# Muscle mechanical work and elastic energy utilization during walking and running near the preferred gait transition speed

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## Abstract

Mechanical and metabolic energy conservation is considered to be a defining characteristic in many common motor tasks. During human gait, the storage and return of elastic energy in compliant structures is an important energy saving mechanism that may reduce the necessary muscle fiber work and be an important determinant of the preferred gait mode (i.e., walk or run) at a given speed. In the present study, the mechanical work done by individual muscle fibers and series-elastic elements (SEE) was quantified using a musculoskeletal model and forward dynamical simulations that emulated a group of young healthy adults walking and running above and below the preferred walk-run transition speed (PTS), and potential advantages associated with the muscle fiber-SEE interactions during these gait modes at each speed were assessed. The simulations revealed that: (1) running below the PTS required more muscle fiber work than walking, and inversely, walking above the PTS required more muscle fiber work than running, and (2) SEE utilization in running was greater above than below the PTS. These results support previous suggestions that muscle mechanical energy expenditure is an important determinant for the preferred gait mode at a given speed.

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*Keywords:* Muscle work; Musculoskeletal model; Forward dynamic simulation; Preferred gait mode

## 1. Introduction

Muscle mechanical energy expenditure is an important quantity to analyze human locomotion since it reflects the neuromotor strategies used by the nervous system and is directly related to the efficiency of the task. Energy conservation is a defining characteristic in many common motor tasks and generally leads to a preferred mode in performing a given locomotor task [1]. Previous studies have suggested that the two primary energy saving mechanisms in walking are the passive exchange of potential and kinetic energy (e.g. [2]) and elastic energy utilization (e.g. [3]). Assuming that walking can be modeled as an inverted-pendulum, the maximum theoretical efficiency of the energetic exchange between kinetic and potential energy (i.e., energy recovery) is only as high as 65% and varies depending on walking speed [4] and stride frequency [5]. In addition, recent simulation analyses using a multi-segmental musculoskeletal model found that considerable muscle work is needed to produce the inverted pendulum-like motion [6]. Thus, the passive energy exchange mechanism in normal walking may not be as significant as that observed in simple inverted-pendulum models.

Elastic energy utilization that stores and returns mechanical energy is considered to be an important metabolic energy saving mechanism, especially in running (e.g. [3,7]). Gravitational potential and kinetic energy have the potential to be stored as elastic energy in compliant connective tissue and tendinous structures, and subsequently released to do positive work at a later point in the gait cycle. The Achilles tendon is one of the most widely studied structures, and previous studies have estimated that nearly 50% of the total mechanical energy of the body is stored in the tendon and arch of the foot during the stance phase in running [8,9]. Other tendons that are rapidly stretched during the loading response (e.g., knee extensor tendons) are also assumed to play an important role [10].

Tendons not only store and return elastic energy, but also act to reduce the corresponding muscle's fiber shortening

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velocity to allow the fibers to operate at a more favorable contractile state. The reduction in fiber velocity increases the contraction efficiency and reduces the corresponding metabolic cost [10]. Such reductions in fiber velocities have been observed in the distal extensor muscles in vivo in hopping and running animals [11,12] and humans during walking [13]. With the reduction of metabolic cost, elastic energy storage and return has been suggested as an important determinant for the preferred gait mode (i.e., walking or running) at a given speed [14,15]. Indeed, the metabolic cost of running is lower than walking at speeds above the preferred walk-run transition speed (PTS), and inversely, running becomes more costly than walking at speeds below the PTS (e.g. [16,17]). However, no study has quantified the relative fiber to tendon work ratios in walking and running and whether the increase in metabolic cost is the result of increased muscle fiber work.

Previous studies have measured muscle force and length in vivo in animals [11,12] and humans (e.g. [18,19]). Methodologically, force and length measurement in vivo is extremely difficult and limited to a few local muscles, either by surgically implanting force and length sensors into muscles [11,12] or using complex imaging techniques to obtain fiber lengths and estimating the corresponding musculotendon forces (e.g. [20–22]). Earlier studies have used traditional gait analysis techniques to compute changes in segmental mechanical energy (e.g. [23–25]) as an indirect approach for estimating fiber and tendon work. However, these methods cannot account for co-contractions of antagonistic muscle groups and separate individual muscle fiber and tendon contributions to mechanical energy of the system [26].

In contrast, a detailed musculoskeletal model with individual musculotendon actuators including contractile (CE) and series elastic (SEE) elements and forward dynamical simulations can be used to estimate the contributions of muscle fibers and elastic structures to the mechanical energetics of a given motor task [6,27]. The overall goal of this study was to use simulations of walking and running at speeds above and below the PTS to examine muscle fiber mechanical work and SEE utilization. Our specific objectives were to assess the hypotheses that: (1) total muscle fiber work is higher in walking than running above the PTS, and inversely, fiber work is higher in running than walking below the PTS, and (2) SEE utilization during stance is greater in running above than below the PTS. These results will provide insight into the role muscle mechanical energy expenditure plays in determining the preferred gait mode at a given speed.

## 2. Methods

### 2.1. Musculoskeletal model

A sagittal-plane musculoskeletal model with nine degrees of freedom (e.g. [28]) was used to generate forward

dynamical simulations emulating young healthy adults walking and running above and below the PTS. The musculoskeletal model was developed using SIMM (MusculoGraphics Inc., Evanston, IL) and a forward dynamical simulation was generated using Dynamics Pipeline (MusculoGraphics Inc., Evanston, IL). The model consisted of a trunk (head, arms, torso and pelvis), both legs (femur, tibia, patella and foot per leg) and fifteen Hill-type musculotendon actuators per leg representing the major lower-extremity muscle groups. Each actuator consisted of a contractile element (CE) that represents the active force generating properties of the muscle fibers governed by force-activation-length-velocity relationships, a non-linear elastic element parallel to the CE representing the passive properties of the muscle fibers (PEE), and a non-linear elastic element in series with the PEE and CE that represents the passive properties of the tendon and aponeurosis (SEE) [29]. The SEE force-length relationship was scaled by CE maximum isometric force and SEE slack length [29]. These muscles were combined into nine functional groups based on anatomical classification, with muscles within each group receiving the same excitation signal. The groups were defined as: GMAX (gluteus maximus, adductor magnus), IL (iliacus, psoas), HAM (biceps femoris long head, medial hamstrings), VAS (three vasti muscles), RF (rectus femoris), BFsh (biceps femoris short head), TA (tibialis anterior), GAS (medial and lateral gastrocnemius) and SOL (soleus). Each muscle's excitation was defined using surface EMG-based patterns (see *Data acquisition and processing* below). Since no surface EMG data were available for IL and BFsh, block excitation patterns were used. The muscle excitation-activation dynamics was described using a first-order differential equation [30] with activation and deactivation time constants of 5 and 10 ms, respectively. These relatively short time constants were chosen because the EMG-based patterns were already heavily low-pass filtered. Passive torques representing the ligaments and other connective tissues were applied to each joint [31]. The contact between the foot and ground was modeled using thirty visco-elastic elements attached to each foot [32].

### 2.2. Dynamic optimization

Well-coordinated walking and running simulations over the gait cycle (i.e., from right foot-strike to right foot-strike) were generated using dynamic optimization to fine-tune the onset, duration and magnitude of the muscle excitation patterns. A simulated annealing algorithm [33] was used to minimize the difference between the simulation and experimentally measured group-averaged kinematics and ground reaction forces (GRFs) (e.g. [34]; see *Data acquisition and processing* below).

### 2.3. Muscle fiber and SEE mechanical work

Muscle fiber (CE) and SEE power were computed independently as the product of the corresponding force and

velocity at each instant in time over the gait cycle. Subsequently, positive (concentric), negative (eccentric) and total mechanical work done by the individual muscle fibers and SEEs during the stance and swing phases were obtained by time-integration of the corresponding power during each phase of the gait cycle as

$$\text{Mechanical work} = \int_{t_1}^{t_2} P \, dt \qquad (1)$$

where $P$ is the positive or negative power in the fiber and SEE and $t_1$ and $t_2$ define the duration of positive or negative power within the stance and swing phases. The total fiber work was obtained by summing the positive and absolute value of the negative fiber work over the gait cycle across all muscles. The net fiber work was computed by summing the positive and negative fiber work across all muscles. Since the SEEs are perfectly elastic, the negative SEE work (energy stored) equals the positive SEE work (energy released). Therefore, only the positive SEE work is presented.

SEE utilization was defined as the ratio of the positive SEE to positive fiber work during each muscle's active region during the stance phase (i.e., when the muscle's active state exceeded 3% of its maximum activation) as

$$\text{SEE utilization} = 100 \times \left( \frac{\text{positive SEE work}}{\text{positive fiber work}} \right) \qquad (2)$$

To assess the total elasticity utilization of all muscles, the same ratio was computed for the total positive SEE and total positive fiber work for all muscles during the stance phase.

## 2.4. Experimental data collection

Body segment kinematic, GRF and EMG data during walking and running above and below the PTS were collected from 10 healthy subjects (5 males and 5 females: age $29.6 \pm 6.1$ years old, height $169.7 \pm 10.9$ cm, body mass $65.6 \pm 10.7$ kg). The two speeds examined were 80% and 120% of the subject's PTS, which correspond to speeds where the difference in metabolic cost between walking and running is clearly observed (e.g. [17]). The PTS was determined using a step protocol [35]. 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.

## 2.5. Data acquisition and processing

The kinematic, GRF and EMG data used in the dynamic optimization were sampled at 120, 480 and 1200 Hz, respectively, for 15 s near the end of a randomly assigned one-minute trial of walking or running on a split-belt treadmill with embedded force plates (Tecmachine,

Andrézieux-Bouthéon, France). The kinematic data were captured using a motion capture system (Motion Analysis Corp, Santa Rosa, CA) with a modified Helen Hayes marker set (one-inch diameter reflective markers). The EMG data were collected using the guidelines provided by Perotto [36] from the gluteus maximus, rectus femoris, vastus medialis, biceps femoris long head, medial gastrocnemius, soleus and tibialis anterior of the right leg. Disposable surface bi-polar EMG electrodes were used (Noraxon, Scottsdale, AZ; 1 cm diameter, 2 cm inter-electrode distance). All data were digitally filtered using fourth-order zero-lag Butterworth filters. The cut-off frequencies for the kinematic and GRF data were 6 and 20 Hz, respectively (e.g. [37,38]). EMG data were processed using a band-pass filter (20–400 Hz), full rectification and low-pass filter (10 Hz) (e.g. [39]). The resultant EMG linear envelopes were then normalized to each muscle's maximum value during the gait cycle. All data were time-normalized to a full gait cycle, and were averaged within each subject and then across subjects to obtain a group average.

## 3. Results

The group-average PTS was $1.96 \pm 0.17$ m/s, yielding simulations of walking and running at 1.6 and 2.4 m/s that corresponded to speeds of 80% and 120% of the PTS, respectively. Hereinafter, walking and running at the slow and fast speeds will be labeled as W80, R80, W120 and R120, respectively. The corresponding walking and running simulations emulated the experimental data almost always within $\pm 2$ S.D. of the group-average (Fig. 1) using the optimized EMG-based muscle excitation patterns.

### 3.1. Comparison between W80 and R80

The total fiber work done by the muscles in running at the slow speed was 25 J greater than in walking (Table 1: Fiber Total, W80 < R80). The difference was primarily due to an increase in VAS negative work in stance during running (~22 J) (Fig. 2: VAS, Fiber-Negative, W80 < R80). The total positive work done by all SEEs was higher in running than in walking (Table 1: Positive SEE Work Total), with the difference due primarily to the ankle plantar flexors (SOL, GAS) and VAS (Fig. 2: SOL, GAS, VAS - SEE-Positive). Overall, the SEE utilization was greater in running than in walking due primarily to the greater SEE work in R80 (Table 1: SEE Utilization, W80 < R80).

### 3.2. Comparison between W120 and R120

The total muscle fiber work was slightly lower in running compared to walking (4 J, Table 1: Fiber Total, W120 > R120). In running, GAS positive work (~3 J) and VAS positive and negative work (~10 and 14 J,
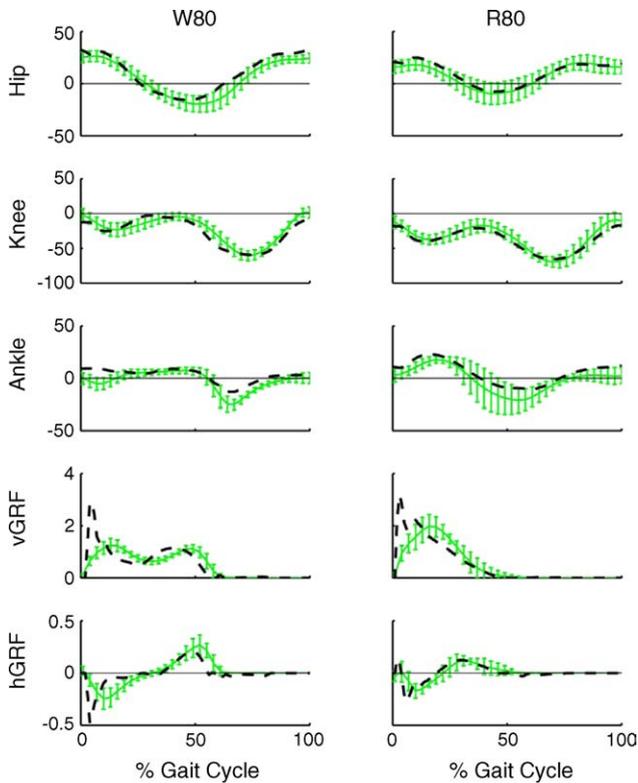
Fig. 1. Hip, knee and ankle joint angles (units: °) and vertical (vGRF) and horizontal (hGRF) ground reaction forces (units: normalized to body weight) in walking (W80) and running (R80) simulations (dashed line) and experimental data (solid line, average ± 2 S.D.). Positive angles indicate flexion, extension and dorsiflexion in the hip, knee and ankle joints, respectively. Similar tracking results were obtained for the 120% PTS walking and running conditions.

Table 1
Mechanical work (units: J) done by all muscle fibers and SEEs during stance, swing and over the gait cycle in walking (W) and running (R) at 80% and 120% PTS

|  | W80 | R80 | W120 | R120 |
|---|---|---|---|---|
| Fiber stance |  |  |  |  |
|   Positive | 58 | 65 | 67 | 67 |
|   Negative | 29 | 52 | 34 | 51 |
| Fiber swing |  |  |  |  |
|   Positive | 28 | 22 | 44 | 27 |
|   Negative | 13 | 14 | 30 | 26 |
| Fiber total | 128 | 153 | 175 | 171 |
| Fiber net | 44 | 21 | 47 | 17 |
| SEE stance |  |  |  |  |
|   Positive | 23 | 34 | 31 | 48 |
| SEE swing |  |  |  |  |
|   Positive | 2 | 2 | 7 | 6 |
| Positive SEE work total | 25 | 36 | 38 | 54 |
| SEE utilization (%) | 40 | 52 | 46 | 72 |

SEE Utilization is the percent ratio of positive SEE work to positive fiber work during stance.

respectively) (Fig. 2: SOL, HAM – Fiber-Positive, W120 > R120). Consequently, fiber negative work increased while overall positive work remained unchanged during stance (Table 1: Fiber Stance – Negative and Positive, compare W120 and R120). In swing, marked decreases in IL (∼15 J), and to a lesser degree in GMAX and HAM, positive work was observed in running (Fig. 3: IL, GMAX, HAM – Fiber-Positive, W120 > R120). Positive SEE work during stance increased 17 J in running (Table 1: SEE Stance), primarily due to increased plantar flexor SEE work (Fig. 2: SOL, GAS – SEE-Positive, W120 < R120). Overall, the SEE utilization was greater in running than in walking due to the increased positive SEE work (Table 1: SEE Utilization, W120 < R120).

respectively) increased during stance (Fig. 2: GAS, VAS – Fiber-Positive, Fiber-Negative, W120 < R120), while SOL and HAM positive work output decreased (∼5 and 8 J,
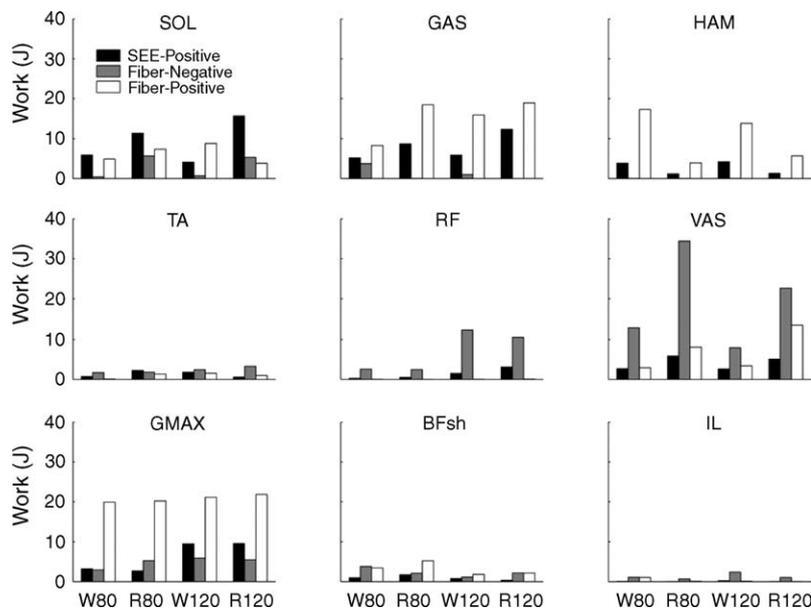


Fig. 2. Mechanical work done by individual muscle fibers and SEEs during stance in walking (W) and running (R) at 80% and 120% PTS.
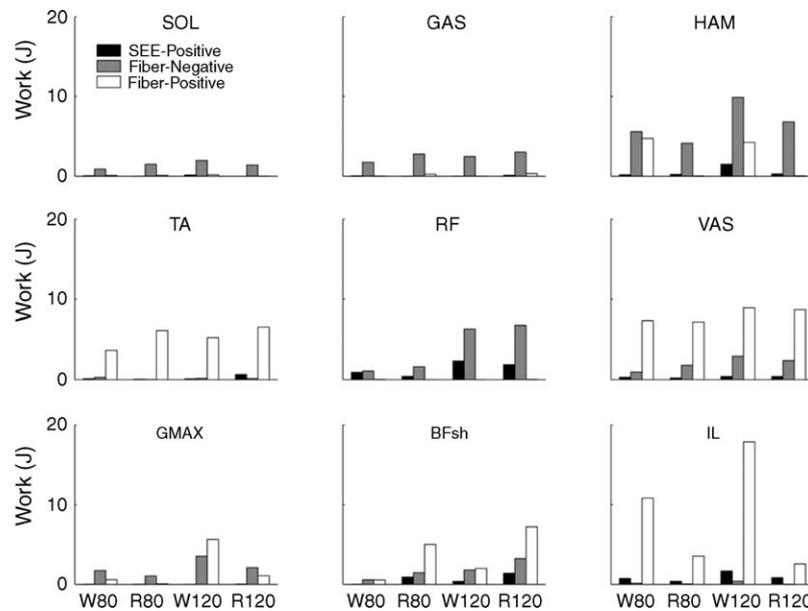
Fig. 3. Mechanical work done by individual muscle fibers and SEEs during swing in walking (W) and running (R) at 80% and 120% PTS.

## 4. Discussion

The overall goal of this study was to use forward dynamical simulations to test the hypotheses that: (1) muscle fiber mechanical work is greater in running than walking below the PTS, and inversely, fiber work is greater in walking than running above the PTS, and (2) SEE utilization is greater in running above than below the PTS.

The simulation results supported these hypotheses. The total fiber work over the gait cycle in running below the PTS was ~20% greater than in walking at the same speed, with the increase due primarily to an increase in fiber work during the stance phase (Table 1: Fiber Total, W80 < R80). In contrast, walking above the PTS showed slightly higher fiber work than in running (Table 1: Fiber Total, W120 > R120). Thus, walking required less fiber work than running below the PTS and more fiber work above the PTS. Although we did not differentiate the relative cost difference between concentric and eccentric work (i.e. eccentric contractions consuming less metabolic energy than concentric contractions, e.g. [40]), the trend of total fiber mechanical work should follow the metabolic cost (e.g. [16,17]) since the negative (eccentric) fiber work was greater in R80 compared to W80, while the positive (concentric) work remained unchanged. Similarly, the difference in total positive work between W120 and R120 (17 J, W120 > R120) was larger than the difference in the total negative work (13 J, W120 < R120).

The increase in fiber work during running compared to walking below the PTS (25 J, Table 1: Fiber Total, W80 < R80) was due primarily to an increase in VAS eccentric work during stance (~22 J, Fig. 2: VAS Fiber-Negative, W80 < R80). The negative work increase in VAS was due to nearly 20° greater knee flexion (Fig. 1: Knee,

W80 < R80, 0–25% gait cycle) and the greater force requirements in running (e.g., the peak VAS muscle force in walking and running was ~2000 and ~3300 N, respectively). In contrast, the slightly higher fiber work in walking compared to running above the PTS (4 J, Table 1: Fiber Total) largely resulted from the greater work by GMAX, HAM and especially IL during the swing phase (Fig. 3: GMAX, HAM, IL Fiber-Negative, Fiber-Positive, W120 > R120). The increased work in IL during swing in walking may be related to the increased demand on the hip flexors to overcome the larger moment of inertia of the extended leg during swing [41]. The IL concentric action to accelerate the hip into flexion in early swing [28] appears to be much more pronounced when walking at higher speeds, which is consistent with measurements of IL EMG activity using fine wire-electrodes [42].

Running has been historically considered a "bouncing" gait that utilizes elastic energy stored and returned in tendinous and other elastic structures primarily during the stance phase (e.g. [7,9]). Effective utilization of this elastic energy has been suggested as an important determinant of a preferred gait mode at a given speed (e.g. [14,15]). In the present study, SEE utilization was quantified as the ratio of SEE to fiber positive work performed during the stance phase, which was shown to be higher in running above the PTS than below the PTS (72% versus 52%, Table 1: SEE Utilization). This relative decrease in SEE work during running below the PTS appears related to the lower force demands during slow running, which is not high enough to stretch the SEEs. Our simulation results showed that the peak muscle forces in SOL and GAS (i.e., those muscles that exhibited the greatest SEE work in running, Fig. 2) were both nearly 20% lower in R80 compared to R120, which resulted in similar decreases in the corresponding SEE excursions.

SEE utilization was greatest in SOL during all conditions, which was substantially higher in R120 than W120 (Fig. 4: SOL, W120 < R120). Although the fiber kinematics were not presented, the high SEE utilization decreased the SOL fiber shortening velocity, which allows SOL to operate at a more efficient contractile state during running above the PTS. Previous studies have shown in animal models during running that the distal muscles with longer tendons contract mostly in an isometric fashion in stance (e.g. [11,12]), which is metabolically more efficient (e.g. [40]). Since the plantar flexor concentric contraction in late stance provides critical support and forward progression in walking [34], the decreased SEE utilization and corresponding increased fiber shortening in SOL and GAS when walking above the PTS is detrimental to their force production. This was illustrated in a recent simulation study showing that plantar flexor force production is greatly impaired at higher walking speeds due to adverse fiber contractile conditions (i.e., fiber length and velocity) [35]. Thus, impaired plantar flexor force production due to poor contractile conditions associated with decreased SEE utilization appears to be an additional disadvantage of walking above the PTS.

The relative decrease in SEE work during slow running may also indicate the need for more precise neuromotor control that is not required during faster running above the PTS, which utilizes more SEE elastic energy. Seyfarth et al. [43] used a spring-mass running model to analyze how leg adjustments in response to altered leg stiffness and angle of attack influences stability in running. Their data showed that as running speed decreases, the leg adjustment becomes more critical for stability, and that the spring-mass system needed to be operated above a certain speed to maintain a stable gait. These results suggest that running below the PTS may not be a stable bouncing gait, and therefore, requires more control from muscle fibers. Biewener and Roberts [44] suggested that muscles with a longer tendon and shorter fibers could save metabolic energy at the expense of accurate control of musculotendon length, and inversely, reducing energy expenditure may be compromised by precise length control in a muscle with longer fibers and a shorter tendon. Such trade-offs between control and efficiency in muscles may also influence the preferred gait mode at a given speed.
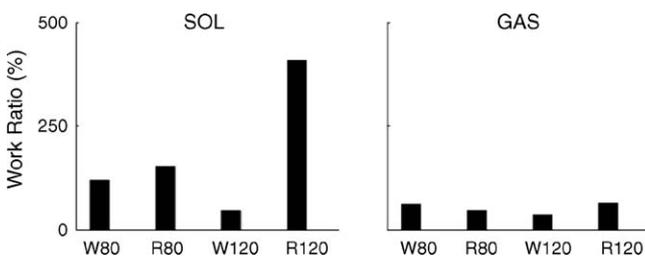


Fig. 4. The SEE utilization in SOL and GAS during each muscle's active region in the stance phase (i.e., when the muscle's active state exceeded 3% of its maximum activation) in walking (W) and running (R) at 80% and 120% PTS.

Due to the limited number of experimental studies on fiber and tendon work, the comparison between experimentally measured tendon work and the present study is only possible in the Achilles tendon. Alexander and Bennet-Clark [8] and Ker et al. [9] estimated the elastic energy storage in the Achilles tendon during running. Ker et al. [9] showed that the tendon stores approximately 35 J during stance when running at 4.5 m/s. Force-length data measured in vivo by Kyrolainen et al. [19] showed that approximately 17 J was stored in the tendon during running at 3 m/s (using linear extrapolation in their force-length curve). Hof et al. [45] indirectly estimated the musculotendon work using an inverse dynamics approach and showed that during slow running (between 2.68 and 3.93 m/s), tendon work varied from ∼10 to 39 J. These results are comparable with our simulation data showing that during running at 2.4 m/s (i.e., R120), the SEE of the plantar flexors returned 28 J during stance (Fig. 2: SOL, GAS, SEE-Positive, R120).

The limitations of the musculoskeletal model used in the present study to interpret muscle function have been previously discussed in detail [6,27,28,34]. One noticeable difference between the simulation and experimental data are the higher GRF impact peaks in the simulation (Fig. 1: vGRF and hGRF). However, these peaks have little influence on the results since they are the result of primarily nonmuscular components (e.g., centripetal and Coriolis effects) [28,46]. An additional potential limitation relevant to the present study is that the non-linear SEE force-length relationship used in the model may influence the amount of fiber work and SEE utilization. To assess this possibility, we performed sensitivity analyses by changing the SEE stiffness by ±20% for all muscles in the model to examine how it influenced our conclusions. As expected, some magnitudes of fiber and SEE work changed. For example, the combined positive SEE work by SOL and GAS during stance at R120 was nominally 28 J, and decreased to 23 J when the stiffness was increased 20%. However, the relative distribution of fiber work and SEE utilization between the gait modes and speeds remained nearly identical. A second potential limitation is that fiber and SEE work could be affected by the rigid foot model. Ker et al. [9] estimated that approximately 17 J is stored in the arch of the foot during running at 4.5 m/s. Thus, the exclusion of a compliant foot in our model could result in an overestimation of the muscle fiber and SEE work. On the other hand, excluding the metatarso-phalangeal joint in the model could underestimate the work, since this joint appears to dissipate mechanical energy into the shoe and foot structures (∼21 J during running at 4 m/s [47]). The consequence of excluding both structures on the musculotendon work remains an area of future research.

In summary, we found that muscle fiber work was lower in walking than running below the PTS, and inversely, that fiber work was slightly higher in walking than running above the PTS, which was consistent with metabolic cost data of

walking and running near the PTS (e.g. [16,17]). Thus, walking below the PTS is a more suitable gait mode due to the lower fiber work required, while running is a more suitable gait mode above the PTS due to the lower fiber work required and greater SEE utilization. These results support previous suggestions that muscle mechanical energy expenditure is an important determinant for the preferred gait mode at a given speed.

## Acknowledgements

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