

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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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

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