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The relationships between muscle, external, internal and joint mechanical work during normal walking

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SUMMARY

Muscle mechanical work is an important biomechanical quantity in human movement analyses and has been estimated using different quantities including external, internal and joint work. The goal of this study was to investigate the relationships between these traditionally used estimates of mechanical work in human walking and to assess whether they can be used as accurate estimates of musculotendon and/or muscle fiber work. A muscle-actuated forward dynamics walking simulation was generated to quantify each of the mechanical work measures. Total joint work (i.e. the time integral of absolute joint power over a full gait cycle) was found to underestimate total musculotendon work due to agonist–antagonist co-contractions, despite the effect of biarticular muscle work and passive joint work, which acted to decrease the underestimation. We did find that when the net passive joint work over the gait cycle is negligible, net joint work (i.e. the time integral of net joint power) was comparable to the net musculotendon work (and net muscle fiber work because net tendon work is zero over a complete gait cycle). Thus, during walking conditions when passive joint work is negligible, net joint work may be used as an estimate of net muscle work. Neither total external nor total internal work (nor their sum) provided a reasonable estimate of total musculotendon work. We conclude that joint work is limited in its ability to estimate musculotendon work, and that external and internal work should not be used as an estimation of musculotendon work.

Key words: gait, musculotendon work, musculoskeletal model, simulation.

INTRODUCTION

Muscle mechanical work (or power) is an important quantity in human movement analyses as it is often used to compare estimates of the work associated with walking, running and other locomotor tasks (Cavagna and Kaneko, 1977; Detrembleur et al., 2003; Devita et al., 2007; Donelan et al., 2002; Minetti et al., 1995; Saibene and Minetti, 2003), analyze energy generation, absorption and/or transfer within body segments (Caldwell and Forrester, 1992; Willems et al., 1995), compare mechanical and metabolic cost (Burdett et al., 1983; Frost et al., 2002; Griffin et al., 2003; Martin et al., 1993; Massaad et al., 2007; Ortega and Farley, 2005; Umberger and Martin, 2007), examine locomotor efficiencies (Aissaoui et al., 1996; Winter, 1979), determine how muscles function (Jacobs et al., 1996; Winter and Eng, 1983), and identify impairments associated with neurological deficits (Mansour et al., 1982; Olney et al., 1991; Parvataneni et al., 2007).

Historically, mechanical work has been quantified using a number of methods and generally classified as external, internal or joint work. External work is the mechanical work done on an external load [e.g. during pedaling (van Ingen Schenau et al., 1990)] and/or the body's center of mass [e.g. during walking (Cavagna et al., 1963)]. Internal work is the work necessary to move the body segments relative to the body's center of mass and is computed as the sum of the absolute changes in body segment kinetic and potential energy (Cavagna and Kaneko, 1977; Winter, 1979). Although used extensively to estimate mechanical energy expenditure, either alone or as a sum (Burdett et al., 1983; Detrembleur et al., 2003; Minetti et al., 1995; Ortega and Farley, 2005; Saibene and Minetti, 2003), external and internal work both have several limitations. For example, there exists ambiguity regarding energy transfer within and among body segments (Willems et al., 1995) and lack of independence between external and internal work that prevents the total mechanical work from being estimated as a simple sum of the two measures (Aleshinsky, 1986a; Kautz and Neptune, 2002). In addition, these estimates provide little insight into the mechanical work generated by individual muscles during locomotor tasks of interest (Aleshinsky, 1986b; Kautz and Neptune, 2002).

Joint work, computed as the time integral of net joint power calculated using standard inverse dynamics techniques, is thought to represent musculotendon work more accurately than external or internal work. The advantages of joint work over the external/internal work approach have been documented in previous studies of pedaling, walking and running (Caldwell and Forrester, 1992; Kautz et al., 1994). Kautz and colleagues showed in pedaling that the change in internal work is not concomitant with the change in joint work, and therefore there is little correlation between these measures (Kautz et al., 1994). However, the joint work approach is not without limitations. The primary limitation is its inability to account for individual muscle contributions to mechanical work, primarily due to co-contraction causing the net moment to be less than the sum of the individual muscle flexor and extensor moments and muscle tendon energy storage and release that allows negative work in one phase to be recovered as positive work in a subsequent phase. For

example, human walking involves substantial muscle co-contraction at the knee and ankle joints (Centomo et al., 2007; Falconer and Winter, 1985; Schmitt and Rudolph, 2007) and elastic energy storage and release in the calcaneus tendon (Fukunaga et al., 2001; Hof, 1998), both of which are difficult to account for using joint work calculations. In addition, the various methods used to account for intercompensation of joint power by biarticular muscles (i.e. power can appear to be absorbed at one joint and generated at the other joint) means that joint work only provides an estimation within upper and lower bounds (Kautz et al., 1994). This was highlighted in a previous analysis of pedaling that showed joint work including biarticular muscle intercompensation greatly underestimates muscle fiber work, while the joint work neglecting intercompensation estimates the muscle work relatively well (Neptune and van den Bogert, 1998). However, whether these relationships hold in other locomotor tasks such as walking is unclear. Walking differs from pedaling in several ways. The feet collide with the ground, which leads to energy losses from friction and damping while, unlike pedaling, little work is done on the environment. Instead, mechanical work is required primarily to provide body support (i.e. to stop the body's downward motion and accelerate it upward during each step), forward propulsion and leg swing.

Although muscle work and tendon elastic energy storage and release have been analyzed in walking using muscle-actuated forward dynamics simulations (Neptune et al., 2008; Sasaki and Neptune, 2006), the extent to which muscle work relates to external, internal and joint work has not been investigated. Therefore, the objective of this study was to use muscle-actuated forward dynamics simulations of walking to investigate the relationships between muscle work and external, internal and joint work. Specifically, we expected that (1) when muscle work was estimated using joint work, co-contraction would lead to an underestimation of musculotendon work, while muscle tendon elastic energy storage and release would overestimate muscle fiber work, and (2) neither external nor internal work (nor their sum) would accurately estimate musculotendon work.

MATERIALS AND METHODS

Musculoskeletal model

A sagittal plane musculoskeletal model was generated using SIMM (MusculoGraphics, Santa Rosa, CA, USA) and consisted of a trunk (head, torso, pelvis and arms), two legs (thigh, shank, patella, rear foot, mid-foot and toes) and 25 Hill-type musculotendon actuators per leg (Fig. 1). There were 13 degrees of freedom in the model, including horizontal and vertical translations and rotation of the trunk, and flexion–extension for each hip, knee, ankle, mid-foot and toe joint. The position and orientation of the patella were prescribed as a function of knee flexion angle (Delp et al., 1990). The muscle actuators were combined into 13 functional groups (Fig. 1), with the muscles within each group receiving the same excitation pattern. The excitation patterns were defined using experimentally measured EMG (see 'Experimental data' below). For those muscles where surface EMG were not available, block patterns were used defined by an onset, duration and magnitude. The muscle activation dynamics were governed by a first-order differential equation (Raasch et al., 1997) with activation and deactivation time constants based on Winters and Stark (Winters and Stark, 1988). For those muscles whose time constants were not specified in Winters and Stark, nominal time constants of 12 and 48 ms were used (seven muscles per leg). Thirty-eight visco-elastic elements were attached to each foot to model the foot–ground contact (Neptune et al., 2000). Passive hip, knee and ankle torques representing ligaments and connective tissues were applied to each joint based on Davy and Audu (Davy and Audu, 1987). The passive torques for the mid-foot and toe joints were defined using the following equation:

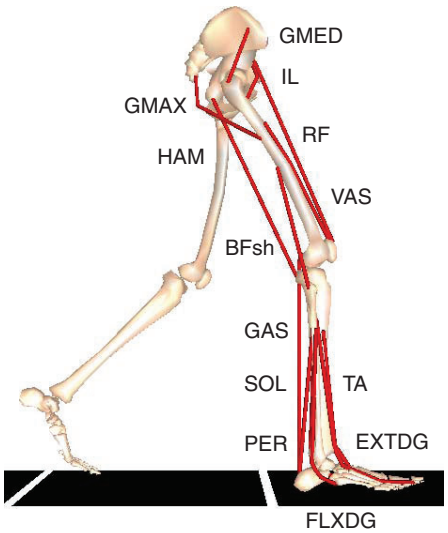

Fig. 1. The 2D-sagittal plane musculoskeletal model consisting of the trunk (head, arms, torso and pelvis) and both legs (femur, tibia, patella, rear-foot, mid-foot and toes). The 13 muscle groups (25 muscles in total) per leg included GMED (anterior and posterior portion of gluteus medius), IL (iliacus, psoas), RF (rectus femoris), VAS (3-component vastus), TA (tibialis anterior, peroneus tertius), PER (peroneus longus, peroneus brevis), FLXDG (flexor hallucis longus, flexor digitorum longus), EXTDG (extensor hallucis longus, extensor digitorum longus), SOL (soleus, tibialis posterior), GAS (medial and lateral gastrocnemius), BFsh (biceps femoris short head), HAM (medial hamstrings, biceps femoris long head) and GMAX (gluteus maximus, adductor magnus). Only the muscle groups in the right leg are shown.

$$T = k_p \times (\text{joint angle}) + k_v \times (\text{joint angular velocity}) , \quad (1)$$

where the coefficients k_p and k_v were 750 N m and 0.05 N m s for the mid-foot joint, and 25 N m and 0.03 N m s for the toe joint, respectively. The joint angles were defined as angular displacement from the anatomical neutral position expressed in radians.

Forward dynamics simulations

A forward dynamics walking simulation was generated using Dynamics Pipeline (MusculoGraphics, Inc., Santa Rosa, CA, USA) and SD/FAST (PTC, Needham, MA, USA). To generate a well-coordinated walking simulation over a full gait cycle (i.e. right heel strike to subsequent right heel strike), dynamic optimization (Neptune and Hull, 1998) was used to fine-tune the muscle excitation patterns with a cost function that minimized the difference between the simulation and experimental kinematics (i.e. the time history of the trunk trajectory and hip, knee and ankle angles) and ground reaction force (GRF) data (see 'Experimental data' below). Constraints were placed on the excitation magnitude and timing in the optimization algorithm to ensure the muscles were generating force in the appropriate region of the gait cycle.

Experimental data

Previously collected experimental kinematic, GRF and EMG data (Neptune and Sasaki, 2005) were used and will be briefly described here. Ten able-bodied subjects (five male and five female; age

29.6±6.1 years, height 169.7±10.9 cm, body mass 65.6±10.7 kg) walked on a split-belt instrumented treadmill (TecMachine, Andrezieux Boutheon, France) at 1.2 m s^{-1}.

Kinematic (Motion Analysis Corp, Santa Rosa, CA, USA; 120 Hz sampling rate using a modified Helen Hays marker set), GRF (480 Hz sampling rate) and surface EMG data (Noraxon, Scottsdale, AZ, USA; 1200 Hz sampling rate) from the soleus, tibialis anterior, medial gastrocnemius, vastus medialis, rectus femoris, biceps femoris long head and gluteus maximus were collected for 15 s to acquire 20 consecutive steps. The kinematic and GRF data were then digitally low-pass filtered at 6 and 20 Hz, respectively. Linear envelope EMG data were generated by applying sequentially a band-pass filter (20–400 Hz), full rectification and low-pass filter (10 Hz). All data were then normalized to the gait cycle, and averaged across steps and then across subjects to obtain group-averaged data.

Mechanical work

To identify the various sources of mechanical work during the walking simulation, various quantities of mechanical work were computed as the time integral over the complete gait cycle of: (1) external power, (2) internal power, (3) joint power, (4) joint power with intercompensation, (5) musculotendon power, (6) muscle fiber power, (7) muscle tendon power, (8) passive joint power, (9) muscle joint power and (10) mechanical power by the visco-elastic elements attached at the foot segment (referred to as shoe elements, hereinafter). Positive, negative, total (absolute sum of positive and negative) and net (direct sum of positive and negative) work values were computed. Below, these measures are described in more detail.

External power was computed as the dot product of the GRF and velocity of the mass center of the body vectors. Internal power was computed as the sum of time derivatives of rotational and translational kinetic energy and potential energy of each body segment. Joint power was computed as the product of net joint torque and corresponding joint angular velocity. Joint power with biarticular muscle intercompensation was obtained using the method described by Kautz and colleagues (Kautz et al., 1994), where power absorbed at one joint was allowed to cancel power generated at the other joint as if only a biarticular muscle were active. Musculotendon, muscle fiber and muscle tendon (series-elastic element) power were computed as the product of corresponding force and velocity vectors obtained from the Hill-type muscle model. The shoe-element power was computed as the product of corresponding force and velocity vectors for each ground contact element, and then summed across elements to obtain the total power. Passive joint power was computed as the product of the passive joint torque and corresponding joint angular velocity. Muscle joint power was computed as the sum of the individual muscle power contributions to each joint power, which was equivalent to joint power excluding passive joint power. The influence of muscle co-contraction on joint work was quantified as the difference between the musculotendon work and muscle joint work.

RESULTS

Walking simulation

The walking simulations emulated well the experimental kinematics and GRFs (Fig. 2) with an average deviation from the group average in the hip, knee and ankle joint angles of 3, 5 and 3 deg., respectively. The average errors in the horizontal and vertical GRFs were 7% and 2% body weight, respectively. The simulation excitation timing also compared well with the experimental EMG data (Fig. 3).

Mechanical work

The total joint work underestimated the total musculotendon work by 46% (126 J) when biarticular intercompensation was included in the joint work computation (Table 1; total intercompensated joint work *vs* total musculotendon work). Without biarticular intercompensation (i.e. joint work was computed independently without the assumption of power cancellation by biarticular muscles), the difference between the total joint work and musculotendon work was only 7% (20 J; Table 1).

Muscle joint work underestimated musculotendon work in all measures. For example, the total muscle joint work was ~35% (96 J) lower than the total musculotendon work (Table 1). This difference represents the influence of muscle co-contraction, which is not accounted for in joint work. Co-contraction occurred primarily during early stance and late swing (Fig. 3; e.g. compare HAM with

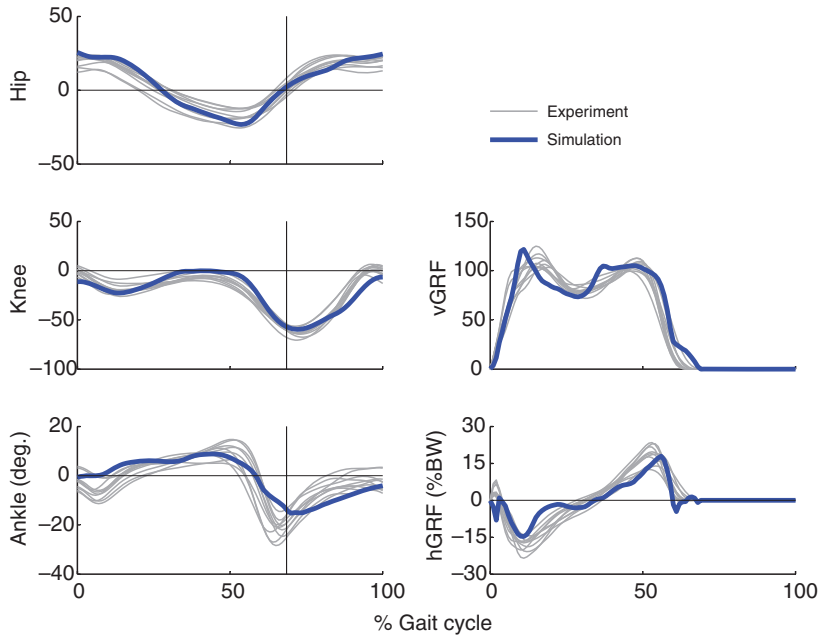

Fig. 2. Experimental joint angles, vertical and horizontal GRFs (vGRF and hGRF, respectively) from 10 subjects and corresponding simulation data over the gait cycle (i.e. from right heel strike to right heel strike). The vertical lines indicate toe-off.

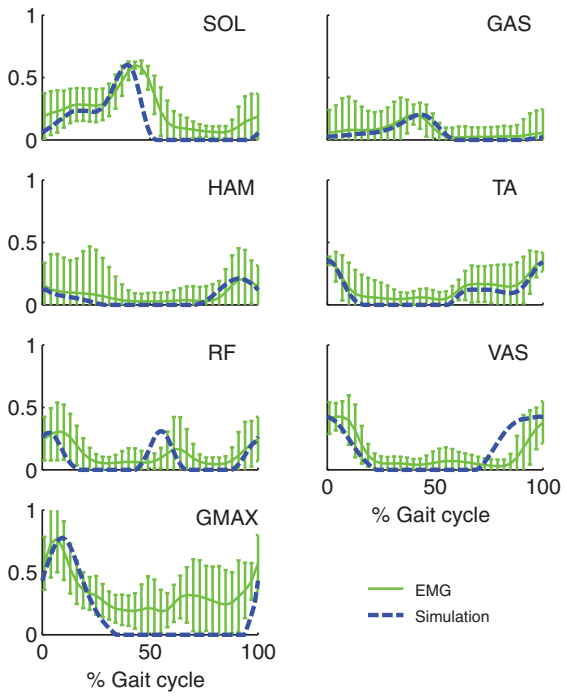

Fig. 3. EMG (group mean ± s.d.) and muscle excitation patterns in the simulation over the gait cycle. The EMG magnitude was normalized to the peak simulation excitation magnitude for each muscle.

RF and VAS excitation). Overall, the net joint and musculotendon work was positive (Table 1), which was necessary to offset the net negative shoe-element work (Table 1; net shoe-element work) such that the net mechanical work over the gait cycle was zero.

The total external and internal work was less than 30% and 40% of the total musculotendon work, respectively (Table 1). The summation of the total external and internal work still underestimated the total musculotendon work by ~100 J. The net musculotendon work was substantially higher than both the net external and internal work, which was near zero (Table 1).

DISCUSSION

The primary goal of this study was to use muscle-driven forward dynamics simulations of walking to assess whether joint, external or internal work can be used as an estimation of either musculotendon or muscle fiber work during human walking. Simulations provide an ideal framework to make the comparison because every source of mechanical work (e.g. from biarticular muscles, tendon and passive joint work) and levels of co-contraction can all be precisely quantified. To our knowledge, no study has quantified these contributions to mechanical work in detail. The simulation not only emulated well the experimental kinematic and GRF data (Fig. 2) but also the simulation joint work was comparable to previous studies using inverse dynamics. For example, Devita and colleagues showed that the positive and negative joint work per leg during stance were 50 J and –34 J, respectively (Devita et al., 2007). When the joint work was quantified only for the stance phase per leg (hip, knee and ankle joints) in our simulation, the positive and negative work were 53 J and –35 J, respectively. Thus, the simulation is representative of normal walking mechanics and sufficient to highlight the potential limitations of the various methods used to estimate muscle mechanical work.

Table 1. Mechanical work during the complete gait cycle of walking

	Positive (J)	Negative (J)	Total (J)	Net (J)
External work	36	–37	73	–1
Internal work	51	–51	102	0
Joint work	141	–113	254	28
Intercompensated joint work	88	–60	148	28
Musculotendon work	152	–122	274	30
Muscle fiber work	143	–113	256	30
Tendon elastic work	42	–42	84	0
Passive joint work	50	–51	101	–1
Muscle joint work	104	–74	178	30
Shoe-element work	5	–33	38	–28

The simulation data showed that total joint work with biarticular muscle intercompensation greatly underestimates the total musculotendon and total muscle fiber work, which was consistent with a previous analysis of pedaling (Neptune and van den Bogert, 1998). The underestimation occurs because the intercompensation model assumes that all the negative power at one joint can be cancelled out by positive power at the other joint by biarticular muscle action, which does not properly account for the contributions of uni-articular muscles to the negative joint power. In general, biarticular muscles act to overestimate musculotendon work from joint work (e.g. Prilutsky et al., 1996), because the muscle joint power is separately time integrated to compute joint work (e.g. see Fig. 4, areas under positive and negative RF power near toe-off). The overestimation of the musculotendon work by the biarticular muscles was ~25 J for both positive and negative work.

Without including joint intercompensation, total joint work underestimated total musculotendon work by ~20 J. The underestimation was due to the combined contributions of antagonist–agonist muscle co-contraction, biarticular muscle work and passive joint work to the total joint work. Muscle co-contraction (i.e. the difference between muscle joint work and musculotendon work) acted to increase the underestimation of total musculotendon work, while biarticular muscle work and passive joint work acted to decrease the underestimation. In our simulation, the total muscle fiber work was less than the total musculotendon work by ~18 J, with the difference due to tendon elastic energy storage and return. As a result, total joint work and muscle fiber work were similar in magnitude (254 J and 256 J, respectively). This result is a coincidence rather than a mechanical requirement, as the difference between joint work and fiber work is influenced by many factors including co-contraction, biarticular muscle work, passive joint work and muscle tendon elastic energy, and these factors vary across subjects and locomotor tasks. For example, we generated an additional simulation that walked with the same overall mechanics but had increased co-contraction (125 J compared with 96 J, i.e. the difference between muscle joint work and musculotendon work in Table 1) and passive joint work (143 J compared with 101 J in Table 1) over the gait cycle. Muscle co-contraction was increased by adding the inverse of the sum of squared muscle powers to the cost function to be minimized while passive joint work was increased by increasing the stiffness and damping coefficients in the model. The total joint, muscle fiber and musculotendon work in this simulation were 276 J, 301 J and 320 J, respectively. Thus, since there is no mechanical requirement that the underestimate of work done due to co-contraction equals the overestimate of work done due to biarticular muscles, passive work and tendon elastic energy, the similar magnitude of total joint work and total fiber work observed in this study should not be generalized. However, the sum of the net musculotendon work and

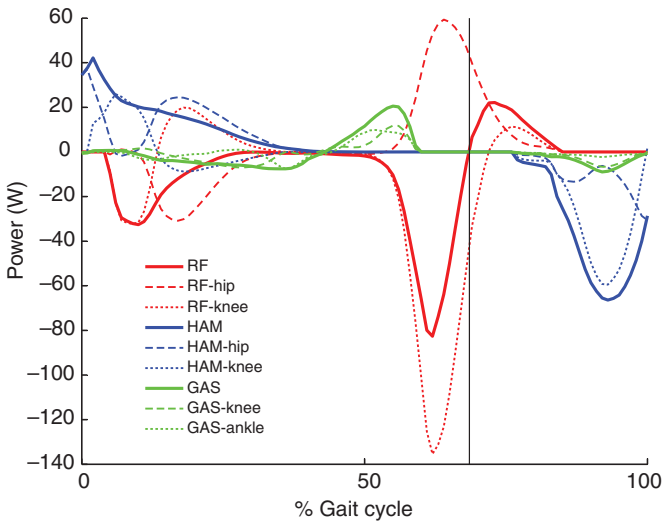

Fig. 4. Biarticular musculotendon power (RF, HAM and GAS) and the corresponding joint power at the hip, knee and ankle over the gait cycle. The vertical line indicates toe-off.

net passive joint work was equal to the net joint work (Table 1, round-off error of 1 J) and, therefore, net joint work can estimate net musculotendon work in locomotor tasks or subjects where net passive joint work is negligible (e.g. slow walking). Also, as the net elastic energy during the gait cycle is zero, the net joint work can be used as an estimate of net muscle fiber work. However, net joint work is not a useful quantity to estimate overall mechanical work, metabolic cost or efficiency.

Previous studies using inverted pendulum walking models have suggested that positive work input is primarily required to overcome the energy loss (negative work) during the step-to-step transition (e.g. Kuo, 2002), and that the external work during the step-to-step transition is the primary determinant of the metabolic cost of walking (Donelan et al., 2002; Kuo et al., 2005). However, our data show that muscles perform considerably more negative work than the negative external work (Table 1; 122 J *vs* –37 J, respectively) and, therefore, the metabolic cost of walking may not be as strongly related to the work associated with the step-to-step transition as previously suggested. We also obtained external work using the individual limbs method of Donelan and colleagues (Donelan et al., 2002) by computing the external work for individual limbs separately. Using this method, the computed negative external work was only –45 J, which was still substantially lower than the negative musculotendon work. This lack of correlation is further supported by a simulation analysis showing that muscle fiber work output is highest when the body's center of mass is raised, not during the step-to-step transition (Neptune et al., 2004).

The net musculotendon work (also net joint work) over the gait cycle was positive (30 J), which is consistent with the results of DeVita and colleagues (DeVita et al., 2007) and Umberger and Martin (Umberger and Martin, 2007), who computed joint work using an inverse dynamics approach. When musculotendon work was quantified only for the stance phase per leg as in Devita et al. (Devita et al., 2007), the net positive work was 18 J, which was comparable to the 16 J in their study. Devita and colleagues (Devita et al., 2007) reasoned that the positive net work was required to offset energy losses by body tissues. In our simulation, the net positive work was offset primarily by the net negative work dissipated in the shoe elements during foot contact, and secondarily by the energy dissipation in the passive joint torques. Although not included in the present model, energy could be lost in other body tissues such as joint cartilage and by muscle damping (e.g. Boyer and Nigg, 2007; Nigg and Liu, 1999). If additional energy-dissipating elements were included in our model, total musculotendon mechanical work would most likely be higher. However, the relationship between net musculotendon (or net muscle fiber) and net joint work would remain unchanged (again, assuming net passive joint work is negligible).

The positive passive joint work was ~35% of the positive joint work. Previous *in vivo* studies analyzing the amount of hip or knee passive joint torque generated during normal walking have produced conflicting results (Mansour and Audu, 1986; Silder et al., 2007; Vrahas et al., 1990; Yoon and Mansour, 1982). The positive work by the hip and knee passive torques in our simulation was approximately 11 J and 3 J, respectively, while the ankle passive work was negligible. The passive joint torques in our model were based on those of Davy and Audu (Davy and Audu, 1987), which are lower in magnitude than those of Silder and colleagues (Silder et al., 2007). Although further investigation is needed to estimate the contributions of the passive joint structures to joint work, the relationships between net joint work and net musculotendon work would remain unchanged because the net joint torque is the net sum of passive and active muscle contributions at the joint.

The total and net external work were substantially lower than the total and net musculotendon work, respectively. Similar to external work, the total and net internal work were markedly lower than the total and net musculotendon work, respectively. Further, the summation of total external and internal work was much lower than the total musculotendon work (175 J *vs* 274 J, respectively). Previous studies have shown that external and internal work are not mutually independent and, therefore, total mechanical work cannot be obtained as the sum of the two measures (Aleshinsky, 1986a; Kautz and Neptune, 2002). Although external and internal work or power have been widely used in previous studies to estimate mechanical work and metabolic cost (Burdett et al., 1983; Cavagna and Kaneko, 1977; Detrembleur et al., 2003; Minetti et al., 1995; Ortega and Farley, 2005; Saibene and Minetti, 2003; Winter, 1979), the present study as well as previous analyses of pedaling (Kautz et al., 1994; Neptune and van den Bogert, 1998) clearly show that neither total external nor total internal work (nor the sum of the two) can be used to estimate total musculotendon work.

While not the purpose of this study, we recognize that the muscle fiber work obtained in this study has implications for estimating mechanical efficiency. There are a number of methods to compute efficiency with different equations and different quantities to represent mechanical work (joint work, external work, muscle work). For example, previous studies have suggested that negative work should be included in the efficiency calculation, in contrast to the traditionally used measures of mechanical efficiency expressed as the ratio of positive work to metabolic cost (Prilutsky, 1997; Woledge, 1997). Recently, Umberger and Martin (Umberger and Martin, 2007) looked at the influence of stride rate during walking on efficiency by including negative joint work (power) in their efficiency calculation. Using the same equation with our joint work and their net metabolic rate data to estimate our metabolic cost (~243 J), our efficiency was ~0.40 [141 J/(243 J+113 J)], which was comparable with the data from Umberger and Martin (Umberger and Martin, 2007), who showed an efficiency of 0.38 when subjects walked at 1.3 m s^{-1} using their preferred stride rate. This value would be higher if negative work was not included in the denominator or

lower if gross, rather than net, metabolic rate data were used. Note that our individual muscle-based estimate of efficiency would be 0.59 using the ratio of positive fiber work relative to metabolic cost (143 J/243 J), demonstrating that net joint work-based measures of mechanical work probably underestimate positive work due to inevitable co-contraction. However, these efficiency values are high compared with traditional values of 0.25–0.30 measured in isolated muscles or muscle fibers (e.g. Astrand and Rodahl, 1977), which could be due to a number of factors including an overestimate of muscle co-contraction in the model, unaccounted or underestimated elasticity in the muscle fibers, tendon and other tissues, unmodeled stretch-induced force enhancement, an overestimate of the energy lost at foot–ground contact, an overestimate of the resting baseline metabolic cost used to determine net metabolic cost, or the fact that the efficiency measured in isolated muscle fibers is not the same as whole-body efficiency. For a detailed discussion of a number of these issues, see target article by van Ingen Schenau and colleagues (van Ingen Schenau et al., 1997) and the various responses. While additional research is clearly needed to validate whole-body efficiency models in human locomotor tasks such as walking, analyses of individual muscle contributions to mechanical work as performed in this study are an important step in the process.

One comment that should be made is that the net external work was not zero over the gait cycle in our study as it should be for steady-state walking, but measured –1 J. This occurred because the walking simulation was not perfectly symmetrical between the right and left steps, although the kinematics and GRFs in the simulations emulated well the experimental data. However, the magnitude of the net external work was much lower than the net musculotendon work (or the net joint work) and, therefore, the overall results would remain unchanged even if the steps were perfectly steady state.

In summary, we found that during walking, (1) total joint work underestimated total musculotendon work due to muscle co-contraction despite the biarticular muscle work and passive joint work that acted to decrease the underestimation, (2) total joint work cannot be used to estimate total muscle fiber work in general because of the influence of tendon elastic energy, muscle co-contraction, biarticular muscle work and passive joint work, (3) net joint work can be used as an estimate of net muscle fiber work over a full gait cycle only if the net passive joint work is known to be negligible, (4) net muscle mechanical work is positive over the gait cycle to overcome energy dissipation during foot–ground contact and other damping effects, and (5) the total and net external and internal work were substantially lower than the total and net musculotendon work, respectively, and therefore cannot be used to estimate the musculotendon work. These results have important implications for studies attempting to estimate metabolic cost from mechanical work measures as external, internal and joint-based work measures do not accurately estimate total muscle work.

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