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Muscle mechanical work requirements during normal walking: the energetic cost of raising the body's center-of-mass is significant

R.R. Neptune[a,b,*], F.E. Zajac[b,e,f], S.A. Kautz[b,c,d,g]

[a] *Department of Mechanical Engineering, University of Texas at Austin, Austin, TX 78712, USA*
[b] *Rehabilitation R&D Center, VA Palo Alto Health Care System, 3801 Miranda Avenue, Palo Alto, CA 94304, USA*
[c] *Brain Rehabilitation Research Center, Malcolm Randall VA Medical Center, Gainesville, FL 32608, USA*
[d] *Brooks Center for Rehabilitation Studies, University of Florida, Gainesville, FL, USA*
[e] *Departments of Mechanical Engineering, Stanford University, Stanford, CA 94305, USA*
[f] *Orthopedic Surgery, Stanford University, Stanford, CA 94305, USA*
[g] *Department of Physical Therapy, University of Florida, Gainesville, FL 32608, USA*

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Abstract

Inverted pendulum models of walking predict that little muscle work is required for the exchange of body potential and kinetic energy in single-limb support. External power during walking (product of the measured ground reaction force and body center-of-mass (COM) velocity) is often analyzed to deduce net work output or mechanical energetic cost by muscles. Based on external power analyses and inverted pendulum theory, it has been suggested that a primary mechanical energetic cost may be associated with the mechanical work required to redirect the COM motion at the step-to-step transition. However, these models do not capture the multi-muscle, multi-segmental properties of walking, co-excitation of muscles to coordinate segmental energetic flow, and simultaneous production of positive and negative muscle work. In this study, a muscle-actuated forward dynamic simulation of walking was used to assess whether: (1) potential and kinetic energy of the body are exchanged with little muscle work; (2) external mechanical power can estimate the mechanical energetic cost for muscles; and (3) the net work output and the mechanical energetic cost for muscles occurs mostly in double support. We found that the net work output by muscles cannot be estimated from external power and was the highest when the COM moved upward in early single-limb support even though kinetic and potential energy were exchanged, and muscle mechanical (and most likely metabolic) energetic cost is dominated not only by the need to redirect the COM in double support but also by the need to raise the COM in single support.

Keywords: Human walking; Forward dynamics simulation; Inverted pendulum models; Muscle work

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1. Introduction

The mechanics of human walking is often modeled as an inverted pendulum since it predicts many characteristics of walking such as the arched trajectory of the body's center-of-mass (COM) and the relatively constant state of mechanical energy during single-limb support, which is assumed to reflect a continuous exchange of kinetic and potential energy (e.g., Cavagna et al., 1977; Cavagna and Margaria, 1966). By assuming that the leg can be represented as very stiff and extended during stance, the simple pendular mechanics of these models allows for an exchange between potential and kinetic energy during stance that requires no muscle mechanical work. However, in reality the theoretical efficiency of this energetic exchange (or energy recovery) is only as high as 60% and varies depending on stride length (Minetti et al., 1995) and walking speed (Cavagna et al., 1976). Furthermore, the metabolic cost of normal walking is significant (e.g., Waters and Mulroy, 1999); thus muscle metabolic energy is being expended somewhere in the gait cycle.

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*Corresponding author. Department of Mechanical Engineering, University of Texas at Austin, Austin, TX 78712-1063, USA. Tel.: +1-512-471-0848; fax: +1-512-471-7682.

E-mail address: rneptune@mail.utexas.edu (R.R. Neptune).

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Recent inverted pendulum-based models have suggested that a primary mechanical energetic cost may be predicted by the mechanical work required to redirect the motion of the body COM at the step-to-step transition (Donelan et al., 2002a; Kuo, 2002). The step-to-step transition is essentially defined as a boundary condition between successive stance phases and is associated with the collision of the leg with the ground and the redirection of the COM, which occurs in double support. The mechanical energy loss at impact by the leading leg can theoretically be minimized by the simultaneous production of mechanical work by the contralateral trailing leg muscles, such as the ankle plantar flexors (Kuo, 2002). To test this hypothesis, Donelan et al. (2002a) computed for a variety of step lengths the negative external mechanical work of a step, which arises predominantly by the leading leg in or near double support. Consistent with their model of inverted pendular mechanics for walking (Kuo, 2002), they found the negative external work by the leading leg to rise with step length. Since the measured metabolic energy consumed by their walking subjects mirrored the measured external work, and both agreed with the predicted relationship for both step length and step width, they concluded that the mechanical work associated with the step-to-step transition appears to be a major determinant of the metabolic cost of walking rather than the mechanical work to support the pendular motion itself.

External work measurements are, however, only indirectly related to the mechanical energetic cost of muscles (e.g., Donelan et al., 2002a). First, external power represents the rate of COM mechanical energy but contains no information on the mechanical energy changes of the body segments relative to the COM (e.g., Willems et al., 1995). However, energy flow among the segments relative to the COM is important (e.g., Willems et al., 1995) and depends critically on muscle force production (Neptune et al., 2003; Zajac et al., 2002, 2003). Second, external power is a resultant quantity but muscles may be simultaneously producing both positive and negative muscle work. Indeed, many leg muscles are co-excited in stance, such as the quadriceps, hamstrings, gluteus maximus from impact into early single-limb support, and the unarticular and biarticular plantar flexors and rectus femoris in late single-limb support through toe-off (Perry, 1992; Winter, 1991). During muscle co-excitation, some muscles shorten (concentric activity) and produce positive work while others lengthen (eccentric activity) and produce negative work output (Neptune et al., 2001, 2003; Zajac et al., 2003). Such co-excitation has been shown to be synergistic and critical to achieve the segmental energetic exchanges observed (Neptune et al., 2001, 2003; Zajac et al., 2003). The mechanical energetic cost associated with simultaneous positive and negative muscle work could be high, even if the net muscle work output is minimal, since there is an energetic cost associated with both positive and negative muscle work. Third, elastic energy storage and release by muscles is unaccounted for with external power analyses. Such energy storage may occur during foot impact or even during single support, with subsequent release in single-limb support or late stance. In fact, the ankle plantar flexors have been shown to produce and store much energy in the musculotendon elastic structures in single-limb support for later release in late stance (e.g., Hof, 1998; Hof et al., 1983, 2002; Neptune et al., 2001). Thus, whether a relationship between external work and the mechanical energetic cost of muscles exists remains to be quantified.

The estimation of timing and magnitude of the mechanical work and mechanical energetic cost of individual muscles with a muscle-based multi-segmental model of the body would be useful to test how much mechanical work is performed by muscles to redirect the body COM during double support, and how much is used during single-limb support (e.g., for extending the knee and raising the COM). Muscle mechanical energy expenditure as the COM rises and descends during single-limb support is not predicted by inverted pendulum models without knees (e.g., Donelan et al., 2002a; Saibene and Minetti, 2003), and even in pendular models with knees since the stance knee is assumed to be locked in extension (e.g., Dankowicz et al., 2001; McGeer, 1990; Rostami and Bessonnet, 2001). A muscle-based multi-segmental model with knees would allow one to test whether the body's COM can be raised in single-limb support with little muscle work and energy through an exchange of body potential and kinetic energy.

The goal of the present study was, therefore, to use a multi-linked muscle-actuated forward dynamic simulation of walking to assess whether: (1) potential and kinetic energy of the body are exchanged with little muscle work; (2) external mechanical power can estimate the mechanical energetic cost by muscles; and (3) the net work output and the mechanical energetic cost by muscles occurs mostly in double support, which is the region in the gait cycle where collision of the leg with the ground occurs and the COM is redirected. Specifically, body segment energetics, and work and energetics of individual muscles, were quantified within specific regions defined by the external power curve. We did not focus on the mechanical costs associated with the swing phase because, even though there are costs associated with moving the swing leg and preparing it for the loading response, we have previously shown that the muscular power output during swing is minimal compared to the output during stance (Neptune et al., 2003).

2. Methods

2.1. Musculoskeletal model

A previously described multi-linked muscle-actuated forward dynamic simulation of normal walking was generated. The bipedal sagittal plane musculoskeletal model and optimization framework used to produce the simulation using optimal tracking has been described in detail (Neptune et al., 2001, 2003). Briefly, the musculoskeletal model and forward dynamic simulation were produced using SIMM and Dynamics Pipeline (MusculoGraphics, Inc.) (Delp and Loan, 1995) and consisted of rigid segments representing the trunk and legs. Each leg consisted of a thigh, shank and foot. The trunk segment included the mass and inertial characteristics of the pelvis, torso, head and arms. The musculoskeletal geometry was based on Delp et al. (1990) and the system dynamical equations-of-motion were generated using SD/FAST (Symbolic Dynamics, Inc.). The contact between the foot and the ground was modeled by 30 discrete visco-elastic elements with coulomb friction attached to the bottom of each foot segment (Neptune et al., 2000). Passive torques representing the forces applied by ligaments, passive tissue and joint structures were applied at the hip, knee and ankle joints based on the work of Davy and Audu (1987).

Fifteen individual Hill-type musculotendon actuators for each leg drove the model. Anatomical classification was used to combine the muscles into groups, with muscles within each group receiving the same excitation signal. The nine muscle groups were defined as IL (iliacus, psoas), GMAX (gluteus maximus, adductor magnus), VAS (3-component vastus), HAM (medial hamstrings, biceps femoris long head), SOL (soleus), BFsh (biceps femoris short head), GAS (medial and lateral gastrocnemius), RF (rectus femoris) and TA (tibialis anterior). EMG patterns (see Fig. 2) were used to define the shape of their respective muscle group's excitation burst(s). Block patterns were used for the IL and BFsh bursts because no EMG data were available for those muscles. A first-order differential equation was used to represent the muscle activation dynamics (Raasch et al., 1997) with activation and deactivation time constants of 5 and 10 ms, respectively.

2.2. Dynamic optimization

Dynamic optimization was used to generate a simulation of normal walking at 1.5 m/s by determining the optimal tracking solution using a simulated annealing optimization algorithm (Goffe et al., 1994). The onset, duration and magnitude of each muscle burst and initial joint angular velocities were optimized to minimize the difference between the simulated and experimentally measured walking data from 10 young healthy adults (5 male, 5 female). The objective function in the optimization was formulated to minimize the squared error normalized by the inter-trial variability for each quantity "tracked" (e.g., Neptune and Hull, 1998; Neptune et al., 2001). The specific quantities evaluated in the objective function included the right and left hip, knee and ankle joint angles, horizontal and vertical ground reaction forces, and the two components (x, y) of the trunk translation. From the experimental data, external mechanical power was computed as the dot product of the measured total ground reaction force and the pelvis velocity, which served as an estimate of the body's COM velocity.

2.3. External power and muscle work calculations

The external mechanical power associated with each leg was also computed from the simulation, as the dot product of the external forces acting on the leg (i.e., the measured ground reaction forces) and the velocity of the body's COM determined from the simulated kinematics of the segments. The external power was further decomposed into contributions from individual muscles, gravity and the passive structures in the model. To perform these calculations, the contribution of each of these sources to the ground reaction force was determined (see Neptune et al., 2001 for details). The external power contributions were then analyzed in four specific regions defined by the zero crossings of the external power curve (see Fig. 4): region (1) the step-to-step transition for the leading leg as it absorbs the mechanical energy of impact (approximately the first region of double support); region (2) the raising of the COM in early single-limb support; region (3) the lowering of the COM in late single-limb support; and region (4) the step-to-step transition of the trailing leg as it propels the body (approximately the second region of double support).

In each region, the net mechanical work produced by an individual muscle (i.e., the musculotendon actuator, which includes both muscle and tendon tissue; Zajac, 1989) was computed by integrating the muscle (musculotendon) power. The net mechanical work produced by a muscle in a region was further partitioned into positive and negative work output by integrating all the positive or negative portions of the muscle power trajectory. The muscle work was further decomposed into the contributions from the in-series elasticity of tendon and muscle aponeuroses (TEN), the passive visco-elasticity of the muscle fibers (PEE), and the active contractile process of the muscle fibers (CE) (Zajac, 1989). The mechanical energetic cost of a muscle in a region was computed by summing the positive work output of the CE with the absolute value of the negative CE work output because negative work output by the CE represents mechanical energy dissipated into heat (Hill, 1938). The positive, negative and net mechanical work from the elastic and dissipative elements associated with the passive joint torques and ground contact elements were also determined. Since the right and left leg muscle coordination patterns were symmetrical, the data were analyzed only for the right leg muscles.

3. Results

The simulated kinematics, kinetics and EMG timing of a similar simulation were previously shown to compare well with the group-averaged experimental data (Neptune et al., 2001) (e.g., Fig. 1). Since experimentally measured muscle EMG patterns were used as control inputs into the model, and the muscle excitation timing was moderately constrained in the optimization to match the EMG data (Fig. 2), the timing of muscle force development throughout the gait cycle is consistent with normal human subject activity. Successful tracking of the experimental data assures a near steady-state solution as evident by the symmetrical potential and kinetic energy trajectories of the body's COM (Fig. 3). Energy balances were checked to ensure the net change in mechanical energy over the gait cycle equaled zero (i.e., the summed positive muscle work equaled the amount of energy dissipated by the muscles, passive structures and ground contact elements).

The simulated single-limb external power compared well with the experimental data (Fig. 4; dashed line) and other published data (e.g., Donelan et al., 2002a). The magnitude of the net musculotendon (muscle) work output in the model was highest when the COM moved upward during the beginning of single-limb support (Fig. 5, region 2). Muscles also produced substantial net work output near double support when the leg became the trailing leg (region 4, pre-swing). Net muscle work output was much lower near impact (region 1), and when the COM descends in single-limb support (region 3).

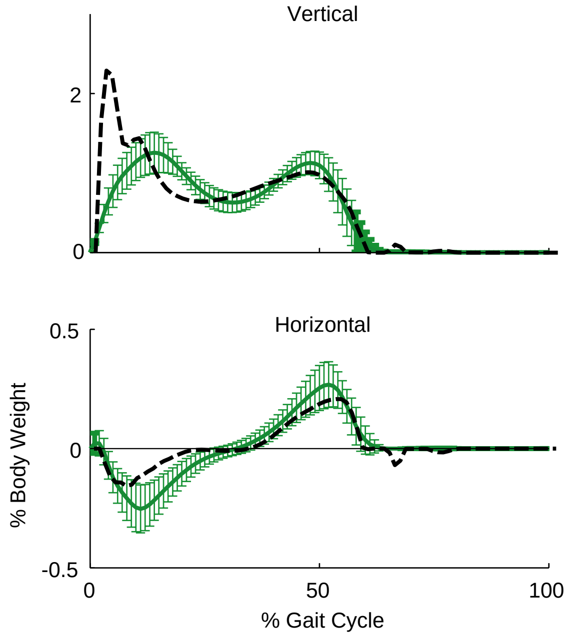

Fig. 1. Comparison of the simulation (dashed line) and group average experimental (solid line, mean ± 1SD) ground reaction forces normalized to body weight over the gait cycle (right heel-strike to right heel-strike). The experimental data are the average of the 10 subjects.

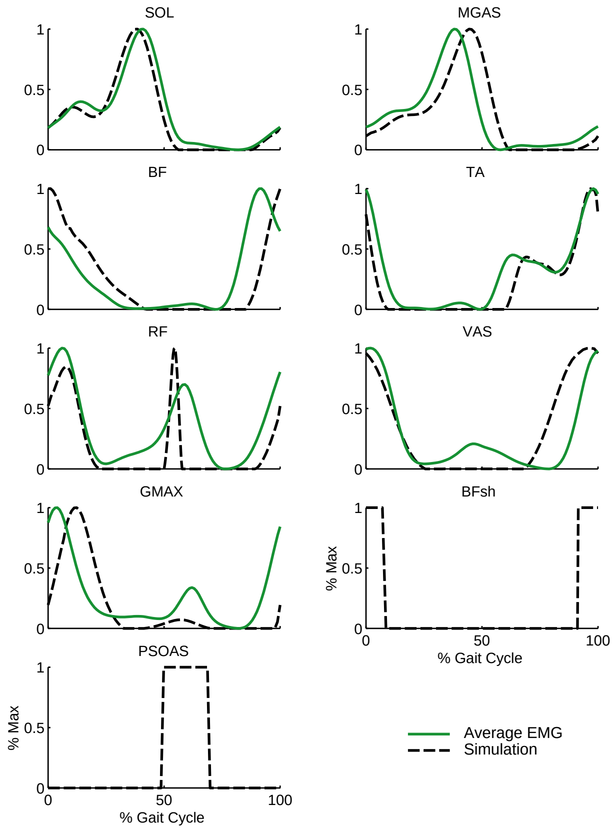

Fig. 2. Comparison of the simulation muscle excitation (dashed line) and group average EMG (solid line) patterns. The EMG data were recorded with surface electrodes at 2000 Hz from 10 young healthy adult subjects (5 male, 5 female) walking at 1.5 m/s on a motorized treadmill from the gluteus maximus (GMAX), vastus medialis (VAS), biceps femoris long head (BFlg), soleus (SOL), medial gastrocnemius (GAS), rectus femoris (RF) and tibialis anterior (TA). The data were rectified and low-pass filtered with a cut-off frequency of 10 Hz. To provide an equivalent base of reference, the simulation excitation and EMG patterns were normalized to the maximum value observed.

Co-excitation of muscles (Fig. 2) produced substantial positive and negative work in every region in stance (Fig. 5). The largest amount of negative (eccentric) work occurred near impact (region 1), primarily by the uniarticular knee extensors, which was largely offset by the positive (concentric) work by HAM and BFsh. The positive work by HAM, VAS, and GMAX when the COM moved upward (region 2) was greater than the net muscle work output because other active and passive

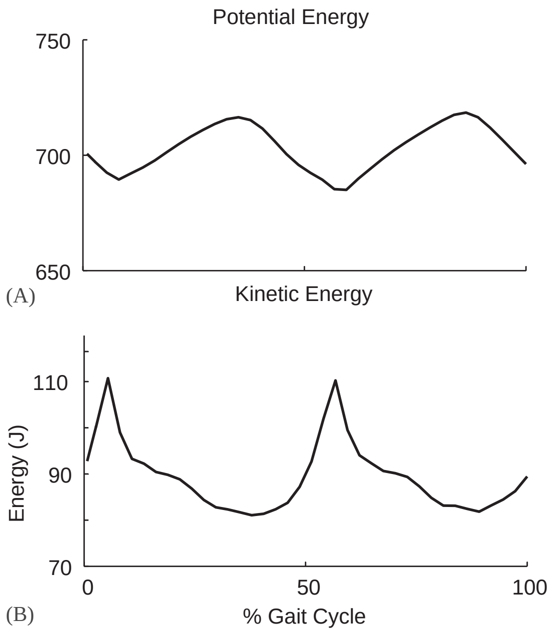

Fig. 3. Mechanical energy of the body during the gait cycle: (A) system potential energy and (B) system kinetic energy.

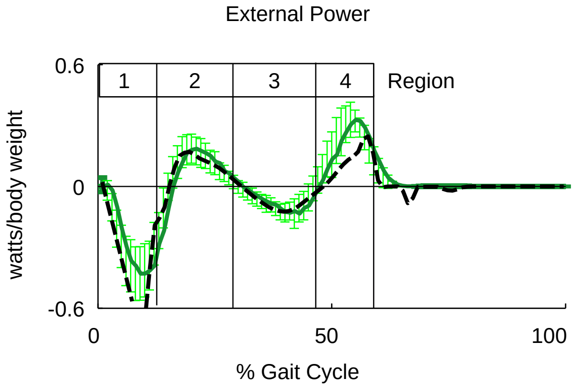

Fig. 4. Comparison of the simulated (dashed line) and experimental external power (solid line, mean ± 1SD). The regions are defined by the zero crossing of the external power curve, which corresponds approximately to double support in regions 1 and 4, and the rise and fall of the COM in regions 2 and 3, respectively.

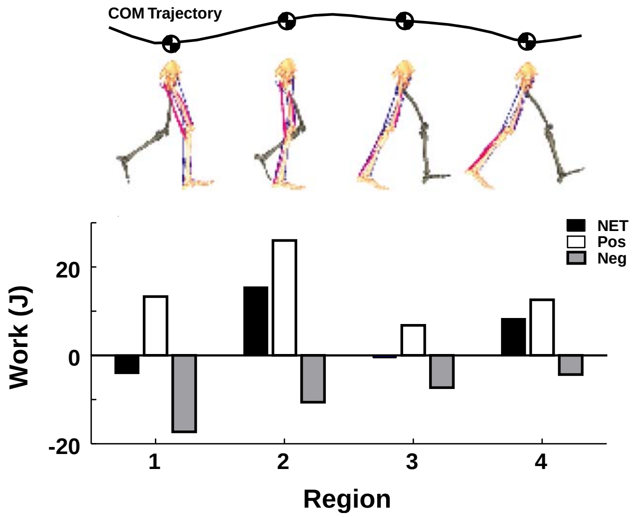

Fig. 5. Positive (*Pos*), negative (*Neg*) and net (*Net*) musculotendon (muscle) work produced in each of the four regions defined by the external power curve (see Fig. 4). Also shown are the COM trajectory of the simulation (not drawn to scale with the model figure to improve resolution) and the corresponding model configuration in each region.

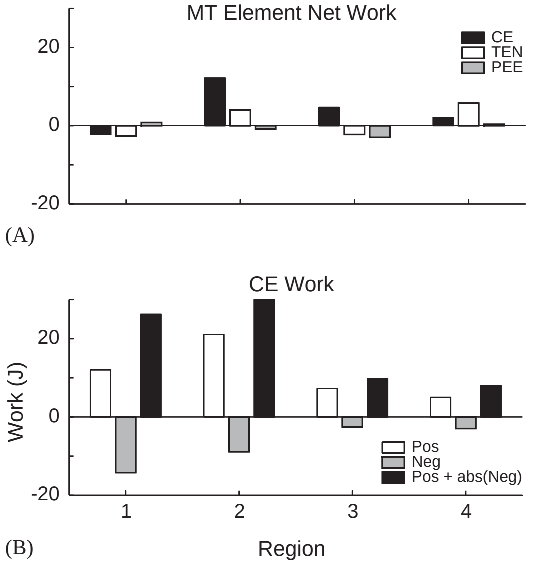

Fig. 6. Muscle mechanical work output and mechanical energetic cost in each of the four regions defined by the external power curve. Each quantity shown is the sum from all the muscles. (A) Work output from the active contractile process of the muscle fibers (*CE*), the in-series musculotendon elasticity (*TEN*) and the passive elasticity of the muscle fibers (*PEE*). (B) Active contractile work (CE in (A)) partitioned into positive (*Pos*) and negative (*Neg*) work. The muscle mechanical energetic cost is given by the sum of the positive and absolute value of the negative work (*Pos + abs (Neg)*).

muscles were simultaneously producing negative work. Similarly, the positive work by the plantar flexors (SOL, GAS) in pre-swing (region 4) was greater than the net muscle work because they were offset primarily by the negative work of RF.

Positive and negative muscle contractile (CE) work mirrored to a large extent the work output from the musculotendon actuators (Fig. 6B compared with Fig. 5). Again, the most positive CE work occurred in region 2 when the COM moved upward and the system potential energy increased (Fig. 3A). The summed mechanical energetic cost associated with the positive and negative CE work was, however, about equal between regions 1 and 2, while a lower cost occurred in region 3 as the COM moved downward and in region 4 where much of the MT work was due to the recovery of elastic energy (Fig. 6A). Some of the elastic energy was stored in the excited, lengthening ankle plantar flexors (Neptune et al., 2001) as the COM descended (Fig. 6A, region 3: TEN < 0). This stored energy was recovered in region 4 (Fig. 6A, region 4: TEN > 0) to augment the net output of the contracting plantar flexors (Fig. 6A, region 4: CE > 0).

4. Discussion

The net work output and the summed mechanical energy developed by individual muscles, computed from a muscle-driven forward dynamic simulation of walking, were used to compare muscle work cost during double support, which is where both collision of the leg with the ground occurs and the COM is redirected, with the cost to maintain the pendulum-like motion of the body COM. Kuo (2002) and Donelan et al. (2002a) hypothesized that much of the net muscle work output for the stance phase can be predicted by the requirements of the step-to-step transition, defined as the boundary condition between single-limb support phases. After testing their hypothesis over a range of step lengths, they concluded that "mechanical work for step-to-step transitions, rather than pendular motion itself, appears to be a major determinant of the metabolic cost of walking" (Donelan et al., 2002a). Though Donelan et al. (2002a) do not explicitly limit the step-to-step transition to double support, we separated muscle work developed in double support from single support in order to estimate the relative cost to redirect the motion of the COM (in double support) and the relative cost of pendular motion (in single support).

We found that the magnitude of the net work output by muscles was the highest when the body COM moves upward at the beginning of single-limb support, rather than in the two regions of double-limb support. In addition, the mechanical energetic cost by muscles was also relatively high in the beginning of single-limb support when the COM rises, and about equal to the cost in each of the two regions of double support (regions 1 and 4). Thus, we conclude that significant muscle work and energy is required to maintain the pendulum-like motion of the body COM since we hypothesize that muscle actions during single-limb support are more directly related to pendular motion than to the collision event (Donelan et al., 2002a) of the step-to-step transition.

The caveats and limitations of the simulation have been thoroughly discussed before in our other studies of walking (Neptune et al., 2001, 2003; Zajac et al., 2003). Nevertheless, recognizing that our results depend on the specific parameters used to generate the simulation, we performed sensitivity analyses and found the basic mechanics and conclusions identified in the present study to be unaltered. For example, elastic energy storage in single-limb support (region 3) and energy release in late single-limb support into pre-swing were found to be insensitive to parameter variations and consistent with other studies of human locomotion (e.g., Alexander, 1991; Hof et al., 1983).

Net muscle work output during region 2, which begins at the onset of knee extension, was the highest of any region as the muscles acted to extend the knee and raise the COM (region 2). The knee flexion angle during the simulation tracked well the experimental data and reached a maximum knee flexion angle of 30° in region 2 (see Fig. 7). Both VAS and GMAX shortened and delivered power to accelerate the knee into extension (Neptune et al., 2003) and the trunk upward (Fig. 3A: potential energy is increasing). But they also redistributed additional segmental power to the trunk by continuing to decelerate the leg (Neptune et al., 2003), which acted to decrease the kinetic energy of the system (Fig. 3B: kinetic energy is decreasing). However, the redistribution of energy by VAS and GMAX from the leg to the trunk required synergistic positive work output from HAM to accelerate the leg and deliver power to it. This concentric action by VAS, GMAX and HAM coincided with an increase in the external power, which was positive (Fig. 4, region 2: external power > 0), and their summed net work output in region 2 represented nearly 80% of the net musculotendon work produced over the entire gait cycle. Thus, our analysis suggests that a major determinant of the net muscle work output required for walking is raising the COM of the body, which is consistent with others' suggestions that a major determinant of the metabolic cost of walking is raising the COM (e.g., Duff-Raffaele et al., 1996; Saunders et al., 1953).

By its very nature, an inverted pendulum model without a knee joint, or a very stiff knee that requires little muscle activity, cannot predict the high net muscle work output we calculated as necessary to raise the COM during single-limb support. Instead, inverted pendulum models hypothesize that the rise of the COM can be represented predominantly by an exchange of body kinetic energy into potential energy

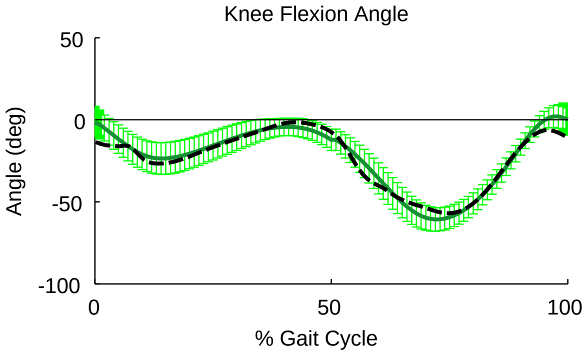

Fig. 7. Comparison of the simulated (dashed line) and experimental (solid line, mean ± 1SD) knee flexion angle over the gait cycle. A maximum knee flexion angle of 30° occurs near 15% of the gait cycle in region 2.

(e.g., Cavagna et al., 1977; Cavagna and Margaria, 1966). However, our simulation results using a more realistic multi-linked anthropometric musculoskeletal model suggest that significant muscle work is needed to raise the COM by extending the knee and hip and increasing the body's potential energy. Without muscle force by VAS, GMAX and HAM, the knee and hip would continue to flex and ultimately collapse. Muscles have also been found to decelerate the COM in the horizontal direction in region 2 (Neptune et al., 2003), a region where the body's kinetic energy is dominated by the horizontal kinetic energy (e.g., Winter, 1990). Thus, muscles directly contribute to both the decrease in kinetic energy and increase in potential energy rather than the passive energetic exchanges that occur in a true inverted pendulum.

The positive external work of region 2 could potentially be due to muscle contractile work, release of stored elastic energy and contralateral swing leg motion. Inverted pendulum models are insufficient to determine the relative contributions from these possible sources (Donelan et al., 2002a). We did observe in region 2 some recovery of elastic energy previously stored in region 1 (Fig. 6A: region 1, $TEN<0$ and region 2, $TEN>0$). However, the majority of the negative muscle work in region 1 (Fig. 5) was not stored as elastic energy in the model's muscles, ground contact elements, or passive structures, but instead, was dissipated into heat (Fig. 6B, region 1: negative CE work ~ -14J; Fig. 6A, region 1: sum of TEN and PEE ~ -2J). In addition, we do not believe that motion of the swing leg during nominal speed walking contributes substantially to external power, since muscular power output by the swing leg is small (Neptune et al., 2003) and velocity-dependent forces contribute little to the ground reaction forces (Anderson and Pandy, 2003). Thus, we believe positive muscle contractile work by the stance leg (Fig. 6A) to be the major determinant of the positive external power in region 2, rather than swing leg motion or the release of elastic energy.

The positive muscle work by the trailing leg in double support (region 4), which was developed by the ankle plantar flexors (SOL and GAS) and accounts for the positive external power (Fig. 4), is consistent with the suggestion of others that muscle work is critically needed then to redirect the COM (Donelan et al., 2002a, 2002b). Indeed, this muscle work has been shown to provide support and forward progression of the body, functions akin to redirecting the COM (Neptune et al., 2001, 2003). Much of this muscle work in region 4 was found in our model to arise from the release of elastic energy stored in the plantar flexors in region 3, which is an efficient mechanism in walking and consistent with other studies (Hof et al., 1983, 2002; Hof, 1998; Neptune et al., 2001). Previous studies have suggested that the positive work generated in region 4 by the contralateral trailing leg is used to offset the negative muscle work by the leading leg in double support (region 1) (Donelan et al., 2002a; Kuo, 2002). We also found this mechanism to exist (Fig. 5). However, we also found much of the negative work was offset by the simultaneous positive muscle work by the same leading leg. VAS was found to dissipate energy in region 1 (Fig. 6B, region 1: negative CE $\sim$ 14J), while simultaneously HAM and GMAX produced offsetting positive ipsilateral contractile work (Fig. 6B, region 1: positive CE $\sim$ 12J). Similarly, in region 4 SOL and GAS provided positive work to offset the synergistic eccentric activity by the ipsilateral RF, which acted to redistribute energy from the leg to the trunk to accelerate it forward (Neptune et al., 2003). Positive muscle work in region 4 is also important for other functions including accelerating the leg into swing (e.g., Neptune et al., 2001) and assuring appropriate limb kinematics during the subsequent swing phase (Piazza and Delp, 1996).

Muscle-based simulations of walking can be analyzed to suggest how active force generation by individual muscles (through the induced forces and accelerations) contribute to external power, coordinate the exchanges of segmental energy, facilitate the storage of elastic energy and replenish the energy dissipated over the gait cycle. We found that muscle synergism is needed to maintain the energetic state of the system. For example, negative work by VAS in region 1 was almost offset by the positive work by HAM and GMAX, and the negative work by RF in region 4 was more than offset by SOL and GAS. HAM, VAS and GMAX produced much positive work in region 2 to offset the negative muscle work. Thus, external power, which represents the net power output of the system from muscle and other forces (e.g., gravity), does not quantify the relative power contributions of muscle, tendon and other structures, nor does it quantify when muscle work is performed. In addition, external power does not estimate well the net power output of muscles (e.g., region 1), and certainly cannot estimate either net positive or negative power output from muscles. Thus, caution should be used when using external power to estimate muscle work.

Though the metabolic cost for active muscles to produce force, work output and dissipate mechanical energy was not computed, our results suggest that much metabolic cost may occur to raise the COM as well as overcome the step-to-step transition mechanical cost. We found that nearly one-third of the total mechanical energetic cost by a leg in stance (regions 1–4) is to raise the COM (region 2) (Fig. 6B). Since positive work output by a muscle consumes more metabolic energy than negative work output (e.g., Abbot et al., 1952), this estimate for the relative amount of metabolic cost to raise the COM is more than likely underestimated because the relative amount of positive work in region 2 is higher compared to the other regions. The ratio will also be affected by non-contributing muscles to positive or negative work (i.e., isometric muscles) that also consume metabolic energy (e.g., Koerhuis et al., 2003; Russ et al., 2002). Nevertheless, our results suggest that there is a high metabolic cost associated with raising the COM as well as overcoming the step-to-step transition.

Inverted pendulum models have been shown to predict remarkably well many facets of human walking mechanics including walking speed–frequency ratios (Bertram and Ruina, 2001), walk–run transition speeds (Kram et al., 1997), preferred walking speed–step length ratios (Kuo, 2001), the influence of preferred step width (Donelan et al., 2001), the effect of gravity (Cavagna et al., 2000; Minetti et al., 1993), stability (Garcia et al., 1998) and the relation between work-rate and stride frequency (Minetti and Saibene, 1992). However, the mathematical elegance of inverted pendulum analyses is confounded when the complexities of the musculoskeletal system are considered. As a result, inverted pendulum-based models cannot identify the timing of work output by muscles (positive, negative or net) or muscle contributions to external power. In addition, we found that the net muscle work output cannot be estimated from the external power trajectory, and the mechanical and metabolic energetic cost by muscles is dominated not only by the need to redirect the COM in double support, but also by the need to raise the COM afterward in single support. Thus, we conclude that the muscle energetic cost to raise the COM is significant and probably related to the metabolic cost of walking.

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