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Human walking isn't all hard work: evidence of soft tissue contributions to energy dissipation and return

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SUMMARY

The muscles and tendons of the lower extremity are generally considered the dominant producers of positive and negative work during gait. However, soft-tissue deformations not captured by joint rotations might also dissipate, store and even return substantial energy to the body. A key locomotion event is the collision of the leg with the ground, which deforms soft tissues appreciably in running. Significant deformation might also result from the impulsive ground collision in walking. In a study of normal human walking (*N*=10; 0.7–2.0 m s^{-1} speeds), we show indirect evidence for both negative and positive work performed by soft tissue, consistent with a damped elastic collision and rebound. We used the difference between measured joint work and another quantity – the work performed on the body center of mass – to indicate possible work performed by soft tissue. At 1.25 m s^{-1}, we estimated that soft tissue performs approximately 7.5 J of negative work per collision. This constitutes approximately 60% of the total negative collision work and 31% of the total negative work per stride. The amount of soft tissue work during collision increases sharply with speed. Each collision is followed by 4 J of soft tissue rebound that is also not captured by joint work measures. Soft tissue deformation may save muscles the effort of actively dissipating energy, and soft tissue elastic rebound could save up to 14% of the total positive work per stride. Soft tissues not only cushion impacts but also appear to perform substantial work.

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Key words: locomotion, mechanical work, soft tissue, walking biomechanics, wobbling mass.

INTRODUCTION

Locomotion is accomplished by performing positive and negative mechanical work with the body. During steady gait on level ground, no net work is performed on the environment, so that mechanical work of the body must sum to zero over a stride. Muscles, in series with tendons, are recognized to provide most of the positive work through rotations of the joints. But it is less appreciated that soft tissues, such as plantar fascia, cartilage and the viscera, may deform and perform significant negative work without necessarily rotating the joints. Although much of this work may be dissipative, some may be elastic, implying the possibility of energy return. Work *via* soft tissue deformation may be helpful for locomotion if it reduces the negative work needed from active muscle or if it performs some of the positive work. How and where this work occurs may influence the likelihood of injuries and degenerative damage to tissues. We therefore seek to quantify the contribution of work from soft-tissue deformations to human walking.

Soft tissues certainly deform during human walking (Collins and Whittle, 1989; Light et al., 1980; Rao and Jones, 1975). For example, empirical data show substantial deformations of the heel pad (Bennett and Ker, 1990; Hsu et al., 1998; Ker et al., 1989; Whittle, 1999) and foot arch (Gefen, 2003; Ker et al., 1987). Forces are transmitted through the rest of the body in a traveling wave (Challis and Pain, 2008; Smeathers, 1989; Voloshin, 2000), and 'wobbling mass' models show that soft-tissue motion can explain the forces transmitted due to impacts from running (Alonso et al., 2007; Liu and Nigg, 2000; Nigg and Liu, 1999) and jumping (Gittoes et al., 2006; Gruber et al., 1998; Günther et al., 2003; Pain and Challis, 2006). Similar effects may apply to walking (Kuo et al., 2005), where the relevant soft tissue work may be performed by motion of the viscera, compression of the intervertebral discs, heel pads or joint cartilage, or even transverse muscle motion (as opposed to active shortening). The prior literature primarily focuses on the effect of soft tissues on vibrations and joint forces and torques. There is, however, little experimental evidence regarding the work performed by soft-tissue deformations during walking.

One reason why evidence is limited is that soft-tissue work is difficult to measure. In human studies, the standard method of quantifying work is inverse dynamics analysis (e.g. Cappozzo, 1991; Vaughan et al., 1992), which estimates the joint torques and powers. The integrated power, or joint work, is the result of both concentric and eccentric muscle actions as well as passive tendon elasticity, acting to rotate the joints. Inverse dynamics is based on an assumption of rigid bodies and does not quantify soft-tissue deformations between or within them. Previous studies have noted how force and torque errors may result from incorrect rigid body assumptions (Günther et al., 2003; Pain and Challis, 2006; Riemer et al., 2008), but few have examined the effect on the mechanical energetics of walking. The unmodeled soft-tissue dynamics mean that joint-work estimates from rigid body models may be insufficient to summarize the work performed by the entire body. For the purposes of this study, we define soft-tissue work as that not performed by lower-limb joint rotations and, therefore, not captured by rigid-body inverse dynamics in traditional gait analysis. An example of such work is that performed by passive dynamic walking machines that can descend a gentle slope with freely swinging joints

(McGeer, 1990). Inverse dynamics would be expected to yield practically no joint work, even though there is clearly energy lost in each leg's collision with the ground and even though the legs appear to be rigid.

Indirect evidence suggests that joint work fails to capture significant work performed elsewhere in the body. Using inverse dynamics, DeVita et al. found that the negative work estimated for the lower extremity joints during stance phase was 32% lower than the positive work (–34 *vs* 50 J step^{-1}, not including swing phase) in subjects walking at 1.5 m s^{-1} (DeVita et al., 2007). We have hypothesized that substantial negative work is performed by soft tissue and cannot be captured by conventional inverse dynamics (Kuo et al., 2005), potentially explaining this work inconsistency. In order to test this hypothesis and study the energetic role of soft tissue, additional methods of quantifying human locomotion are needed to complement inverse dynamics.

As a point of comparison, we propose using a second measure: that of the work performed on the body's center of mass (COM). The COM work is defined as the vector dot product of each limb's ground reaction force with the COM velocity (Fig. 1) obtained by integrating the ground reaction forces (Donelan et al., 2002b). We have used this method to show that the collision of the leg with the ground performs negative work on the body's COM (Adamczyk and Kuo, 2009; Donelan et al., 2002a) in the first 15% of a stride (beginning with heel-strike). The collision work is approximately 14 J at 1.25 m s^{-1}, and increases sharply with walking speed (Adamczyk and Kuo, 2009; Donelan et al., 2002b). The COM work analysis makes no assumptions about rigid bodies and, therefore, captures both joint and soft-tissue work. However, it does not estimate individual joint contributions or work performed relative to the COM, the latter generally considered small during stance phase (Cavagna and Kaneko, 1977; Ralston and Lukin, 1969; Willems et al., 1995). Despite these limitations, the comparison of COM and joint work may provide insight into the nature of soft-tissue work that is not captured by the lower extremity joints. We use the difference between these two measures, along with additional supporting evidence, as an indirect indicator of soft tissue work in human walking.

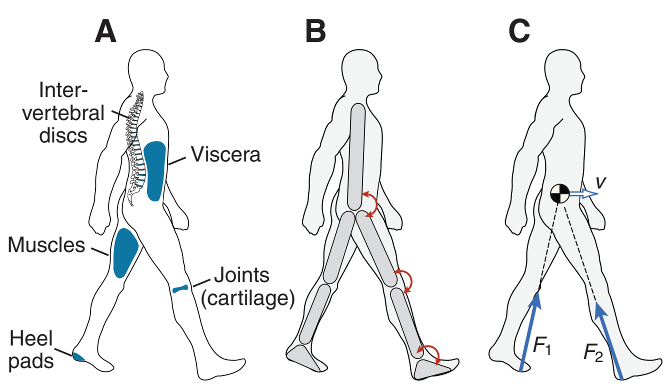

Fig. 1. Soft tissues of the body and models for estimating work. (A) Deformation of tissues such as the heel pad, joint surfaces, muscles, viscera and intervertebral discs may affect walking. (B) The standard inverse dynamics model for gait analysis includes the ankle, knee and hip joints of each leg, and computes joint work from force and torque balances between body segments that are assumed to be rigid. (C) Analysis of center-of-mass (COM) work (defined as the dot product of ground reaction forces, F_1 and F_2, and COM velocity, *v*) does not assume rigid bodies, but quantifies the work performed by the two legs to move the COM, treated as a point mass. We compare estimates of joint work and COM work during normal human walking and propose that differences between these methods may be indicative of soft-tissue contributions.

The purpose of this study was to quantify the contribution of soft-tissue work to human walking. We propose that mechanical work captured by COM work, but not by inverse dynamics, is indicative of such soft-tissue work. This comparison does not specify the location or type of tissue performing the work, but it does roughly indicate the magnitude and timing. Based on dynamic walking principles (Kuo, 2007; Kuo et al., 2005), we hypothesize that: (1) soft tissue performs significant negative work during the collision of the leg with the ground and (2) soft tissue dissipates more collision energy at faster walking speeds. These hypotheses were tested using measurements of steady walking performed by normal human participants.

MATERIALS AND METHODS

We compared mechanical work estimated from conventional inverse dynamics and COM work analysis for subjects walking across a range of speeds. We used the difference between rigid-body joint work from inverse dynamics and the whole-body COM work as an indicator of soft tissue deformations. These differences were examined in terms of individual phases of the gait cycle as well as over the entire gait cycle. We hypothesized that soft-tissue work would increase with greater ground collisions at faster walking speeds. Consequently, we predicted that, at higher speeds, inverse dynamics would show greater net positive work over a stride whereas COM work per stride would sum to zero regardless of speed. We measured kinematics and ground reaction forces for 10 subjects walking in normal street shoes on an instrumented treadmill at eight speeds ranging from 0.7 to 2.0 m s^{-1}. All subjects (seven males, three females) were healthy and had no known gait impairments or abnormalities (24±2.5 years old, 73.5±15 kg, 1.76±0.11 m in height). This study was approved by the University of Michigan Institutional Review Board and all subjects gave informed consent prior to participation in the experiment.

Ground reaction forces and lower-body kinematics were collected according to standard gait analysis procedures. Forces were recorded on a custom-built split-belt instrumented treadmill located in the Human Neuromechanics Laboratory at the University of Michigan. Separate force plates (Bertec, Columbus, OH, USA) mounted beneath each belt of the treadmill independently measured reaction forces under each foot at 1200 Hz. Force plates were calibrated based on methods described previously (Collins et al., 2009). Kinematic data were collected at 120 Hz *via* an eight-camera motion capture system and software (Motion Analysis Corp., Santa Rosa, CA, USA). Passive, reflective markers were placed bilaterally on the ankle (lateral malleolus), knee (lateral epicondyle) and hip (greater trochanter). Additionally, we placed stiff marker triads on each thigh and shank, three markers on the pelvis (sacrum, left/right anterior superior iliac spine) and two markers on each foot (calcaneous, fifth metatarsal).

Randomized experimental trials consisted of subjects walking at self-selected stride frequency at each of the following eight speeds: 0.7, 0.9, 1.1, 1.25, 1.4, 1.6, 1.8 and 2.0 m s^{-1}. Walking trials at each speed lasted 60 s, of which the middle 40 s were analyzed as representative of steady-state walking. The number of steps per trial varied based on subject and speed, but typically included at least 20 strides. Crossover steps on the split-belt treadmill, in which both feet simultaneously affected the same force plate, were omitted from analysis because of the need for limb-specific forces. Prior to the study, subjects were allowed a short acclimation period to adjust to treadmill walking. Of the 80 total trials (10 subjects, eight trials each), three were excluded from analysis owing to errors in data acquisition.

Inverse dynamics calculations (Fig. 2) were performed using standard commercial software (Visual3D, C-Motion, Germantown, MD, USA) and its associated anthropomorphic model. We used a commercial package because it is representative of the procedure used by many laboratories and because any standard method would be expected to yield similar trends. Analog force data were filtered at 25 Hz and marker motion was filtered at 6 Hz (Butterworth low-pass) prior to inverse dynamics calculations. Joint moments and powers were computed in all three dimensions. To facilitate comparison with COM work rate, we summed joint power in all planes and refer to this as summed ankle–knee–hip power, or total joint power. We produced summary measures of net work by integrating power over the entire gait cycle (defined as one stride, from heel-strike to subsequent heel-strike of the same limb), as well as over individual phases of gait, as defined below.

We computed COM work rate independently for each limb (Fig. 1C). The work rate was calculated from the three-dimensional dot product of each limb's ground reaction force with COM velocity (Donelan et al., 2002b). COM velocity was determined from integration of ground reaction forces, assuming steady-state, periodic strides. We defined positive and negative COM work as the integrals over regions of positive and negative COM work rate, respectively. This work summarizes fluctuations in the energy of the COM, but not of motions relative to the COM, which appear to contribute less to the overall energy of the body (Cavagna and Kaneko, 1977; Willems et al., 1995). From the beginning to the end of a periodic stride of level walking, no net mechanical work is performed on the COM, assuming negligible air resistance and ground deformation. For many imperfectly periodic strides, we still expect the average summed positive and negative COM work for the body to be approximately zero.

One reason that net joint work may be non-zero is because soft-tissue deformations may also perform work. We have previously hypothesized that this may occur during the collision of the leg with the ground following heel-strike, and have also speculated that there may be some passive elastic rebound following the collision (Kuo et al., 2005). Soft tissues may perform negative work and then return some fraction as positive work, and thus perform net negative work over an entire stride. Because joint work is predicted not to capture soft-tissue work, we predict the summed ankle–knee–hip work to be measured as net positive over a stride. To determine when the soft-tissue work might occur within a gait cycle, we compared summed joint power against COM work rate. Even though the two are different measures of work, their difference may serve as a rough indicator of soft-tissue work. To perform this comparison, we found it convenient to divide the gait cycle into five phases defined by major regions of positive and negative COM work (Fig. 3): collision (approximately 0–15% of stride), rebound (15–30%), pre-load (30–45%), push-off (45–65%) and swing (65–100%). We predicted that the greatest mismatch between joint work and COM work would occur during collision and that this mismatch would increase with walking speed.

All analysis was performed on a stride-by-stride basis. For example, work values were computed for each stride in a trial, and these were averaged across strides to yield mean work for a given trial. All power and work analyses were performed with non-dimensionalized values to account for size differences between subjects, using body mass (M), leg length (L) and gravitational acceleration ($\boldsymbol{g}$) as base units. Mean normalization constants were then used to re-dimensionalize values for reporting purposes. Mean power and work normalization constants were $Mg^{3/2}L^{1/2}$=2357 W and MgL=727 J, respectively.

Primary statistical analysis was performed using analysis of covariance (ANCOVA) to determine the significance of work trends and offsets across speed. To examine work per stride and work per phase of gait trends across walking speed (v), we performed a one-way ANCOVA with $v^{2.8}$ as the predictor variable and work as the response. The 2.8 exponent was based on a prediction of collision work (W) per step $W \propto v^2 l^2$ (where l is the step length) from dynamic walking models (Donelan et al., 2002a; Kuo, 2002), combined with the empirical relationship $l \propto v^{0.42}$ (Grieve, 1968; Kuo, 2001). We have previously found normal walking data to fit this relationship well (Adamczyk and Kuo, 2009), although for statistical

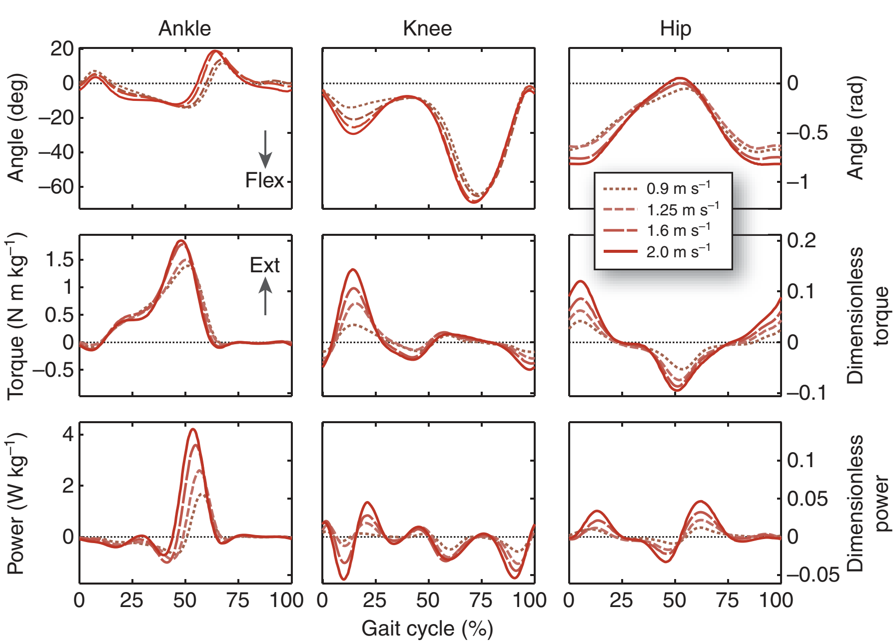

Fig. 2. Mean joint angle, torque and power trajectories *vs* time, as recorded for four walking speeds. Torques and powers were calculated from standard inverse dynamics methods and were found to scale relatively consistently with walking speed. Data shown are sagittal plane values, averaged across subjects (N=10) and normalized to a gait cycle beginning with heel-strike, although calculations of work were performed in all three dimensions. Angles and torques are defined as positive in extension. Standard gait analysis units are shown on the left-hand axes, and dimensionless scales are shown on the right-hand axes, using body mass, leg length and gravitational acceleration as base units. Ext, extension; Flex, flexion.

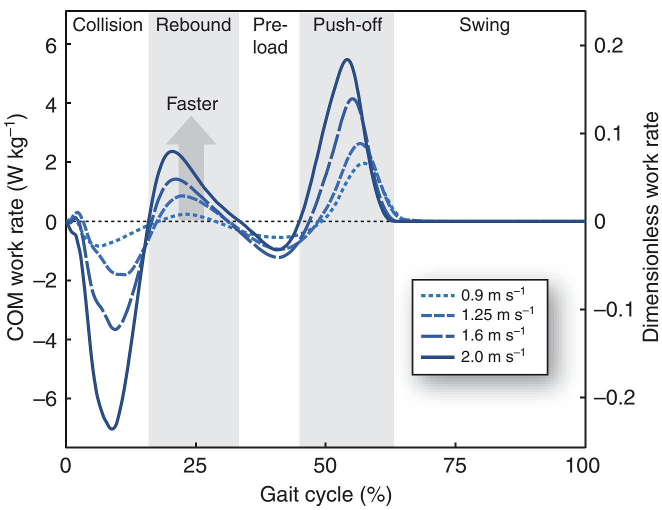

Fig. 3. Mean center-of-mass (COM) work rate for a single limb *vs* time for a gait cycle, at four walking speeds. The COM work rate generally followed a consistent pattern of negative and positive work fluctuations, used to define five gait phases: collision, rebound, pre-load, push-off and swing. Data shown are averaged across all subjects (N=10).

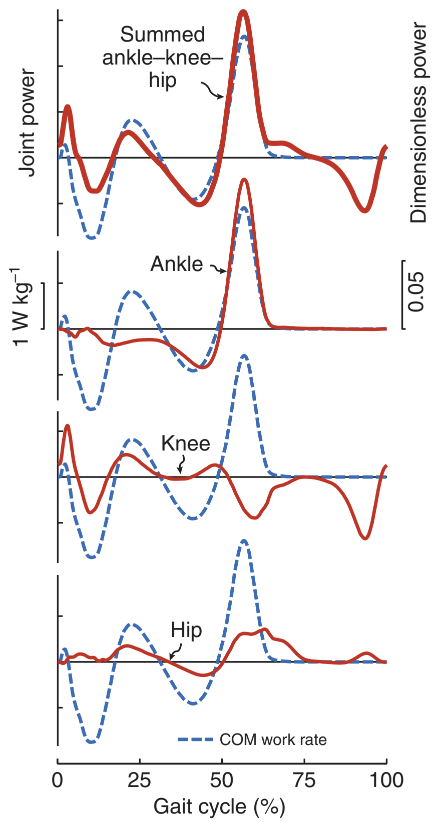

Fig. 4. Single limb joint powers (solid lines) over a gait cycle compared with center-of-mass (COM) work rate (dashed lines) for walking at 1.25 m s^{-1}. Ankle, knee, hip and summed ankle–knee–hip powers for a single stride are shown averaged across subjects. Summed ankle–knee–hip power was found to fluctuate between negative and positive work in rough correspondence with COM work rate.

comparisons we do not consider the particular exponent to be crucial. Work trends were fit to $W=Cv^{2.8}+D$, where C is the coefficient and D is an offset. In some instances, paired Student's t-tests were used as a secondary statistical means to compare COM and summed ankle–knee–hip work at each walking speed. In all analyses, P-values less than 0.05 were considered statistically significant.

RESULTS

We observed a qualitative correspondence between joint power and COM work rate (Fig. 4). The summed ankle–knee–hip power generally displayed regions of negative work during collision and pre-load, and positive work during rebound and push-off, as is typical of COM work rates. The correspondence was less strong during collision, where the summed ankle–knee–hip power was more positive than the COM work, indicating less overall negative joint work. Another difference was at the end of the swing phase, where the knee performs negative work over the final 20% of the stride. By contrast, the COM work rate is calculated through the stance leg and is not suitable for quantifying work of the swing limb. Therefore, COM and joint work were not directly compared during the swing phase. At the level of the joints, the COM work of the collision and rebound phases could largely be attributed to the knee, and pre-load and push-off to the ankle, with less obvious correspondence at the hip.

A quantitative comparison of the work performed over each phase revealed notable trends with walking speed. The magnitudes of summed joint work and of COM work increased roughly with $v^{2.8}$ for all phases (Fig. 5) except for pre-load, where the magnitudes actually decreased slightly. The largest difference between COM and ankle–knee–hip work was during collision. This difference increased with walking speed, from 3.8 J at 0.7 m s^{-1} to 33.0 J at 2.0 m s^{-1}. The trends were significantly different, in both the curve fit proportionality coefficient (P=2E–25, N=10 for all reported statistics) and offset (P=0.03). Furthermore, at all walking speeds, the COM collision work was significantly larger in magnitude than summed ankle–knee–hip work (paired t-tests, P<0.05). These results are consistent with our expectations that joint work would not fully capture collision work, with the uncaptured amount increasing with gait speed.

Another substantial difference was in the positive work of the rebound phase, with consistently less ankle–knee–hip work than COM work. This difference averaged 3.9±0.4 J (mean ± s.d.), with a maximum of 4.4 J at 2 m s^{-1} and a minimum of 3.4 J at 1.4 m s^{-1}. ANCOVA revealed no significant difference in fit coefficients (P=0.85), but significantly different offsets (P=0.001). Paired t-tests at each speed also showed significant differences (P<0.05) at five of the eight walking speeds (0.7, 0.9, 1.1, 1.25 and 1.6 m s^{-1}) and marginally significant differences (P<0.08) at the remaining speeds. These results are consistent with a damped elastic rebound of soft tissues that is not captured by joint work.

The observed COM and summed ankle–knee–hip work during the pre-load and push-off phases were in strong agreement. Neither phase showed a significant difference in fit coefficients or offsets (P>0.05). Examining each speed separately, COM and summed ankle–knee–hip work magnitudes were not significantly different in push-off or pre-load phase across speeds (t-test, P>0.20), with the single exception of push-off work at 1.25 m s^{-1} (t-test, P=0.04).

Net ankle–knee–hip work per stride increased with speed (Fig. 6). On average, summed joint work for a single limb over the gait cycle was close to zero at slower walking speeds (e.g. –2.70±7.38 J at 0.7 m s^{-1}) and was increasingly net positive at faster speeds (e.g. 17.75±16.63 J at 2.0 m s^{-1}). By contrast, net COM work was consistently small across walking speeds, as expected. At 1.25 m s^{-1},

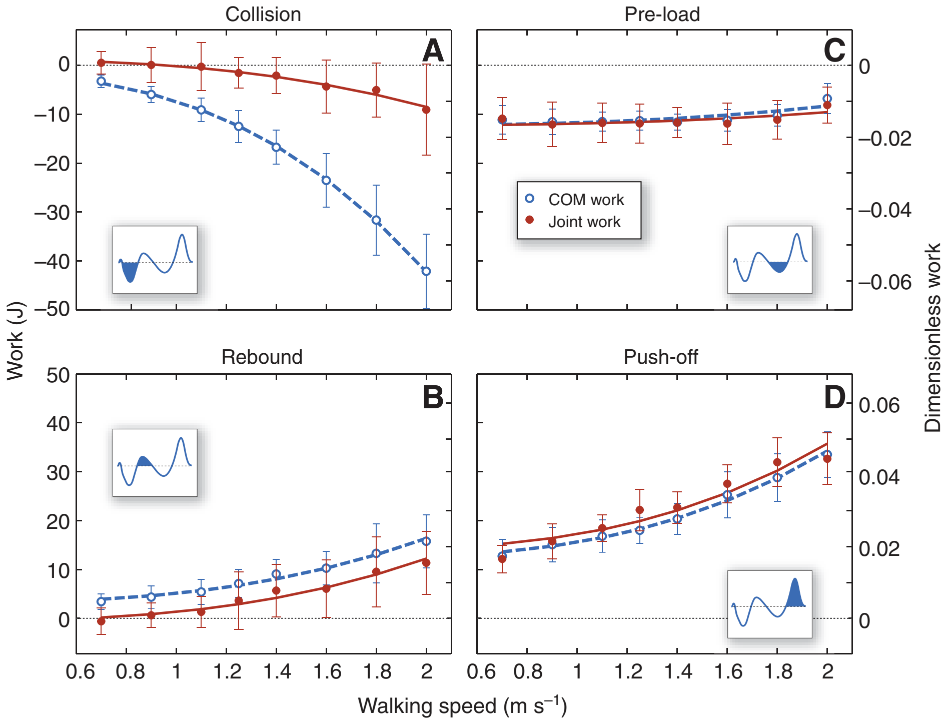

Fig. 5. Mean center-of-mass (COM) and summed ankle–knee–hip joint work for each phase of the gait cycle, plotted across walking speeds. Phases shown are (A) collision, (B) rebound, (C) pre-load and (D) push-off. The summed joint work (filled circles) failed to capture significant negative work during collision as compared with COM work (open circles), with a difference increasing significantly with walking speed (v). An approximately constant but significant work difference was observed in rebound. There was greater agreement during pre-load and push-off. Data were fitted with trends increasing with $v^{2.8}$ based on dynamic walking model predictions for collision (Kuo, 2001; Donelan et al., 2002a; Adamczyk and Kuo, 2009). Data shown are means ± s.d. across all subjects (N=10). Curve fit R^2 values, fit coefficients and offsets are reported in the supplementary material Tables S1–S3.

net ankle–knee–hip work was approximately five times greater than net COM work (6.33 *vs* 1.28 J) and, at 2 m s^{-1}, it was approximately 50 times greater (17.75 *vs* 0.35 J). Curve fits of $v^{2.8}$ revealed significant coefficient differences between COM and joint work (P=3E–8). Meanwhile, regression offsets were not significantly different (P=0.09).

DISCUSSION

There is a collision in gait
When the foot hits the ground and bears weight,
  Joint work measures miss
  Three-fifths of the squish,
Which soft tissues perhaps dissipate.

We used non-joint work – that not captured by inverse dynamics – as an estimate of soft-tissue contributions to determine whether soft tissues contribute significant work to human walking. We tested for evidence of such work and whether its magnitude increased with walking speed. Our results suggest that negative work is indeed performed by soft tissues, to a degree perhaps comparable to the joints themselves. This dissipative soft-tissue work occurs primarily during collision and increases with gait speed. Therefore, the joint work captured by rigid-body inverse dynamics may seriously underestimate the total negative work performed by the body, and perhaps even some of the positive work. We next examine these findings in detail, along with their underlying assumptions.

We found two indicators of soft-tissue work, the first coming from the joint work results alone. Net ankle–knee–hip work over a stride was measured as positive for most speeds (Fig. 6). Negative ankle–knee–hip work over a stride was 6.3 J or approximately 18.6% less than the positive work at 1.25 m s^{-1}. This represents a self-inconsistency in joint work measurements because the net mechanical work performed over a stride of steady walking must be zero. Inverse dynamics consistently fails to capture a significant percentage of work, especially negative work, performed by the body during gait.

The second indicator comes from the difference between joint work and COM work, which indicates when in the gait cycle soft-tissue work might be performed. Results suggest that substantial negative soft-tissue work is performed during collision. At the nominal 1.25 m s^{-1}, negative ankle–knee–hip work (ignoring the early positive transient; see Fig. 4) failed to capture approximately 7.5 J during collision, which amounts to approximately 31% of the negative work per stride, using COM work for comparison. Across all walking speeds, this soft-tissue work appears to constitute approximately 60% of the negative collision work. The high forces and rate of work associated with the collision phase appear well suited for deforming soft tissues in human walking. As a point of

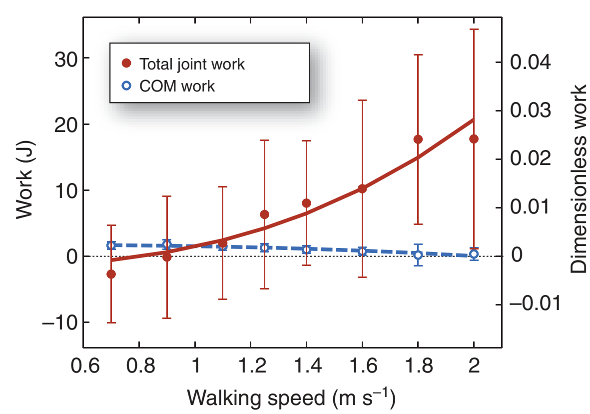

Fig. 6. Mean summed ankle–knee–hip work and center-of-mass (COM) work per stride across walking speeds. Net COM work (open circles) was close to zero at all speeds, as is required for steady gait. By contrast, summed ankle–knee–hip work (filled circles) showed a strong increase with speed, with less negative work captured than positive work at most speeds, indicating an inconsistency in joint work estimates. Data shown are means ± s.d. across all subjects (N=10). Curve fit R^2 values, fit coefficients and offsets are reported in the supplementary material Tables S1–S3.

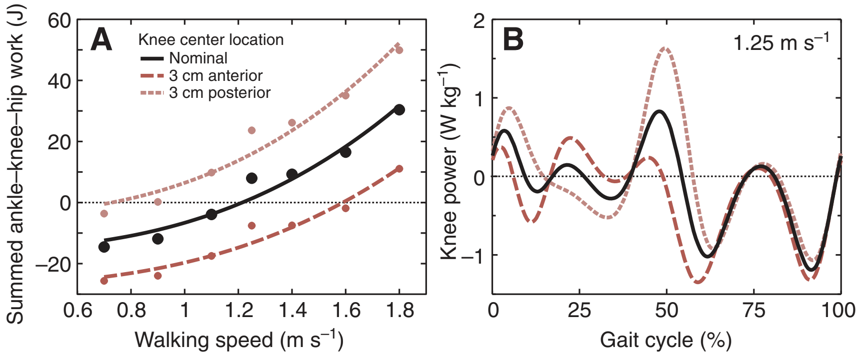

Fig. 7. Sensitivity of inverse dynamics to knee joint center location, examined with data from a single subject. (A) Joint work sensitivity. Perturbation of the observed knee joint center by 3 cm in anterior and posterior directions caused offsets in the magnitude of net ankle–knee–hip work per stride, but did not affect the speed-dependent trend. (B) Knee power sensitivity. Perturbations caused substantial changes in knee power trajectory, but the overall discrepancies in joint work are not explained by possible methodological errors in marker placement. The nominal knee joint center was defined by motion-capture markers on the medial and lateral epicondyles of the femur.

comparison, a passive dynamic walking machine descending a 2.3% slope with step lengths similar to humans would perform an equivalent amount of negative collision work (~12.5 J step^{-1} at 1.25 m s^{-1}), even though it performs no work through joint rotations. Our present results suggest that soft-tissue deformation in humans may account for most of the negative work following heel-strike, with joint work of the ankle, knee and hip capturing only a fraction of the total energy dissipated in collision.

The COM *versus* joint work comparison also indicates that some positive soft-tissue work is performed during rebound. The observed difference in positive rebound work was less substantial, approximately 4 J, and varied little with speed. At 1.25 m s^{-1}, this difference constituted approximately 10% of the positive work per stride performed by the lower extremity joints and 14% of the positive COM work. Soft-tissue contributions to rebound were not proportional to the difference in the collision, but nonetheless might represent a damped elastic recoil not attributable to ankle–knee–hip joint rotations. Elastic energy return by soft tissue could perform 10–14% of the positive work otherwise required of active muscle, perhaps saving a roughly proportionate amount of metabolic energy.

Several trends were observed in mechanical work as a function of walking speed. The magnitude of COM collision work increased approximately with speed raised to the 2.8 power (R^2=0.89; Fig. 5), as predicted by dynamic walking models (Kuo, 2001; Kuo, 2002). The positive COM work during push-off also increased at that rate (R^2=0.77), as it largely offsets the negative collision work (Adamczyk and Kuo, 2009; Donelan et al., 2002b). The slight pre-load work trend, for which there was no prediction, decreased in magnitude with speed. There was also no explicit trend predicted for net ankle–knee–hip work (Fig. 6) other than an increase with speed. The measured net joint work over a stride did in fact increase with speed, and its difference with COM work also increased during collision. These findings are consistent with our hypothesis that substantial negative work is performed by soft-tissue deformations during collision.

Our conclusions are based on experimental estimates for mechanical work. To minimize methodological errors, we followed standard gait analysis procedures for motion capture and inverse dynamics, and found that our results were in good agreement with prior joint kinetics literature (Vaughan et al., 1992). One area of sensitivity affecting mechanical work estimates is joint center location (Schwartz and Rozumalski, 2005; Vaughan et al., 1992), for example at the knee (Silva and Ambrosio, 2004). We therefore performed a sensitivity analysis in which the knee joint center was artificially translated fore–aft by ±3 cm from the nominal rigid-body model. This changed the summed ankle–knee–hip work results by a substantial offset of 12–20 J across all speeds but had virtually no effect on the trend with walking speed (see Fig. 7). Our results also appear consistent with prior estimates using independent measurement and filtering methodologies to estimate joint work (DeVita et al., 2007; Vaughan et al., 1992) and COM work [using overground force plates (Donelan et al., 2002b)]. Similar trends regarding soft-tissue work are also reported by Soo and Donelan, who applied analogous comparisons to a task that isolates step-to-step transitions from human walking (Soo and Donelan, 2010).

There are limitations to directly comparing COM and joint work. COM analysis quantifies only the work performed on the COM and assumes most of it to be performed by the legs. Large rotational motions such as pitching of the trunk or swinging of the arms could, therefore, potentially cause misattribution of work to the legs. However, these motions are typically assumed to contribute little to the joint work of normal walking and are often not included in inverse dynamics measurements (Vaughan et al., 1992), as was the case here. COM work also does not capture the work performed to move body segments relative to the COM [sometimes referred to as 'internal work' as opposed to 'external work' (e.g. Cavagna, 1963)]. There is substantial work performed relative to the COM during the swing phase, especially to slow the swing knee (Willems et al., 1995), which is one reason why we did not directly compare COM and joint work estimates during that phase. As for the stance phase, estimates from the literature show that positive work is performed relative to the COM during push-off as the trailing limb accelerates rotationally (Cavagna and Kaneko, 1977; Ralston and Lukin, 1969; Willems et al., 1995), in an amount perhaps sufficient to explain the (statistically insignificant) difference we observed between COM and joint work (Fig. 5D). Similarly, collision also showed a relatively small amount of positive work relative to the COM (<3 J) that offsets the negative COM work slightly but explains, at most, a third of the difference between COM and joint work (Fig. 5A). It therefore appears that COM work might be an overestimate, and joint work an underestimate, of the actual negative work of the entire body during collision.

Rigid-body assumptions made in standard inverse dynamics also complicate the definition and interpretation of soft-tissue work. We have treated a substantial difference between COM and joint work as indirect evidence of soft tissue work, but it is possible that work is performed by joints whose associated bodies might be rigid (but perhaps difficult to measure) as opposed to 'soft'. It is also possible that the work estimates for each individual joint are simply inaccurate. However, soft-tissue deformations are a reasonable explanation for these joint work inaccuracies, because of well-recognized force and torque errors induced by wobbling mass and rigid-body assumptions (Gruber et al., 1998; Pain and Challis, 2006; Riemer et al., 2008). All of these issues could potentially be addressed by measuring additional rigid-body segments that are not conventionally captured, or by modeling a wobbling mass with additional rigid bodies, albeit with limits to practicality. In gait analysis, much effort is devoted to reducing 'skin marker artifact' or 'soft-tissue motion artifact' (e.g. Cappozzo, 1991; Günther et al., 2003). Our results suggest that the complete elimination of such artifacts would still leave a 'rigid-tissue motion artifact' because the skeleton accounts for much less than 20% of total body mass in humans and most other animals (Prange et al., 1979). To be truly accurate, inverse dynamics would require the correct displacements and inertias of all moving body parts, which are distributed and continuous as opposed to lumped and discrete. Given these limitations, we interpret our results conservatively by observing work trends across a range of walking speeds, which we believe to be relatively insensitive to errors in absolute work estimates.

This study is not intended to indict inverse dynamics as a method. It is well recognized that rigid-body assumptions lead to errors in torques and forces, and our results suggest that these may, in turn, cause substantial errors in estimates of mechanical work during walking. Most studies using inverse dynamics draw conclusions based on controlled comparisons that require precision but not absolute accuracy. We believe that the inverse dynamics method is quite consistent and provides good precision, despite limitations in absolute accuracy. Of course, COM work also has several limitations, as discussed above, and both methods are indirect indicators of mechanical work performed on the body. Overall, the two methods have different limitations and should be treated as imperfect but complementary indicators of mechanical work.

We have presented preliminary evidence of soft-tissue energy absorption and return. The difference between COM and ankle–knee–hip work provides indirect evidence of soft-tissue work, roughly indicating when but not where in the body it is performed. The greatest impacts are experienced near the ground, and so the heel pad (Ker et al., 1989; Gruber et al., 1998; Pain and Challis, 2006; Riemer et al., 2008), plantar fascia (e.g. Cappozzo, 1991; Günther et al., 2003; Ker et al., 1987) and other tissues of the shank might dissipate substantial energy. They might also provide some damped elastic recoil, but other possible contributors include intervertebral discs (Virgin, 1951), articular cartilage (Hayes and Mockros, 1971; Ker, 1996; Ker et al., 1989) and the viscera (Baudinette, 1991; Minetti and Belli, 1994), supported by the elasticity of the peritoneum. Further research is needed to understand the distribution of soft tissue work throughout the body. Our findings also require corroboration, perhaps with more direct observational techniques such as imaging (e.g. Armstrong et al., 1979; Eckstein et al., 2001; Ophir et al., 1999) and direct strain or force measurements (Armstrong et al., 1979). A challenge in most estimates of soft-tissue work is the need for material and other parameters that are difficult to identify from independent experiments, and internal forces and displacements that are difficult to measure. It is therefore helpful to study soft-tissue work using multiple approaches.

We believe that soft tissues play an underappreciated role in walking. Not only do they reduce peak impact loads, but they also dissipate, store and even return energy. Their deformation is well recognized at the level of localized tissues, but the associated work is not considered in most studies of overall gait. The total amount of collisional negative work is largely dictated by the pendulum-like walking motion (Kuo et al., 2005) and may be distributed between muscle fibers, tendon and soft-tissue deformations (Gefen, 2003; Ker et al., 1987). Soft-tissue deformation may, in fact, account for much of the collisional work, and thus reduce the proportion of negative work performed by muscle and perhaps even the subsequent positive work, if there is appreciable elastic rebound. Also perhaps underappreciated is negative work as a whole, as its existence is the reason why positive work must be performed at all. We propose that negative work is equal to positive work, not only in quantity but also in scientific importance.

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