Differences in muscle function during walking and running at the same speed

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Abstract

Individual muscle contributions to body segment mechanical energetics and the functional tasks of body support and forward propulsion in walking and running at the same speed were quantified using forward dynamical simulations to elucidate differences in muscle function between the two different gait modes. Simulations that emulated experimentally measured kinesiological data of young adults walking and running at the preferred walk-to-run transition speed revealed that muscles use similar biomechanical mechanisms to provide support and forward propulsion during the two tasks. The primary exception was a decreased contribution of the soleus to forward propulsion in running, which was previously found to be significant in walking. In addition, the soleus distributed its mechanical power differently to individual body segments between the two gait modes from mid- to late stance. In walking, the soleus transferred mechanical energy from the leg to the trunk to provide support, but in running it delivered energy to both the leg and trunk. In running, earlier soleus excitation resulted in it working in synergy with the hip and knee extensors near mid-stance to provide the vertical acceleration for the subsequent flight phase in running. In addition, greater power output was produced by the soleus and hip and knee extensors in running. All other muscle groups distributed mechanical power among the body segments and provided support and forward propulsion in a qualitatively similar manner in both walking and running.
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1. Introduction

Walking and running are the two most common forms of human gait, with many of the basic kinetics and kinematics of walking and running being similar between the two modes (e.g., Nilsson and Thorstensson, 1989; Nilsson et al., 1985). However, one of the most noticeable differences is the existence of a flight phase in running, rather than the double support phase that occurs in walking, which suggests that muscles generate greater body support (defined as vertical acceleration of the body center of mass) in running. In walking, recent

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modeling and simulation studies have shown that body support is provided by the uni-articular hip and knee extensors in early stance, and the ankle plantar flexors as primary contributors in late stance (Anderson and Pandy, 2003; Neptune et al., 2004a). However, it is unknown whether these muscle groups provide body support in a similar manner during running.

Similarly, forward propulsion (defined as horizontal acceleration of the center of mass) in walking is provided by the hip and knee extensors in early stance and the plantar flexors in late stance (Neptune et al., 2004a; Zajac et al., 2003). However, which muscle groups are the primary contributors to forward propulsion in running is not well understood. Previous inverse dynamics-based analyses of running have suggested that the knee extensors and ankle plantar flexors contribute to forward propulsion from mid- to late stance

(Ounpuu, 1990; Novacheck, 1998), but others have suggested that the hip extensors are the primary contributors (Simonsen et al., 1985; Belli et al., 2002). Analyzing EMG data, other studies have suggested that the plantar flexors contribute little to push-off in late stance, since their peak muscle activity occurs in mid-stance and then rapidly decreases in late stance (e.g., Mann et al., 1986; Reber et al., 1993). Part of the discrepancy among studies could be related to the inability of inverse dynamics and EMG-based analyses to identify individual muscle contributions to accelerations and mechanical energetics of individual body segments (Zajac et al., 2002), which is essential for assessing muscle function, since individual muscle contributions can vary greatly even within the same muscle group (e.g., ankle plantar flexors, Neptune et al., 2001; Zajac et al., 2003).

To help clarify differences in muscle function between walking and running, the overall objective of this study was to use forward dynamical simulations of walking and running at the same speed to identify how differences in task mechanics influence individual muscle contributions to the mechanical energetics of the two gait modes. Comparing muscle function at the same gait speed is particularly informative, since many of the task requirements remain the same (e.g., the net contributions to forward propulsion). The specific objective was to access whether individual muscle contributions to the body segment mechanical energetics and body support and forward propulsion remain invariant during the two gait modes.

2. Methods

2.1. Musculoskeletal model

A 2D bipedal musculoskeletal model and forward dynamical simulations of walking and running at the preferred transition speed (PTS; i.e., the speed where a voluntary transition from walking to running occurs) were generated to quantify individual muscle contributions to the body segment mechanical energetics and body support and forward propulsion. The musculoskeletal model has been previously described in detail (Neptune and Sasaki, 2005; Sasaki and Neptune, 2005) and will be described briefly here. The model consisted of a trunk, right and left legs and 15 Hill-type musculotendon actuators per leg to actuate the model, which were combined into ten functional groups with muscles within each group receiving the same excitation pattern (Fig. 1). The excitation patterns were derived from EMG data (see Experimental data collection below) and defined by three parameters: excitation onset, duration and magnitude. For the muscles from which EMG was not measured (i.e., GMED, IL and
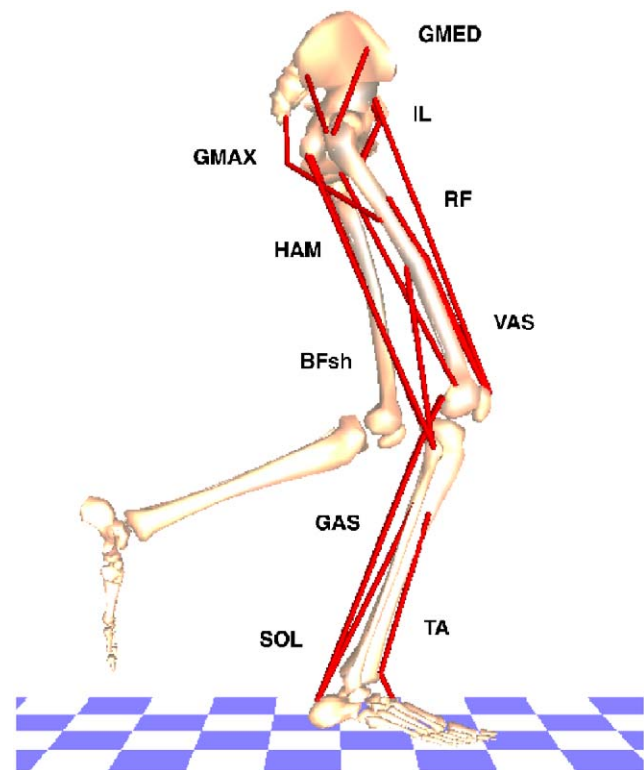

Fig. 1. 2D-musculoskeletal model consisting of the HAT (head, arms and torso) and right and left legs (femur, tibia, patella and foot). Ten muscle groups per leg were used to drive the model: GMAX (gluteus maximus, adductor magnus), GMED (anterior and posterior portion of gluteus medius), IL (iliacus, psoas), HAM (biceps femoris long head, medial hamstrings), VAS (three-component vasti), RF (rectus femoris), BFsh (biceps femoris short head), TA (tibialis anterior), GAS (medial and lateral gastrocnemius) and SOL (soleus). Muscles within each group received the same excitation signal and the muscle excitation–contraction dynamics were governed by Hill-type muscle properties.

BFsh), block patterns were used to define the excitation. The contact between foot and ground was modeled using 30 visco-elastic elements attached to each foot segment (Neptune et al., 2000).

2.2. Dynamic optimization

Dynamic optimization using a simulated annealing algorithm (Goffe et al., 1994) was used to generate simulations that emulated the average mechanics of a group of subjects walking and running at the group's PTS (see Experimental data collection below). The algorithm fine-tuned each muscle's excitation onset, duration and magnitude until the difference between the simulation and experimental kinematics (i.e., trunk anterior–posterior tilting and translation, and the hip, knee and ankle joint angles), and horizontal and vertical ground reaction forces (GRFs) over the gait cycle was minimized.

2.3. Muscle function

Muscle function was quantified by determining the individual muscle contributions to body support and forward propulsion and body segment mechanical energetics over the gait cycle, using ground reaction force decomposition and segment power analyses (Fregly and Zajac, 1996; Neptune et al., 2001). The segment power analysis (Fregly and Zajac, 1996) was performed to identify mechanical power generated, absorbed or transferred to each body segment by each muscle. Positive power generated by a muscle to a segment indicates that the muscle accelerated the segment in the direction of its motion; negative power indicates the muscle decelerated the segment in the direction of its motion. Mechanical power was further analyzed by quantifying the muscle's contribution to each segment's vertical (defined as the time rate of change in the segment's potential and vertical kinetic energy) and horizontal (defined as the time rate of change in its horizontal kinetic energy) power.

2.4. Experimental data collection

Experimental kinematic, GRF and EMG data were collected for the dynamic optimization to generate the simulations. Ten healthy subjects (5 males and 5 females: age 29.6 ± 6.1 years old, height 169.7 ± 10.9 cm, body mass 65.6 ± 10.7 kg), free from any known neuromusculoskeletal disorders, participated in the experiments. Informed consent approved by The Cleveland Clinic Foundation and The University of Texas at Austin was obtained from each subject before participating in the experiments. All data were collected at The Cleveland Clinic Foundation in Cleveland, OH. Kinematic, GRF and EMG data were measured while walking and running on a split-belt treadmill with embedded force plates at each subject's PTS. Details of the protocol to determine the PTS, and data acquisition and processing of experimental data are provided in Neptune and Sasaki (2005). All data were time-normalized to a full gait cycle, averaged within each subject and then across all subjects to obtain a group average.

3. Results

The generated walking and running simulations at the PTS (1.96 ± 0.17 m/s: group average and s.d.) matched the group-averaged kinematics and ground reaction forces, with most tracking variables within ± 2 s.d. (Fig. 2: Walking, Running). The corresponding muscle excitation patterns also compared well with the human subject EMG linear envelopes (Fig. 3).

The segment power analysis revealed that the only muscle that exhibited a distinct functional difference between walking and running was SOL. In walking, SOL absorbed ipsilateral leg power and transferred much of that power to the trunk from mid- to late stance (Fig. 4: SOL, Walking ~20–50% gait cycle, dashed line >0, dash–dot line <0), then in late stance, simultaneously, generated power directly to the trunk (Fig. 4: SOL, Walking, ~30–50% gait cycle, solid line >0) to provide body support during mid- to late stance (Fig. 5: SOL, Walking, Vertical, ~20–100% stance) and forward propulsion during late stance (Fig. 5: SOL, Walking, Horizontal, ~75–100% stance). In running, SOL initially absorbed power from the ipsilateral leg and trunk from the beginning of stance to mid-stance (Fig. 4: SOL, Running, ~5–20% gait cycle, dashed and dash–dot lines <0) and then generated power to the leg and trunk from mid- to late stance (Fig. 4: SOL, Running, ~20–40% gait cycle, dashed and dash–dot lines >0). The power absorbed from the leg primarily decelerated the leg in the horizontal direction (Fig. 6: SOL, Leg, ~5–40% stance, dash–dot line <0). SOL also acted to decelerate the trunk horizontally for a longer duration compared to walking (Fig. 7B: compare dash–dot lines). Then, in late stance SOL contributed very little to forward propulsion of the body (Fig. 5: SOL, Running Horizontal, ~50–100% stance), as seen in its small contributions to the horizontal leg and trunk power during this period (Fig. 6: SOL, Leg, ~40–70% stance, Trunk, ~60–100% stance, dash–dot lines >0). However, similar to walking SOL contributed much to body support (Fig. 5: SOL, Running, Vertical), by decelerating the downward motion of the trunk in the beginning of stance (Fig. 6: SOL, Trunk, 0–30% stance, dashed line <0), and then accelerating the trunk as well as the leg upward from mid- to late stance (Fig. 6: SOL, Trunk, Leg, ~35–80% stance, dashed lines >0).

Although there were some quantitative differences, all other muscles generated consistent body segment mechanical energetics and contributions to body support and forward propulsion in both walking and running. For example, the uni-articular hip extensor GMAX functioned similarly in both walking and running to primarily deliver power to the trunk (Fig. 4: GMAX, Walking ~10–25% gait cycle, Running ~15–35% gait cycle, dashed line >0), which provided body support and forward propulsion from the beginning to mid-stance (Fig. 5: GMAX, Vertical, Horizontal). However, both contributions extended beyond mid-stance and the magnitude of the horizontal contribution was much more pronounced in running.

4. Discussion

The overall objective of this study was to use forward dynamical simulations to identify differences in muscle function between walking and running at the preferred
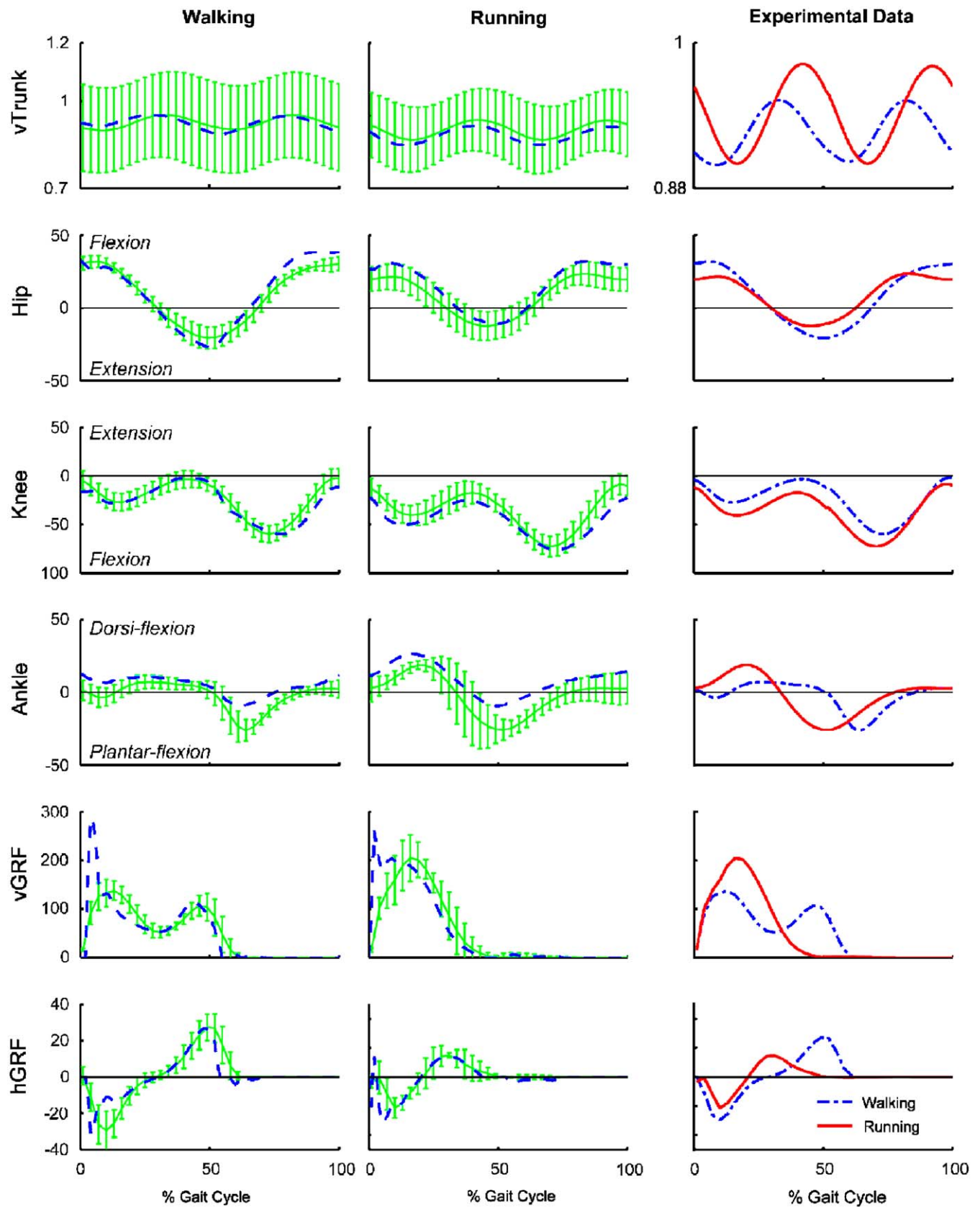
Fig. 2. Trunk vertical displacement (vTrunk, units: m), hip, knee and ankle joint angles (units: degrees) and vertical (vGRF) and horizontal (hGRF) ground reaction forces (units: percent body weight) in walking and running simulations (dashed line) and experimental data (solid line, average±2 s.d.) over the gait cycle (right foot-strike to right foot-strike). Experimental Data compares the kinesiological data in walking and running. Positive angles indicate flexion, extension and dorsiflexion in the hip, knee and ankle joints, respectively.
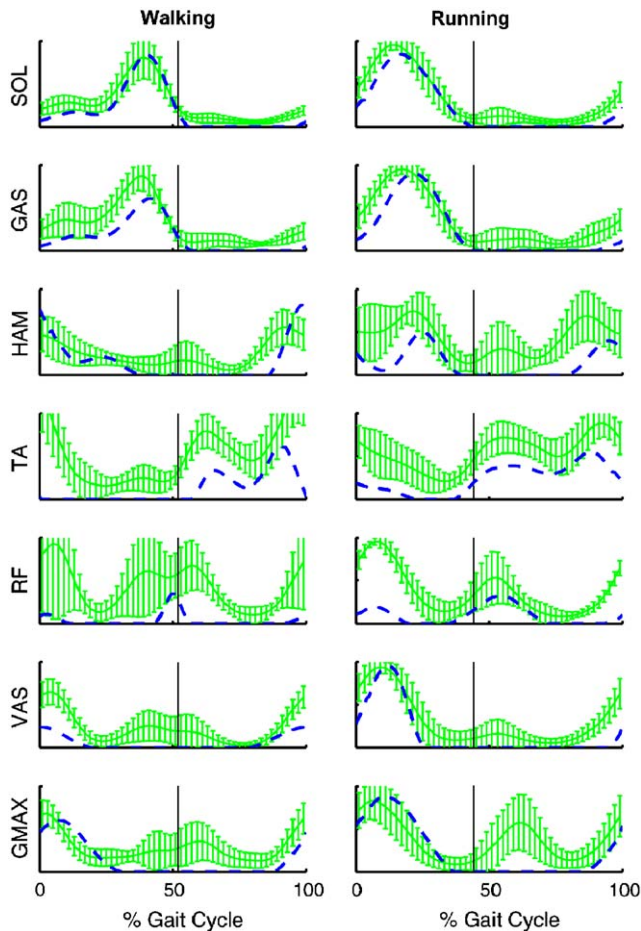
Fig. 3. Muscle excitation patterns for walking and running simulations (dashed line) and group average EMG linear envelopes (solid line, average±s.d.) at the preferred transition speed. EMG data were normalized to the maximum value observed over the gait cycle during running for each muscle. Thus, caution is needed when comparing the excitation magnitudes. Vertical lines indicate toe-off.

Fig. 4. Distribution of muscle mechanical power (Total, solid line) to the trunk (Trunk, dashed line), ipsilateral leg (IpsiLeg, dash–dot line) and contralateral leg (ContraLeg, dotted line) during walking and running at the preferred transition speed over the gait cycle (right heel-strike to right heel-strike). The vertical lines indicate toe-off. All units are in Watts. Note that the scale is adjusted for each muscle.

transition speed (PTS). The specific objective was to access whether individual muscle contributions to body segment mechanical energetics, and support and forward propulsion remain invariant when walking and running at the same speed. The simulations successfully emulated the salient features of kinesiological data collected from a group of young healthy subjects walking and running at the PTS.

Potential limitations of using a planar musculoskeletal model to interpret muscle function in human gait have been previously discussed in detail (Neptune et al., 2001, 2004a, b; Zajac et al., 2003). In the present study, there existed a higher impact peak in both walking and running (Fig. 2: vGRF, 0–10% gait cycle) compared to previous modeling studies of normal walking (e.g., Anderson and Pandy, 2003; Neptune et al., 2004a). These peaks were composed primarily of non-muscular forces (i.e., gravity and velocity-dependent forces) and were accentuated due to the higher gait speeds analyzed
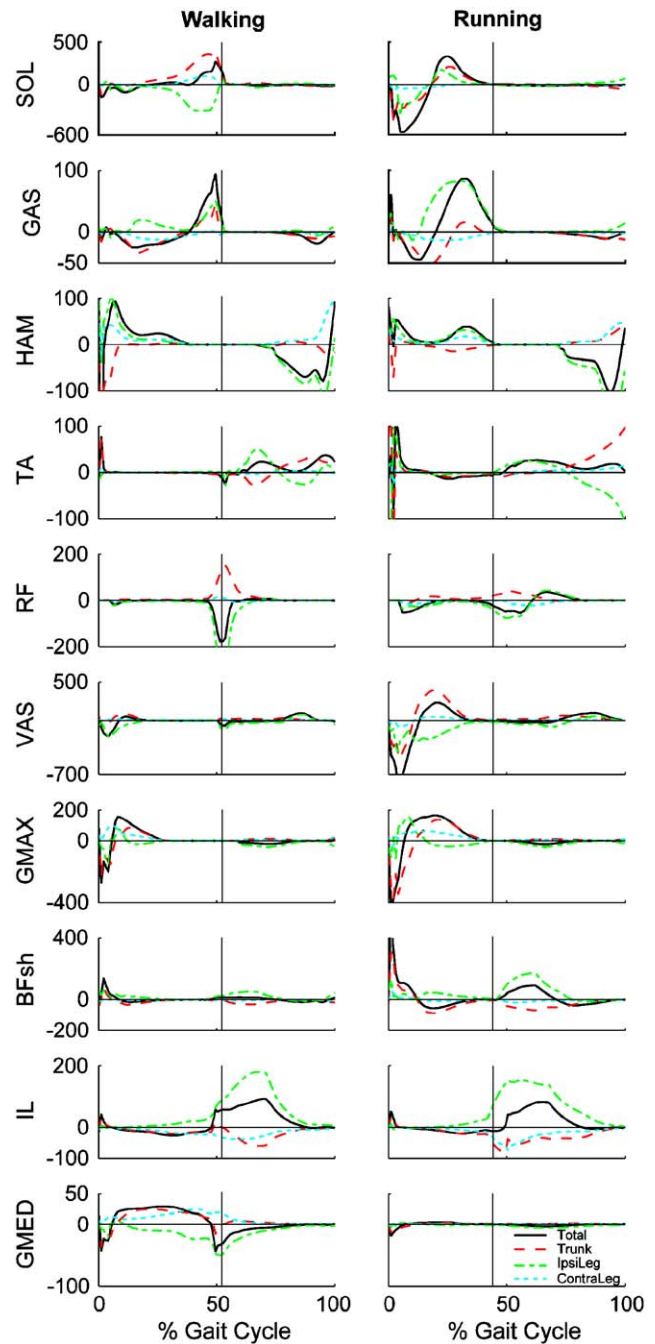
in the present study (∼2 m/s). Reductions in impact peaks may be achieved by adding additional degrees-of-freedom or wobbling masses to the model that would act as viscous dampers at impact (e.g., Schache et al., 1999; Liu and Nigg, 2000). However, such improvements would not alter our interpretation of muscle function in
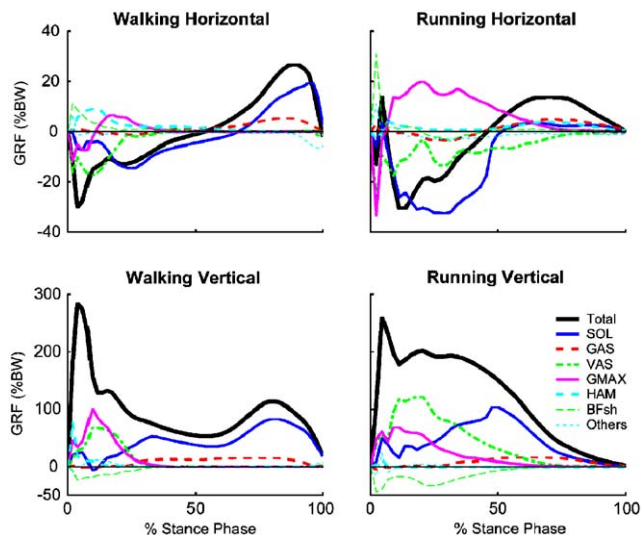
Fig. 5. Individual muscle contributions to body support (vertical GRF) and forward propulsion (horizontal GRF) during stance in walking and running (units: percent body weight). Total denotes the sum of the contributions by non-muscular and muscular components. The stance phase is defined from heel-strike to toe-off of the ipsilateral leg.
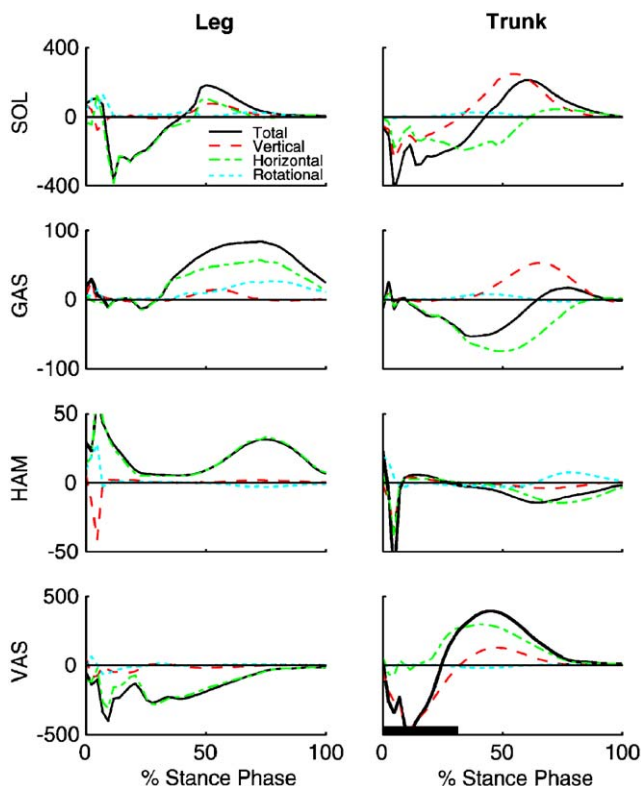

Fig. 6. Power distributions in leg and trunk segments by SOL, GAS, HAM and VAS during stance in running. All units are in Watts (Total: net power generated by a muscle in the segment; Vertical: vertical kinetic and potential power; Horizontal: horizontal kinetic power; Rotational: rotational power). The horizontal bar indicates the period when the trunk motion is downward.
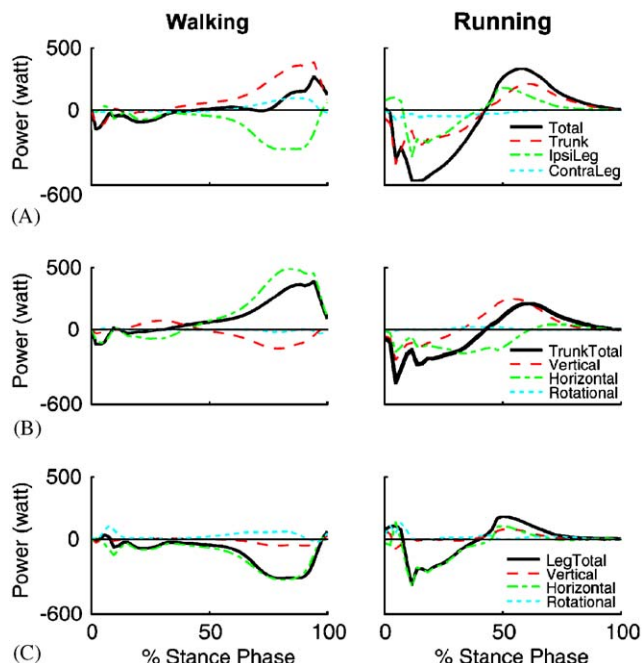

Fig. 7. (A) Soleus (SOL) mechanical power distribution during stance in walking and running at the preferred transition speed. (B) Trunk power distribution by SOL during stance (TrunkTotal: net trunk power; Vertical: trunk vertical kinetic and potential power; Horizontal: trunk horizontal kinetic power; Rotational: trunk rotational power). (C) Ipsilateral leg power distribution by SOL during stance (LegTotal: net leg power; Vertical: leg vertical kinetic and potential power; Horizontal: leg horizontal kinetic power; Rotational: leg rotational power).

this region, as the impact peak is primarily due to non-muscular contributions.

Another potential limitation is the exclusion of upper-extremities in the musculoskeletal model. Arm movement during running appears to stabilize the body by providing angular momentum along the long axis of the body that counteracts the momentum in the lower body (Hinrichs, 1990). In addition, the upper-extremities provide an impulse in the vertical direction that could possibly contribute to body support. However, such contributions are small during stance (~5% of the total impulse), especially during slower running speeds such as those in the present study (Hinrichs, 1990). Thus, the lack of upper extremities in the running simulation in the present study would appear to have little affect on the results.

The simulation results showed that in running, the primary contributors to body support were the hip and knee extensors (VAS and GMAX) and uni-articular plantar flexors (SOL). With SOL excitation occurring from beginning to mid-stance (Fig. 3: SOL, Running; see also Mann et al., 1986; Reber et al., 1993), SOL combined with VAS and GMAX to accelerate the body vertically (Fig. 5: Running, Vertical). Forward propulsion was provided primarily by GMAX from beginning

to mid-stance, and the plantar flexors (SOL and GAS), and HAM in mid- to late stance (Fig. 5: GMAX, SOL, GAS and HAM, Running, Horizontal).

Previous studies of running have suggested that the primary contribution of the plantar flexors is to provide forward propulsion in the second half of the stance phase (e.g., Brandell, 1973; Novacheck, 1998), while others disagree, noting that plantar flexor excitation ceases well before toe-off (e.g., Mann et al., 1986; Reber et al., 1993). Our simulation analysis has shown that the plantar flexors contribute to forward propulsion with a slightly greater contribution by GAS (Fig. 5: SOL, GAS, Running, Horizontal). However, SOL appears to have a greater role in providing body support. Previous studies have shown that in running, SOL EMG activity is significantly lower than GAS in late stance (Reber et al., 1993), and that the duration of GAS activity is prolonged relative to SOL activity (Swanson and Caldwell, 2000). The difference in muscle activity appears to be related to functional differences between SOL and GAS, with SOL providing support in mid-stance and GAS accelerating the leg into swing from mid- to late stance (Fig. 6: GAS, Leg, dash–dot line).

The large GMAX contribution to forward propulsion in running is consistent with previous inverse dynamic analyses (e.g., Belli et al., 2002; Novacheck, 1998; Simonsen et al., 1985; Simpson and Bates, 1990). However, the present results do not support previous suggestions that VAS is the primary contributor to forward propulsion (e.g., Novacheck, 1998; Simpson and Bates, 1990). VAS transferred power from the leg to the trunk from mid- to late stance (Fig. 4: VAS, Running, ~20–40% gait cycle), which provided forward acceleration of the trunk (Fig. 6: VAS, Trunk, dash–dot line). However, VAS acted to decelerate the leg forward (Fig. 6: VAS, Leg, dash–dot line). Thus, the net effect was that VAS acted to hinder forward propulsion of the body (Fig. 5: VAS, Running, Horizontal), while simultaneously providing body support (Fig. 5: VAS, Running, Vertical).

HAM contributed to forward propulsion during the second half of stance (i.e., the propulsive phase) in running (Fig. 5: HAM, Running, Horizontal, ~50–100% stance). Although the magnitude of power generated by HAM during this period was relatively small (~40 W, Fig. 4: HAM, Running, ~20–40% gait cycle), HAM delivered power almost exclusively to the leg to accelerate it forward (Fig. 6: HAM, Leg, dash–dot line). This forward acceleration of the leg by HAM in late stance, combined with the contribution from GAS to initiate swing, was necessary to meet the increased mechanical energetic demands of the leg in running compared to walking (e.g., the peak horizontal power of the thigh and shank after toe-off was greater in running by 20 and 16 W, respectively). Previous studies have suggested that HAM plays a major role in running,

especially at higher speeds (e.g., Belli et al., 2002; Mann and Sprague, 1980). Kyrolainen et al. (1999) found that the biceps femoris long-head had the largest increase in EMG activity among muscles examined in their study as running speed increased from just over 3 m/s to each subject's maximal speed. As the mechanical energetic demands increase with running speed, the contribution from HAM during the propulsive phase would be expected to increase.

The most noticeable difference in individual muscle function between walking and running was observed in SOL, generating a different distribution of body segment power between the two gait modes. In walking, weakly eccentric and then concentric SOL action from early stance to toe-off absorbed power from the leg and delivered that power to the trunk, while simultaneously generating energy directly to the trunk in late stance (Fig. 4: SOL, Walking ~20–50% stance). In contrast, in running SOL initially absorbed much power from both the leg and trunk (Fig. 4: SOL, Running, ~5–20% gait cycle, all curves negative), and then in mid- to late stance, SOL generated positive power to both the leg and the trunk (Fig. 4: SOL, Running, ~20–40% gait cycle). The power delivered to the trunk in running was primarily in the vertical direction to provide support, whereas in walking, it was primarily in the horizontal direction to provide forward propulsion (Fig. 7B: Walking ~50–100% stance, dash–dot line >0; Running ~50–80% stance, dashed line >0). The decreased SOL contribution to forward propulsion in running was surprising considering the increase in power production by SOL (Fig. 4: SOL, Walking and Running, compare solid lines), which is attributed to an increase in force production due to an improved contractile state (Neptune and Sasaki, 2005). The decreased contribution to forward propulsion in running is attributed to a change in kinematics. In running, the foot is located below the trunk when the propulsive GRF reaches its peak value (Fig. 8: Running), which limits the ability of SOL to generate positive horizontal power to the trunk (Fig. 7B: Running ~60–100% stance, dash–dot line ~0). In contrast, the foot placement in walking (Fig. 8: Walking) is more suited for SOL to generate a large contribution to the trunk horizontal power during late stance (Fig. 7B: Walking ~50–100% stance, dash–dot line >0).

The change in the contribution of SOL to support produces the primary difference in the mechanics of walking and running (i.e., the flight phase in running versus the double support phase in walking). In running, the increased and phase-advanced SOL power output combined with VAS and GMAX to provide body support (Fig. 5: SOL, VAS and GMAX, Vertical). This support of the body continued to lift the trunk upward from mid-stance until the foot left the ground (Fig. 2: Experimental Data, vTrunk, solid line, ~20–45% gait
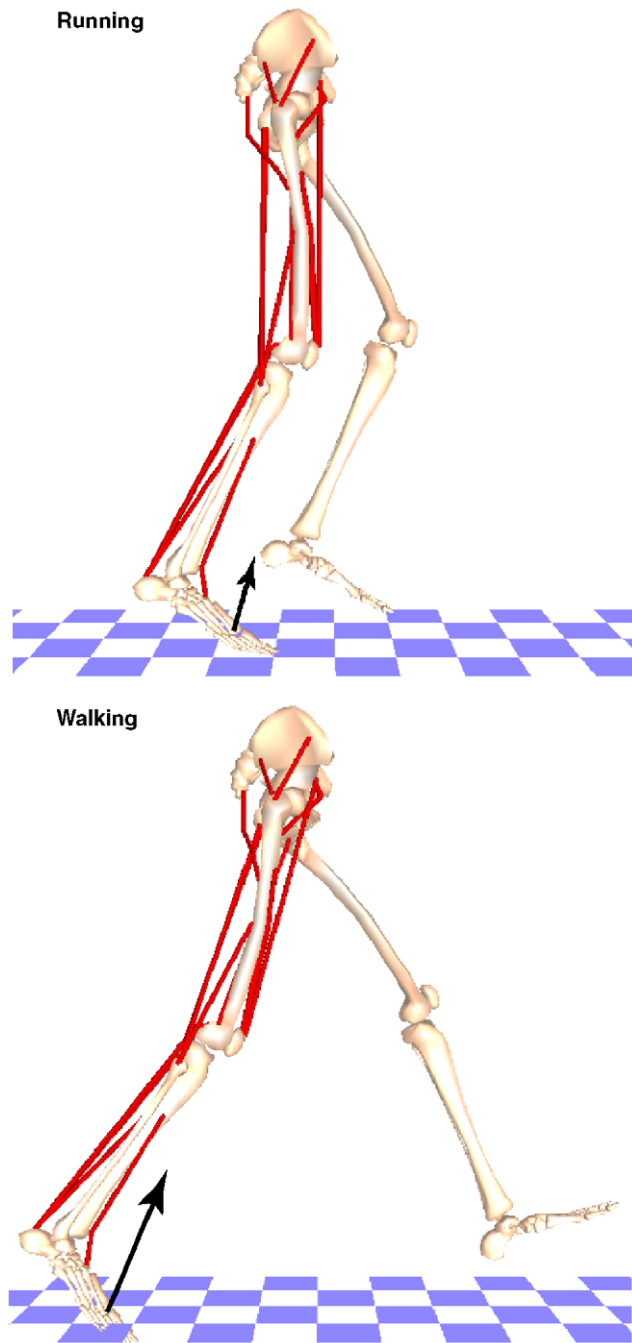
Fig. 8. Configuration of the body segments in walking and running when the propulsive GRF is maximal.

cycle) to generate the subsequent flight phase. In contrast, the hip and knee extensors (VAS and GMAX) and plantar flexors (SOL and GAS) during walking act in succession to provide body support, with VAS and GMAX providing support in the beginning of stance, and SOL and GAS providing support later from mid- to late stance (Neptune et al., 2004a). This muscle coordination pattern results in a vertical trunk trajectory that reaches its apex near 30% of the gait cycle and then begins to descend (Fig. 2: Experimental Data,

vTrunk, dash–dot line). The phase-advance of SOL activity in running also causes the ankle to begin plantar flexing earlier in the gait cycle (Fig. 2: Experimental Data, Ankle, solid versus dash-dot lines). All other joint angle trajectories remain similar between walking and running (Fig. 2: Experimental Data, Hip and Knee, compare solid and dash–dot lines).

Besides SOL, all other muscles showed qualitatively similar distributions of body segment power and contributions to support and forward propulsion during walking and running, despite some differences in muscle excitation timing (e.g., Fig. 3: GAS and HAM). GAS peak activity occurred earlier in stance during running compared to walking, although GAS functioned similarly to deliver power to the leg and, to a lesser degree, to the trunk in both tasks during its peak power output (Fig. 4: GAS). The primary function of HAM was also consistent in both tasks, which acted to deliver power to the leg in early stance and absorb power from the leg in late swing (Fig. 4: HAM). VAS, GMAX and BFsh maintained similar power distributions and contributions to support and forward propulsion in walking and running, although the contributions were generally greater in magnitude and duration in running (Figs. 4 and 5: VAS, GMAX and BFsh). TA, RF, IL and GMED also maintained consistent power distributions (Fig. 4: TA, RF, IL and GMED), although their contributions to support and forward propulsion were minimal in both walking and running. These similarities of the muscle function were consistent with previous EMG studies showing that the hip flexors (IL) and hip and knee extensors (GMAX and VAS) have similar activity patterns during walking and running at the same speeds (Andersson et al., 1997; Nilsson et al., 1985). The limited contribution to body support by GMED is most likely related to the musculoskeletal model being limited to the sagittal plane and not allowing hip ad/abduction. A 3D model has shown GMED to be an important contributor to support (Anderson and Pandy, 2003), although no study has assessed its contribution to body propulsion. This remains an area for future work.

In summary, our simulation analyses of walking and running at the preferred transition speed revealed that muscles contribute to the mechanical energetics of the body, and functional tasks of support and forward propulsion in a similar manner between the two tasks. The primary exception was the decreased contribution of SOL to forward propulsion in running and its increased contribution to support. In addition, the biomechanical mechanism (i.e., mechanical power distribution) used by SOL to provide support and forward propulsion in running was also different from that in walking. All other muscles showed qualitatively similar functional roles to distribute mechanical power among the body segments and provide support and forward propulsion in walking and running.

Acknowledgements

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