Neuromechanical adaptation to hopping with an elastic ankle-foot orthosis

Daniel P. Ferris,1,2,3 Zaineb A. Bohra,1 Jamie R. Lukos,1 and Catherine R. Kinnaird1

1Division of Kinesiology, 2Department of Biomedical Engineering, and 3Department of Physical Medicine and Rehabilitation, University of Michigan, Ann Arbor, Michigan

Submitted 11 July 2005; accepted in final form 18 September 2005

HUMAN LEGS NORMALLY BEHAVE like compression springs during hopping and running (16, 34, 42). During the first half of stance, leg length decreases as ankle and knee joints flex. During the second half of stance, leg length increases as ankle and knee joints extend. This behavior has led biomechanists to model hopping and running animals with a simple spring-mass model (3, 18 –22, 25, 26, 29, 34, 42). In the model, a point mass represents body mass and a compression spring represents the leg (or legs) in contact with the ground (Fig. 1). The stiffness of the leg spring is very important to hopping and running mechanics because it influences peak ground reaction force, ground contact time, center of mass displacement, and stride frequency (19, 42).

When humans hop or run on compliant elastic surfaces, they adjust their leg stiffness to compensate for the stiffness of the surface (20, 22, 25, 26, 36). Elastic surfaces essentially place a second spring in series with the human leg. As surface stiffness increases, humans increase leg stiffness to maintain a constant overall stiffness for the series combination of leg spring and surface spring (22, 26). The invariant overall stiffness allows humans to maintain a similar movement pattern regardless of surface stiffness. Center of mass displacement, foot-ground contact time, and peak ground reaction force are all independent of surface stiffness during hopping and running on elastic surfaces because of leg stiffness adjustments (22, 26).

Whereas elastic surfaces add a spring in series with the human leg, an orthosis (i.e., brace) can add a spring in parallel with the human leg. Lower limb orthoses are normally free moving, rigid, or have limited elasticity with very high stiffness. Alternatively, an orthosis could be fabricated that has elasticity over a large range of joint motion. A few investigators have suggested that elastic orthoses could reduce effort during walking (30, 58) but walking depends less on elastic energy storage than hopping and running (1, 5). Adding springs in parallel with lower extremity joints may better benefit hopping or running given the springlike behavior of human legs during these locomotor movements.

Studies have shown neuromechanical adaptations to hopping with springs in series with the leg, but it is not known how humans adjust neuromechanical control and movement dynamics in response to springs in parallel with the leg. There is a fundamental difference in the neuromuscular control required for these two perturbations. When a spring is added in series with the leg, subjects must increase leg stiffness to preserve overall stiffness. In contrast, when a spring is added in parallel with the leg, subjects must decrease leg stiffness to preserve overall stiffness. No study has yet determined whether humans decrease biological stiffness during functional movements to preserve center of mass dynamics.

The specific purpose of this study was to determine whether humans adjust leg stiffness when a spring is added to a lower limb orthosis. For this initial experiment, we focused on hopping in place because it has similar spring-mass mechanics as forward running (42) but much simpler joint kinematics (17). Previous studies indicate that the ankle joint stiffness is primarily responsible for determining leg stiffness during human hopping (20, 21). On the basis of the importance of the ankle joint, we compared humans hopping with and without an orthosis spring providing plantar flexor torque (i.e., dorsiflexion resistance). We hypothesized that subjects would decrease their biological ankle stiffness to offset the added ankle stiffness from the orthosis spring, keeping overall leg stiffness constant. It is possible to hop with a range of leg stiffness values at any given hopping frequency by altering the relative time spent in the air vs. on the ground (21, 22). Thus it was not mechanically required that subjects keep overall leg stiffness constant when the orthosis spring was added. We recorded...
orthosis conditions. In one condition (Spring), the subjects hopped while wearing a custom-built ankle-foot orthosis with a linear extension spring (Century Spring, Los Angeles, CA; Fig. 1). The linear extension spring provided plantar flexor torque when the ankle was moved into dorsiflexion (extension stiffness 6.7 kN/m resulting in \( \sim 1.04 \text{ N-m/}^\circ \)). We chose the spring stiffness based on preliminary trials on a few subjects with different springs. The spring was the stiffest that subjects felt comfortable with during one-legged hopping without extensive practice. In the second condition (No Spring), subjects hopped while wearing the ankle-foot orthosis without the spring attached. Subjects followed the beat of a digital metronome for the 2.2- and 2.6-Hz hopping frequencies. Testing more than one frequency allowed us to verify that the results were consistent across different leg stiffness and ground contact times (16). We chose 2.2 and 2.6 Hz because they were greater than the preferred hopping frequency found in previous studies (16, 43). Frequencies below the preferred frequency typically do not display springlike leg behavior (16). Actual hopping frequencies of the subjects had a <3% standard deviation from the desired hopping frequency. In the preferred frequency trials, subjects were instructed to hop at their most comfortable frequency while the metronome was off. The preferred hopping frequency also was not significantly different between orthosis conditions [Spring 2.12 Hz (SD 0.11) and No Spring 2.11 Hz (SD 0.10); \( P = 0.261 \)]. For all trials, subjects hopped with their hands on their hips. Subjects practiced hopping with and without the spring until they felt comfortable performing the task (\( \sim 30 \) s). Subjects hopped at the three frequencies for both conditions. Two repetitions of each trial were collected in a randomized order with rest between trials. Subjects were instructed to rest for additional time if they felt fatigued. We collected 10 s of kinematic, kinetic, and electromyographic data for each trial.

**Ankle-foot orthosis.** Each ankle-foot orthosis was custom-built, made from carbon-fiber, polypropylene, and metal hinges (24), allowing for a full range of motion in the sagittal plane (Fig. 1C). Orthosis average mass was 1.3 kg. The spring was attached to the orthosis with stainless steel brackets and metal links with an average moment arm of 8.9 cm. We set the resting position of the spring to \( \sim 127^\circ \) of plantar flexion (foot-to-shank angle) by individually adjusting the number of links for each subject. This angle was found to be the approximate touchdown ankle angle during hopping in place at preferred frequencies (21). We attached a single-axis compression load cell (Omega-dyne, Sunbury, OH) above the top steel bracket to measure tension in the spring (Fig. 1C).

**Data collection.** We used a six-camera motion analysis system to record segment and joint kinematics (120 Hz, Motion Analysis, Santa Rosa, CA). We placed sets of three retroreflective markers on each subject’s left foot, shank, thigh, and pelvis. Subjects hopped on a force plate (1,200 Hz, Advanced Mechanical Technology, Watertown, MA) to collect ground reaction force data.

We recorded electromyography of eight lower limb muscles: soleus, medial gastrocnemius, lateral gastrocnemius, tibialis anterior, rectus femoris, vastus lateralis, vastus medialis, and medial hamstrings (Konigsberg Instruments, Pasadena, CA). Each subject’s skin was shaved and prepared with alcohol before attaching bipolar surface electrodes. Electrodes were centered over the belly of each muscle along its long axis (interelectrode distance: 3.5 cm). We taped electrodes and wires to the skin and, if necessary, wrapped elastic bandages around the upper and lower legs to minimize movement artifact. Before data collection, we visually examined each electromyography signal for noise and cross talk, moving the electrodes as necessary (60). We sampled electromyography data at 1,200 Hz via an analog-to-digital board.

**Data analysis.** We used commercial software (Visual3D, C-Motion, Rockville, MD) for data filtering and processing. From each trial, we extracted five consecutive hops for analysis. All values reported in

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**METHODS**

**Subjects.** Seven healthy subjects participated in this study [5 women, 2 men; age 26 yr (SD 2.7), mass 66 kg (SD 9.0)]. Past studies have found no differences in leg stiffness or hopping dynamics by gender when normalized by body mass (48). The University of Michigan Institutional Review Board granted approval for this project, and all participants gave informed, written consent.

**General procedure.** Each subject hopped on his or her left leg at three frequencies (2.2, 2.6 Hz, and preferred frequency) under two
this study represent data averaged across 10 hops per subject per condition and frequency (5 hops per trial for 2 trials). We defined hop cycle as ground contact to ground contact using ground reaction force data. We filtered marker data with a fourth-order Butterworth low-pass filter with zero lag (cutoff frequency 6 Hz). We calculated internal muscle moments about the lower limb joints based on kinematic marker and force platform data. Lower limb inertial properties were estimated based on subject anthropometric measurements (62). For the inverse dynamics calculations, we modified segmental inertial parameters of the lower limb for orthosis mass and moment of inertia. Electromyography data were filtered with a fourth-order Butterworth low-pass filter with zero lag (cutoff frequency 20 Hz) to attenuate movement artifacts. We calculated normalized root-mean-squared amplitude of the high-pass-filtered electromyography after full wave rectification to compare muscle activation amplitudes across conditions. We also created linear envelopes of electromyography data using a fourth-order Butterworth high-pass filter with zero lag (cutoff frequency 6 Hz). To reduce intersubject variability (61), we normalized electromyography amplitudes to the peak values recorded during hopping at the preferred frequency in the No Spring trials. To assess muscle activation timing, we calculated the time in the hop cycle when the linear envelopes reached their peak.

Joint angle definitions. All joint angles were defined in the sagittal plane (Fig. 1B). The ankle angle was the anterior angle between the foot and the shank. The knee angle was the posterior angle between the shank and the thigh. The hip angle was the anterior angle between the thigh and pelvis.

Stiffness calculations. We calculated leg stiffness by finding the ratio of vertical ground reaction force to the center of mass displacement (i.e., leg compression) during stance using a linear regression. Center of mass displacement was found by twice integrating the vertical ground reaction force with respect to time (4). We calculated the constant of integration for center of mass velocity on the basis of the assumption that the mean velocity of the center of mass was zero over one complete hop cycle (4). We used a zero constant of integration for calculating center of mass position because we only needed center of mass displacement, not absolute position (4). We took the slope of the best linear fit as the average stiffness of the leg during ground contact (Fig. 2) (32). In a similar manner, we took the slope of the best linear fit after plotting joint torque vs. joint displacement in the sagittal plane during stance to calculate average torsional joint stiffness values about the ankle, knee, and hip. To calculate orthosis ankle torque, we multiplied spring force recorded with the load cell by the spring moment arm. To calculate biological ankle torque, we subtracted orthosis ankle torque from the total ankle torque derived from inverse dynamics analyses (Visual3D Software). This allowed us to calculate three separate ankle stiffness values for the Spring condition: biological ankle stiffness, orthosis ankle stiffness, and total ankle stiffness. They equate to:

Total Ankle Stiffness = Biological Ankle Stiffness
+ Orthosis Ankle Stiffness

Statistical analyses. We used a three-way ANOVA (subject, frequency, condition) to determine significant differences in kinematic, kinetic, and electromyographic data between Spring and No Spring conditions ($P < 0.05$ as significance level). Because our focus was on the differences between the two orthosis conditions, we did not analyze differences related to hopping frequency or intersubject variation, which have been reported previously. Leg and ankle stiffness increase with hopping frequency (2, 16) and larger subjects tend to have stiffer legs (6, 48). To determine whether significant variations occurred between controlled frequency hopping and preferred frequency hopping, we conducted additional analyses using separate ANOVAs for controlled frequencies (2.2 Hz, 2.6 Hz) and preferred frequency separately. These analyses revealed almost identical results as one ANOVA for all frequencies (2.2 Hz, 2.6 Hz, preferred frequency) together. Therefore, we only present results for all frequencies grouped together. All statistical analyses were performed with JMP IN software (SAS Institute).

RESULTS

Overall leg stiffness was not significantly different between Spring and No Spring conditions ($P = 0.07$; Fig. 3). Post hoc analysis on leg stiffness revealed a least significant value of 0.81. Because the overall leg stiffness difference between conditions was 1.50, the lack of statistical significance is not likely due to an inadequate sample size (i.e., type II error). Subjects maintained leg stiffness by hopping with the same hip, knee, and total ankle stiffnesses between the two conditions. Post hoc analysis on total ankle stiffness revealed a least significant value of 0.144. The total ankle stiffness difference between conditions was 0.153, indicating again that sample size was not likely the cause for lack of statistical significance. Biological ankle stiffness was lower in the Spring condition compared with the No Spring condition ($P < 0.0001$; Fig. 3). At the preferred hopping frequency, the orthosis spring contributed 24% (SD 6.6) of total ankle stiffness during the Spring condition. At faster hopping frequencies, the orthosis spring contributed less to total ankle stiffness because total ankle stiffness was greater. At 2.6 Hz, the orthosis spring contributed 18% (SD 4.7) of total ankle stiffness.

Most joint kinematic and kinetic parameters were similar for the two orthosis conditions (Table 1). The main exceptions to this were ankle and knee angles at touchdown. Even though the spring was preset to resting length at an ankle angle of $\sim 127^\circ$, subjects landed with a slightly straighter leg (i.e., ankle was...
DISCUSSION

Our results indicate that humans maintain constant leg stiffness when an orthosis spring is added to their lower limb during hopping in place. To achieve constant leg stiffness, subjects decreased biological ankle stiffness to offset added stiffness from the orthosis spring. The adjustment in biological ankle stiffness presumably occurred by reducing plantar flexor muscle activation. Several previous studies have demonstrated that ankle joint stiffness will decrease in response to reduced plantar flexor muscle activation (14, 47, 59). Soleus, medial gastrocnemius, and lateral gastrocnemius all had lower electromyograph amplitudes during the Spring condition compared with the No Spring condition. Isolated muscle studies (8, 56, 57) suggest that shifting plantar flexor muscle activation earlier in the stance phase could have increased ankle stiffness, but there were not large differences in plantar flexor muscle activation timing between conditions. Only the soleus had an earlier peak muscle activity when hopping in the No Spring condition, and that difference was relatively small (~3% of the cycle period).

Overall movement dynamics were similar for both conditions, but there were small changes in ground contact time and peak ground reaction force. These differences were partially caused by the straighter leg posture at ground contact in the Spring condition. Landing with more extended lower limb joints can increase overall leg stiffness, decrease contact time, and increase peak ground reaction force (20). However, the discrepancy in leg posture at touchdown was not enough to significantly alter leg stiffness between conditions. Another reason why we could have found significant differences in ground contact time and peak ground reaction force is the nonlinear dynamics of a spring-mass system. There is not a one-to-one correlation between changes in leg stiffness and changes in ground contact time or peak ground reaction force (42). As a result, smaller and more variable changes in one parameter could lead to larger or more consistent changes in other parameters. In addition, differences in leg stiffness linearity (Table 1) and hysteresis between orthosis conditions could have affected ground contact time and peak ground reaction force in a manner dissimilar to a true spring-mass system. Human legs behave similar to linear springs during hopping, but they clearly are not real mechanical springs. Any variation away from perfect springlike behavior can result in discrepancies between experimental measurements and spring-mass model predictions.

Although our data indicate that humans adjust biological ankle stiffness to offset added stiffness from an orthosis, it is not clear why subjects maintained the invariant total ankle stiffness. Subjects could have kept the same biological ankle stiffness for both conditions and hopped with greater leg stiffness for the Spring condition. Alternatively, subjects could have lowered biological ankle stiffness more than they did so that total ankle stiffness and leg stiffness decreased. Instead of choosing either of these possibilities, subjects offset the added orthosis stiffness with biological stiffness reductions.
Table 1. Kinematic and kinetic data summary

<table>
<thead>
<tr>
<th></th>
<th>Preferred</th>
<th>2.2 Hz</th>
<th>2.6 Hz</th>
<th>ANOVA P Value</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>No Spring</td>
<td>Spring</td>
<td>No Spring</td>
<td>Spring</td>
</tr>
<tr>
<td>Ground contact time, s</td>
<td>0.36 (0.04)</td>
<td>0.35 (0.04)</td>
<td>0.34 (0.03)</td>
<td>0.33 (0.03)</td>
</tr>
<tr>
<td>Peak ground reaction force, N</td>
<td>1,659 (316)</td>
<td>1,760 (318)</td>
<td>1,756 (371)</td>
<td>1,814 (353)</td>
</tr>
<tr>
<td>Leg compression, m</td>
<td>0.08 (0.01)</td>
<td>0.08 (0.01)</td>
<td>0.08 (0.01)</td>
<td>0.07 (0.01)</td>
</tr>
<tr>
<td>Leg stiffness, kN/m</td>
<td>18.80 (5.02)</td>
<td>19.90 (4.61)</td>
<td>20.86 (3.78)</td>
<td>22.11 (4.12)</td>
</tr>
<tr>
<td>Correlation coefficient for leg stiffness</td>
<td>0.91 (0.24)</td>
<td>0.95 (0.02)</td>
<td>0.98 (0.01)</td>
<td>0.99 (0.01)</td>
</tr>
<tr>
<td>Total ankle stiffness, N/m³/°</td>
<td>4.23 (0.73)</td>
<td>4.42 (0.96)</td>
<td>4.70 (0.78)</td>
<td>4.59 (0.71)</td>
</tr>
<tr>
<td>Correlation coefficient for ankle stiffness</td>
<td>0.95 (0.01)</td>
<td>0.97 (0.02)</td>
<td>0.94 (0.02)</td>
<td>0.96 (0.02)</td>
</tr>
<tr>
<td>Biological ankle stiffness, N/m²/°</td>
<td>4.23 (0.73)</td>
<td>3.37 (0.94)</td>
<td>4.70 (0.78)</td>
<td>3.55 (0.81)</td>
</tr>
<tr>
<td>Orthosis stiffness, N/m²/°</td>
<td>0.00 (0.00)</td>
<td>1.04 (0.24)</td>
<td>0.00 (0.00)</td>
<td>1.04 (0.27)</td>
</tr>
<tr>
<td>Knee stiffness, N/m²/°</td>
<td>5.65 (1.61)</td>
<td>5.66 (1.29)</td>
<td>6.08 (1.25)</td>
<td>5.87 (1.43)</td>
</tr>
<tr>
<td>Correlation coefficient for knee stiffness</td>
<td>0.87 (0.04)</td>
<td>0.83 (0.19)</td>
<td>0.87 (0.03)</td>
<td>0.87 (0.04)</td>
</tr>
<tr>
<td>Hip stiffness, N/m²/°</td>
<td>3.96 (3.52)</td>
<td>4.68 (4.43)</td>
<td>4.23 (3.66)</td>
<td>3.92 (3.60)</td>
</tr>
<tr>
<td>Correlation coefficient for hip stiffness</td>
<td>0.32 (0.17)</td>
<td>0.41 (0.22)</td>
<td>0.36 (0.16)</td>
<td>0.41 (0.24)</td>
</tr>
<tr>
<td>Ankle angle at touchdown, °</td>
<td>128 (6)</td>
<td>138 (4)</td>
<td>126 (5)</td>
<td>137 (5)</td>
</tr>
<tr>
<td>Knee angle at touchdown, °</td>
<td>153 (5)</td>
<td>157 (5)</td>
<td>151 (5)</td>
<td>158 (5)</td>
</tr>
<tr>
<td>Hip angle at touchdown, °</td>
<td>170 (7)</td>
<td>171 (8)</td>
<td>168 (9)</td>
<td>170 (8)</td>
</tr>
<tr>
<td>Ankle displacement, °</td>
<td>33 (4)</td>
<td>35 (5)</td>
<td>32 (3)</td>
<td>34 (3)</td>
</tr>
<tr>
<td>Knee displacement, °</td>
<td>24 (5)</td>
<td>24 (4)</td>
<td>22 (4)</td>
<td>23 (3)</td>
</tr>
<tr>
<td>Hip displacement, °</td>
<td>5 (3)</td>
<td>6 (2)</td>
<td>4 (3)</td>
<td>6 (2)</td>
</tr>
<tr>
<td>Hip peak moment, N-m</td>
<td>163 (30)</td>
<td>170 (36)</td>
<td>172 (33)</td>
<td>172 (36)</td>
</tr>
<tr>
<td>Knee peak moment, N-m</td>
<td>166 (48)</td>
<td>142 (28)</td>
<td>172 (35)</td>
<td>153 (34)</td>
</tr>
<tr>
<td>Hip peak moment, N-m</td>
<td>77 (52)</td>
<td>69 (41)</td>
<td>73 (49)</td>
<td>71 (43)</td>
</tr>
</tbody>
</table>

Values are means (SD); n = 7 subjects. See METHODS for calculations. *P < 0.05, showing significant differences between conditions.

One explanation for invariant total ankle stiffness (and invariant leg stiffness) is that subjects attempted to maximize elastic energy storage and return in tendons and ligaments. Mathematical models suggest that movement dynamics can optimize recoil of tendons and ligaments with the appropriate cycle timing (7, 35). Adjusting ground contact time via effective leg stiffness could conceivably maximize elastic energy storage and return. This would then minimize muscle fiber work for the given conditions (35, 53). It would be interesting to measure muscle fiber displacements with ultrasonography (27) while humans hopped with different leg stiffness values on compliant surfaces or with elastic orthoses. This would provide direct evidence of how muscle fiber work varies when humans make adjustments to their biological leg stiffness.

A second possible explanation for the invariant total ankle stiffness is based on reflex pathways. Melville-Jones and Watt (43) proposed that preferred hopping dynamics make optimal use of stretch reflex timing to activate extensor muscles. A recent study by Granata et al. (33) found that stretch reflex timing can result in automatic decreases in joint stiffness when compliant elastic elements are added in parallel with the ankle. However, in that study, they used random unexpected perturbations to a preset stationary ankle posture. It is not clear how those findings would translate to dynamic functional movements like hopping. Indeed, the main finding of that study was dependent on a change in the frequency of ankle motion. That was not the case in the present study because ankle motion occurred at the same frequency for both orthosis conditions. Given the studies of Dietz (9), Dietz et al. (11), and Komi (38), it seems likely that stretch reflex dynamics contribute substantially to leg stiffness during bouncing gaits. A number of research groups have provided mounting evidence for the importance of muscle activation pathways from Ib afferents during legged locomotion (10, 12, 13, 23, 31, 49, 50). As muscle force increases, it can trigger increased muscle activation in a positive-force feedback loop that is stable due to inherent properties of the musculoskeletal mechanics (51, 52). Simulations have demonstrated that the combination of stretch reflexes and positive-force feedback can provide adequate control for bouncing gaits and springlike leg behavior (28). It would be interesting to extend these simulations by including parallel elastic elements to determine whether decreases in biological stiffness can be predicted based on the reflex pathways. In the present study, the slightly straighter leg posture observed at ground contact in the Spring condition could reduce the muscle force and stretch due to a smaller ground reaction force moment arm (46).

A third possible explanation for the invariant overall leg stiffness is that the human nervous system could plan movement dynamics during hopping and running to achieve a desired center of mass trajectory. The studies showing that humans maintain invariant center of mass dynamics by abandoning spring-like leg behavior on extremely compliant surfaces and energy-dissipating surfaces suggest that center of mass movement is especially important to the neuromechanical control of hopping (44, 45). Recent simulation studies found that spring-mass systems self-stabilize to movement perturbations due to inherent dynamics (54, 55). Humans may choose to emulate a spring-mass movement trajectory to simplify the control of hopping and running. It would be helpful to test this theory by examining simulation stability to external perturbations when the leg is not acting like a spring but the center of mass trajectory is similar to a spring mass system (e.g., on energy-dissipating surfaces).

There were limitations to this study that may have affected the results. The resting length of the orthosis spring was set for a constant angle based on a previous study’s results (21). It
would have been preferable to adjust the resting spring length to each subject’s preferred ankle angle at touchdown for each frequency. Pilot experiments performing this adjustment required considerably longer data collection periods to calculate touchdown angles at each frequency and adjust spring length between trials. In addition, on a limited number of subjects we collected data at shorter resting spring lengths and found no difference in results. As such, we chose to use one set angle for adjusting the spring resting length based on the previous study (21). Another limitation was the stiffness of the orthosis spring. A stiffer spring would have forced subjects to make a greater adjustment in biological ankle stiffness if they maintained invariant total ankle stiffness. Pilot experiments with springs of different stiffnesses indicated that the spring used in this study was near the maximum stiffness that would not unduly perturb subjects’ balance. Studying two-legged hopping in the future could alleviate this limitation as hopping on two legs results in reduced leg stiffness and increased stability compared with hopping on one leg (D. P. Ferris, personal observations). Lastly, we only examined hopping in place. It is possible that our results will not apply to forward running. Additional studies need to examine subjects running with elastic orthoses to determine whether humans follow a similar neuromechanical control principle for all bouncing gaits.

Future applications. If human runners adjust biological joint stiffness in a similar manner as human hoppers, an elastic exoskeleton could improve running performance. The hopping subjects in this study decreased muscle activation and reduced muscle-tendon work when using the elastic ankle-foot orthosis. These changes should provide concomitant reductions in metabolic energy expenditure during steady speed running (39, 40). It is also possible that an elastic exoskeleton could increase maximum running speed in humans. During sprinting, the main goal of a runner is to run as fast as possible, not minimize muscle mechanical work or metabolic energy expenditure. Previous studies suggest that sprinters may maximize leg stiffness to achieve the fastest running speed (6, 15, 37, 41). If a sprinter’s goal is to increase leg stiffness as much as possible, an elastic exoskeleton might allow runners to increase leg stiffness if they maintain constant biological leg stiffness. This would be in contrast to our present findings for hopping in place at a steady pace but is a reasonable possibility given previous studies of maximal speed sprinting (6, 41). It would be informative to test these possibilities in future studies examining humans running while wearing elastic exoskeletons.

Fig. 4. Electromyographic (EMG) output of the 8 recorded leg muscles during both the No Spring (solid line) and Spring (dashed line) conditions at 2.2 Hz. Aerial phase begins to the right of the vertical lines. Data were normalized and averaged across subjects. Decreases in EMG were mostly evident during the stance phase of the hop cycle. Sol, soleus; TA, tibialis anterior; MG, medial gastrocnemius; LG, lateral gastrocnemius; RF, rectus femoris; VL, vastus lateralis; VM, vastus medialis; MH, medial hamstrings.

Table 2. Electromyography root-mean-squared amplitudes

<table>
<thead>
<tr>
<th></th>
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<th>2.6 Hz</th>
<th>ANOVA P Value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No Spring</td>
<td>Spring</td>
<td>No Spring</td>
<td>Spring</td>
</tr>
<tr>
<td>TA</td>
<td>1.00 (0.00)</td>
<td>1.03 (0.15)</td>
<td>0.93 (0.16)</td>
<td>1.15 (0.28)</td>
</tr>
<tr>
<td>Sol</td>
<td>1.00 (0.00)</td>
<td>0.75 (0.08)</td>
<td>0.86 (0.16)</td>
<td>0.71 (0.13)</td>
</tr>
<tr>
<td>MG</td>
<td>1.00 (0.00)</td>
<td>0.83 (0.10)</td>
<td>0.88 (0.15)</td>
<td>0.79 (0.17)</td>
</tr>
<tr>
<td>LG</td>
<td>1.00 (0.00)</td>
<td>0.82 (0.11)</td>
<td>0.92 (0.17)</td>
<td>0.78 (0.17)</td>
</tr>
<tr>
<td>VL</td>
<td>1.00 (0.00)</td>
<td>0.92 (0.10)</td>
<td>0.93 (0.18)</td>
<td>0.80 (0.14)</td>
</tr>
<tr>
<td>RF</td>
<td>1.00 (0.00)</td>
<td>0.89 (0.20)</td>
<td>0.96 (0.22)</td>
<td>0.85 (0.30)</td>
</tr>
<tr>
<td>VM</td>
<td>1.00 (0.00)</td>
<td>0.91 (0.07)</td>
<td>0.99 (0.20)</td>
<td>0.87 (0.15)</td>
</tr>
<tr>
<td>MH</td>
<td>1.00 (0.00)</td>
<td>1.04 (0.11)</td>
<td>0.95 (0.23)</td>
<td>0.88 (0.27)</td>
</tr>
</tbody>
</table>

Values are means (SD) for 7 subjects. Data are unitless because of normalization. See METHODS for calculations. TA, tibialis anterior; Sol, soleus; MG, medial gastrocnemius; LG, lateral gastrocnemius; VL, vastus lateralis; RF, rectus femoris; VM, vastus medialis; MH, medial hamstrings. *P < 0.05, showing significant differences between conditions.
ACKNOWLEDGMENTS

The authors thank Ammanath Peethambaran and other staff of the University of Michigan Orthotics and Prosthetics Center for help with designing and fabricating the orthoses. The authors also appreciate helpful feedback from members of the University of Michigan Human Neuromechanics Laboratory on earlier versions of this manuscript.

GRANTS

This project was funded by National Institute of Neurological Disorders and Stroke Grant R01 NS-045486 and National Science Foundation Grant BES-0347479.

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