by the return of elastic energy from the SEE. Whole body net metabolic power was significantly less for S than NS (−19%, \(P = 0.010\)) and NE (−13%, \(P = 0.016\)).

**DISCUSSION**

This study aimed to assess, in vivo, the effects on muscle-tendon mechanics of providing parallel assistance to a MTU that has a compliant SEE. As predicted, SO fascicle length change increased when assistance was provided, although this did not lead to an increase in \(F_{\text{FAS}} \). This was due to reductions in SO activity and the resulting force production as discussed below. It should be noted that more common locomotor tasks (i.e., walking and running) utilize more complex kinematics than hopping and thus care should be taken in extrapolating these findings to such tasks. However, plantar flexor stretch-shortening cycles are important in walking and running, and, therefore, it is relevant to these tasks to study the effects of a parallel spring on SO stretch-shortening mechanics in a simpler motion.

**Muscle activation and force production.** Based on previous studies using similar devices, the first hypothesis was that SO activation levels would be reduced when exoskeleton assistance was provided. As can be seen from Fig. 2A and Table 1, this hypothesis was supported because there were reductions in RMS EMG for SO during the aerial phase (60–70%) and ground contact (≈30%). Most notably, reductions occurred late in the aerial phase and early in stance (Fig. 2A). These timings of reductions in SO activation agree well with data from hopping in a similar device (17).

Also as predicted, there was a concurrent reduction in \(FSO \) during the stance phase when hopping with assistance compared with both other conditions (Fig. 2B, Table 1). In fact, the onset of force production during stance was later, and the peak \(FSO \) was less (≈30%) when hopping with assistance. The later onset of force production may have been facilitated by the lesser preactivation of SO at the end of the aerial phase and lower activation in early stance (Fig. 2A). It seems that parallel assistance in the form of a spring-loaded ankle exoskeleton was able to effectively reduce the activation and loading of SO during hopping.

One potential benefit of reduced force and activation is that the metabolic costs associated with producing muscular force could be reduced. These costs have been considered to account for ≈50% of the metabolic cost of transport in humans (24). Biewener (4) proposed that two factors influence the energy cost of producing muscular force in mammalian locomotion: 1) the magnitude of force generated per unit time; and 2) the
rate of force development and frequency of activation. As indicated by Fig. 2B, the magnitude of $F_{SO}$ was always less when assistance was provided. Hop cycle time was constant, and thus the magnitude of force per unit time was less for hopping with assistance. Furthermore, Fig. 2C shows that $F_{SO}$ was significantly less (≈50%) when the spring-loaded exoskeletons were being used. Because the frequency of the cyclic hopping task was controlled, the frequency of SO activation should not have changed. Overall, the metabolic cost of producing force in SO should have been reduced when assistance was provided. Consistent with this, whole body net metabolic power was significantly reduced with assistance (Fig. 4). However, studies of whole body mechanics have suggested that the cost of force production accounts for ≈50% of net metabolic costs (24), and so there may be other factors to consider at the muscular level.

**Muscle-tendon mechanics and energetics.** In addition to muscle force, mechanical work done by muscle has been cited as the other major factor in determining metabolic energy consumption during gait (10, 13, 24). The mechanical work done by muscle is determined by the length change of contractile elements and the force they produce during this length change. It was predicted that reduced force production by SO would result in a smaller stretch of the SEE, and that this would have to be compensated for by increased length changes of muscle fascicles, resulting in greater average fascicle rate of work ($P_{\text{FAS}}$).

The changes in the length of the SEE were not different when assistance was added (Table 1, Fig. 3B). Initially, this seems improbable given the elastic nature of the SEE and the noted reductions in $F_{SO}$. However, the fact that the average length of the SEE and the whole MTU were both significantly reduced when assistance was used (Table 1) may provide a clue. Tendons typically exhibit a nonlinear “toe region” in their force-elongation relationship at shorter lengths (2). This region has been specifically observed for the SEE of the human plantar flexors (34). In this region, the SEE will lengthen more for a given increase in force than in the stiffer linear region that exists at longer lengths. Without individual force-length plots for each of the study participants, it is hard to conclusively say when their SEE was and was not in the toe region. However, this would help to explain why, despite the smaller increase in force observed in the S condition, the SEE undergoes similar changes in length to NE and NS but at shorter absolute lengths. It could even be that, in the S condition, the SEE was shorter than its slack length early in stance. Again, without individual force-length data, this is hard to confirm, but, in the S condition, SO was contributing no force early (and very late) in stance. At these times, the entire plantar flexion moment was due to forces in the spring of the exoskeleton (Fig. 2B). This was despite small amounts of SO activation and could be explained by a slack SEE.

With the SEE being at shorter lengths with assistance, one might have expected the fascicles to have to have compensated and operated at longer lengths and over greater excursions. However, the ankle kinematics changed with the addition of the spring, and the ankle joint was significantly more plantar flexed on average (Table 1). This resulted in a shorter average length of the whole MTU and SEE, but there was no change in average fascicle length (Table 1). That said, there were differences in fascicle length changes for S compared with NE and NS.
As expected, the total excursion of SO fascicles was increased by 4–5 mm (≈2–3 mm of increased lengthening and shortening) compared with the unassisted conditions (Fig. 3, Table 1). This was as hypothesized, but, contrary to predictions, the increased excursion did not lead to any significant changes in $P_{FAS}^+$ (Fig. 4). This is because the work done by a fascicle is dependent on its length change and its force production during that length change. In the present study, although with assistance there was increased $\Delta L_{FAS}$ (shortening results in positive work), there was also a concurrent reduction in force production. The result of this trade-off was no change in $P_{FAS}^+$. Thus the hypothesis that parallel assistance would have some negative impact on metabolic cost by increasing fascicle work was not supported. This also meant that a reduction in overall net metabolic cost was achieved without altering work done by the SO muscle. Thus the metabolic costs associated with doing work may not be as important as those associated with producing force for SO during bouncing gaits.

While $P_{FAS}^+$ was not increased by assistance, the ratio of $P_{FAS}^+$ to $P_{SEE}^+$ was altered. $P_{SEE}^+$ accounted for 74–78% of $P_{MTU}^+$ without assistance and only 63% with assistance (Fig. 4). This should not increase metabolic cost, but it may affect the apparent efficiency of SO mechanical work. Apparent efficiency is high for MTUs when most of the positive work is provided by energy returned from stretch of the tendon and minimal work is done by active muscle (38). By reducing the energy stored and returned in the SEE, apparent efficiency of $P_{MTU}^+$ may have been reduced in the assisted condition.

**Contributions from other muscles.** Several of the central discussion points of this paper have attempted to relate SO mechanics to whole body net metabolic power. Clearly there are other muscles driving this cost, both at the ankle and at other joints. Based on PCSA, SO is the largest of the plantar flexors, accounting for ≈54% of the summed PCSA of this muscle group (23). SO was chosen because of this, and it was anticipated that it would make the largest contribution to ankle plantar flexion moments. However, it should be noted that a significant portion of plantar flexor force and work may come from the gastrocnemius, and this may influence metabolic energy consumption. However, the fact that MG and LG activations during ground contact did not change with assistance may indicate that much of the change in ankle mechanics is due to the change in SO activation.

On a similar theme, hopping was chosen partly because the overall power production of the task can be controlled, and the ankle joint is the primary power source, making it ideal for studying muscle-tendon mechanics and energetics of the plantar flexors. As such, we note that hop heights and duty factors were not significantly different between experimental conditions (Table 1). This, combined with the controlled hopping frequency, indicated that the total external power requirements of the hopping task were consistent across conditions. Although the ankle dominates overall power output of the task (≈60% at 2.5 Hz), the muscles acting at the knee (37%) and hip (3%) also contribute to mechanical power output and, because of their lesser series compliance, may do so less efficiently (39). This would not affect the changes in metabolic cost observed between conditions if knee and hip contributions were constant across conditions. However, there was a reduction in the contribution at the knee from 37 to 29% in the assisted condition. This probably contributed to some of the observed reduction in metabolic cost. The reduction in average positive power at the knee (≈0.2 W/kg) was much less than at the ankle (≈1.0 W/kg). If a typical muscle efficiency of 0.25 were assumed for the muscles acting at the knee (39), this reduction would account for 0.8 W/kg of the 1.5 W/kg reduction in whole body net metabolic power that was observed (Fig. 4). Despite some metabolic reduction coming from reduced knee mechanical power, a significant portion (≈0.7 W/kg) of the total reduction in metabolic power can still be attributed to reductions in mechanical power output at the ankle joint, most of which is due to reductions in force, but not work, of the SO muscle fascicles.

**Force sharing considerations.** The force sharing between SO, MG, and LG was determined purely on their relative PCSAs. This approach assumes that their relative activations (relative to their own maximum) are similar and fluctuate similarly. Maximums were not tested but, if different muscles’ relative activation were different within an experimental condition, it would have introduced a systematic error that would not change the main results of this study. Of greater concern with the present study design is whether or not their relative activations remained similar when assistance was added. From Table 1, it can be seen that SO activation during stance was reduced with assistance but MG’s and LG’s was not. This would imply that relative activation changed for SO, but not for LG and MG. However, because of the direction of this change (i.e., SO is at a lower percentage of its maximum activation in the S condition), the present result would only be strengthened, because accounting for this change would further reduce $F_{SO}$.

Furthermore, it must be considered that the net joint moment includes an antagonistic contribution from TA that was ignored. This would only cause a systematic underestimate of $F_{SO}$, if TA activation were constant across conditions. Unfortunately, this was not the case, as introducing the spring increased TA activation (Table 1). However, this increase was small for the stance phase, which is when the key dependent variables were evaluated, and TA was minimally active. The small increase in stance phase activity in TA would not explain the large reductions in $F_{SO}$ that were observed. A detailed discussion of why TA’s activation increased in the S condition has been previously published (15).

**Exoskeletons and injury prevention.** Aside from reducing metabolic energy consumption, exoskeletons could be used to reduce musculoskeletal injury risk by unloading musculoskeletal structures. For example, chronic joint or tendon conditions might be due to high volumes of repetitive loading, such as experienced during prolonged walking and running on a daily basis. Alternatively, acute injuries may occur due to instances of excessive loading of tissues. Intuitively, one might consider the reduced loading observed here to indicate a reduction in risk level for such injuries. This may be true for certain stress-related injuries, but muscular injuries have been more closely linked to excessive muscle strain (33). It was shown here that unloading SO actually increased $\Delta L_{FAS}$ by 2–3 mm (Fig. 3A), and fascicles reached a maximum length of 43 mm. Average fascicle lengths during hopping were 38–40 mm, and this is similar to resting SO fascicle lengths previously reported (28). Taking 38 mm as a resting length, the exoskeleton increased fascicle strain by 5–8% to a maximum of 8%. This is still well below the 25% strain that has been reported as a...
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Author Contributions

No conflicts of interest, financial or otherwise, are declared by the author(s).

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