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RESEARCH ARTICLE

Six degree-of-freedom analysis of hip, knee, ankle and foot provides updated understanding of biomechanical work during human walking

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ABSTRACT

Measuring biomechanical work performed by humans and other animals is critical for understanding muscle–tendon function, joint-specific contributions and energy-saving mechanisms during locomotion. Inverse dynamics is often employed to estimate joint-level contributions, and deformable body estimates can be used to study work performed by the foot. We recently discovered that these commonly used experimental estimates fail to explain whole-body energy changes observed during human walking. By re-analyzing previously published data, we found that about 25% (8 J) of total positive energy changes of/about the body's center-of-mass and >30% of the energy changes during the Push-off phase of walking were not explained by conventional joint- and segment-level work estimates, exposing a gap in our fundamental understanding of work production during gait. Here, we present a novel Energy-Accounting analysis that integrates various empirical measures of work and energy to elucidate the source of unexplained biomechanical work. We discovered that by extending conventional 3 degree-of-freedom (DOF) inverse dynamics (estimating rotational work about joints) to 6DOF (rotational and translational) analysis of the hip, knee, ankle and foot, we could fully explain the missing positive work. This revealed that Push-off work performed about the hip may be >50% greater than conventionally estimated (9.3 versus 6.0 J, P=0.0002, at 1.4 m s^{-1}). Our findings demonstrate that 6DOF analysis (of hip–knee–ankle–foot) better captures energy changes of the body than more conventional 3DOF estimates. These findings refine our fundamental understanding of how work is distributed within the body, which has implications for assistive technology, biomechanical simulations and potentially clinical treatment.

KEY WORDS: Biomechanics, Foot work, Gait analysis, Inverse dynamics, Joint work, Mechanical work

INTRODUCTION

Human walking results from a coordinated sequence of energy generation and absorption (Gordon et al., 1980). During level-ground walking at steady speed, there is an equal balance between positive and negative work production as the body undergoes no net acceleration (assuming negligible external losses). This mechanical work is performed by diverse and distributed physiological tissues, including contributions from both active muscle contractions and passive soft tissue deformations, and affects the kinetic and potential energy of the body. To maintain consistent walking speed, any mechanical energy losses (whether in muscles or in other soft tissues) must be compensated for by net positive work generated by muscles (Kuo et al., 2005). Understanding how, when and where in the body this work is performed is useful for discerning fundamental mechanisms underlying locomotion and can inform applications related to clinical treatment, rehabilitation and assistive technology.

Biomechanical work is often measured at the level of specific joints and body segments, representing the net contributions from underlying muscles, tendons and other tissues. Empirical observations indicate that during walking, substantial positive work is performed about the lower-limb joints (Elftman, 1939; Gordon et al., 1980). For convenience, we use the term 'joint work' to describe work performed by muscles, tendons and other structures at/about each joint (e.g. ankle work signifies work performed at/about the ankle joint). The main burst of positive work, termed Push-off, is performed largely by muscles and tendons about the ankle at the end of the Stance phase of gait (Farris and Sawicki, 2012a; Kuo et al., 2005; Winter, 1991) and facilitates economical walking by redirecting the body during step-to-step transitions (Donelan et al., 2002a; Kuo et al., 2005; Ruina et al., 2005).

Joint work estimates, based on inverse dynamics, fail to capture negative work performed by passive soft tissue (DeVita et al., 2007; Zelik and Kuo, 2010) and shoe deformations (Sasaki et al., 2009; Shorten, 1993). For an individual walking on level ground at constant speed, experimental estimates indicate that there is substantially more positive work performed about the lower-limb ankle, knee and hip joints than negative work (DeVita et al., 2007). As positive and negative work must be of equal magnitude for steady-state walking, this difference suggests that the joint-level measures may only capture a portion of the work performed by the body during gait. Additional evidence is based on the comparison of joint work with a separate estimate of the body's center-of-mass (COM) kinetics (Fu et al., 2014; Soo and Donelan, 2010; Zelik and Kuo, 2010, 2012). The mismatch between these estimates indicates that negative work is performed by the body, which cannot be attributed to a specific joint or muscle–tendon source. Also, this mismatch in negative work is larger for obese than for non-obese individuals (Fu et al., 2014), further suggesting that the source may be dissipation by soft tissue deformations in the body.

A similar missing work problem exists for positive work; however, this discrepancy cannot be resolved by invoking soft tissue deformations (as only muscles can perform net positive work). Specifically, if one sums conventional 3 degree-of-freedom (DOF) work measures about the hip, knee and ankle joints (e.g. Zelik and Kuo, 2010) with segment-level contributions from the foot (e.g. Takahashi and Stanhope, 2013), then these estimates fail

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List of symbols and abbreviations

Collision	phase of gait immediately after footstrike impact, occurring at ~0–15% of the stride cycle at typical speeds, primarily characterized by a period of negative individual-limb COM power, but also inclusive of positive power transient immediately after footstrike (Fig. 2)
COM	center-of-mass
DOF	degree-of-freedom
$\dot{E}_{com}$	rate of energy change of the COM
$\dot{E}_{per}$	Peripheral rate of energy change, due to motion of body segments relative to the COM
$\dot{E}_{total}$	Total rate of energy change of the body
Energy-Accounting analysis	the name given to our general methodological approach, in which we compare summed joint- and segment-level work estimates with an estimate of the total energy change of the body (depending on the task or animal being studied, the precise formulation of these estimates may vary; see Materials and methods for computations used in this study of human gait)
$\vec{F}_i$	ground reaction force under the foot
$\vec{I}$	inertia
j	joint
Joint+Segment	in this manuscript, this term refers to contributions from the hip, knee, ankle and foot (although theoretically it could also include additional body joints and segments, if measured)
m	mass
$\vec{M}$	moment
P_{3d}	3DOF joint power
P_{6d}	6DOF joint power
P_{com}	COM power
P_{foot}	Foot power
Peripheral	refers to contributions relative to the body's COM
Preload	phase of gait following Rebound, occurring at ~30–45% of the stride cycle at typical speeds, characterized by negative individual-limb COM power (Fig. 2)
Push-off	phase of gait following Preload, occurring at ~45–65% of the stride cycle at typical speeds, characterized by positive individual-limb COM power (Fig. 2)
Rebound	phase of gait following Collision, occurring at ~15–30% of the stride cycle at typical speeds, characterized by positive individual-limb COM power (Fig. 2)
s	segment
Stance	period of gait when the ipsilateral foot is on the ground; consists of Collision, Rebound, Preload and Push-off phases of gait
Swing	phase of gait following Push-off, occurring at ~65–100% of the stride cycle at typical speeds, characterized by zero individual-limb COM power as the ipsilateral limb is not in contact with the ground (Fig. 2)
Total energy change	sum of COM and Peripheral changes in energy
$\vec{v}_{com}$	COM velocity
ω	angular velocity
3DOF work	rotational joint work (based on conventional inverse dynamics)
3DOF+Foot work	sum of rotational joint work and work performed by foot segment deformation
6DOF work	rotational and translational joint work
6DOF+Foot work	sum of rotational and translational joint work and work performed by foot segment deformation

to account for substantial positive work that is performed by the body (see Materials and methods for complete computational details). When re-analyzing a typical walking data set (Zelik and Kuo, 2010), we found that >30% (~8 J) of the positive energy change of the body during Push-off, which amounts to ~25% of the positive energy changes throughout the entire gait cycle, is not captured by conventional joint and foot work estimates (Fig. 1). This is problematic because our measures of work in healthy human gait contribute to our fundamental understanding of locomotion, as well as inform assistive technology development and clinical treatment (e.g. surgical decision-making for children with cerebral palsy; Gage, 1994; Wren et al., 2011).

In this study, we aimed to find and explain the missing positive work; specifically, to determine whether experimental joint and foot work estimates could collectively account for the total mechanical energy change of the body during gait, if estimated with a more sophisticated biomechanical analysis. To accomplish this goal, we extended conventional 3DOF inverse dynamics to a full 6DOF analysis (Buczek et al., 1994; Duncan et al., 1997), and performed a novel 'Energy-Accounting' analysis to evaluate biomechanical work and energy. This Energy-Accounting analysis was previously presented in a rudimentary form (Zelik and Kuo, 2012), and builds upon the analytical framework detailed by Aleshinsky (1986). It involves computing several complementary biomechanical estimates (see equations and full details in Materials and methods). Two measures summarize whole-body dynamics: COM and Peripheral rates of energy change, due to motion of the COM and to motion of the limb segments relative to the body's COM, respectively. We refer to the sum of these as the Total rate of energy change of the body. Power estimates were also computed for individual lower-limb joints, based on both 3DOF and 6DOF inverse dynamics. A final power estimate was then computed for the foot.

The specific purpose of this Energy-Accounting analysis was to determine whether and when summed joint and foot segment power (and work) estimates account for the body's Total rate of energy change (and the magnitude of energy change). During human walking, the muscles, tendons and other biological tissues of the lower limb perform work at/about the hip, knee and ankle joints, and in the feet. One of the most common biomechanical estimates is rotational joint power, computed from 3DOF inverse dynamics and denoted as 3DOF power in this study. Recently, foot power estimates computed assuming a deformable segment model have also become more widely used and accepted (Prince et al., 1994; Takahashi et al., 2012). In the absence of a true gold standard (e.g. from a comprehensive array of implantable force and strain gauge measurements), these 3DOF and foot power estimates represent the most commonly used standards for measuring and interpreting contributions from joint- and segment-level sources in the human lower limb. By comparing summed 3DOF+Foot power with the body's Total rate of energy change (of/about the COM), it is then possible to assess the ability of the joint- and segment-level measures to explain whole-body kinetics. In this study, we also extended the conventional 3DOF joint estimates by computing full 6DOF inverse dynamics (Buczek et al., 1994; Duncan et al., 1997), which includes both rotational and translational power terms, and performed a similar comparison of 6DOF+Foot power with Total rate of energy change.

Here, we briefly clarify the work versus energy terminology used in this study. We computed total, COM and Peripheral rate of energy change, then integrated these over time to report energy change (in units of J). In much of the previous biomechanics literature, including our own (Zelik and Kuo, 2012), these integrated values

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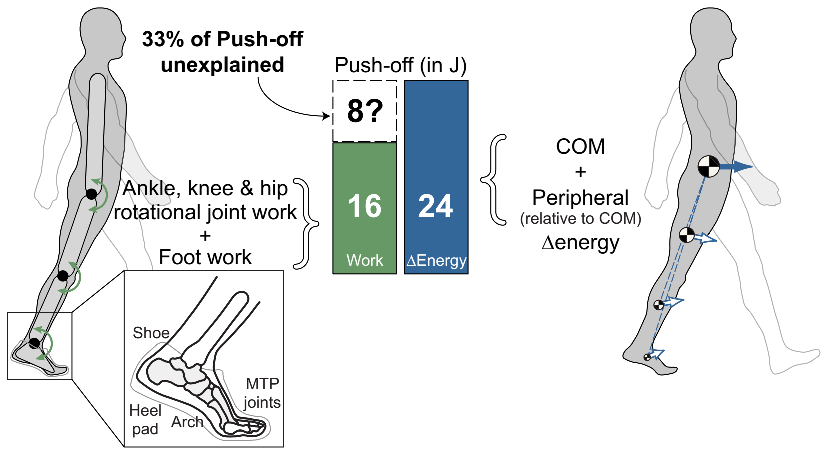

Fig. 1. Unmeasured positive work. Push-off kinetics are not explained by conventional joint- and segment-level biomechanical measures, based on our re-analysis of previously published data (Zelik and Kuo, 2010). At 1.4 m s^{-1} there is about 24 J of total positive energy change (Δenergy) during Push-off, which reflects the redirection of the body's center-of-mass (COM) velocity, and also the motion of segmental masses relative to the COM (termed Peripheral energy change). We can compare this total energy change estimate with the mechanical work computed from commonly used joint- and segment-level estimates. We observe that the Push-off work performed by the stance limb joints and foot segment – work performed rotationally (represented by green arrows) about the hip, knee and ankle joints [from 3 degree-of-freedom (DOF) inverse dynamics] and work performed by the foot [a combination of metatarsophalangeal (MTP) joint rotations and other deformations within the foot and shoe] – only sums to about 16 J. Thus, these conventional measures fail to account for 8 J (33%) of the Push-off kinetics.

were called work (e.g. COM work, Peripheral work). However, for clarity, it is preferable here to describe these measurements in terms of changes in energy. In particular, Peripheral estimates (see Eqn 3 in Materials and methods) are based solely on changes in kinetic energy, rather than defined by a specific force acting over a displacement (the classical definition of work). COM kinetics are often reported in the literature as the work done to move the body's COM and are indeed calculated from force and displacement (integral of Eqn 1); however, this terminology may be confusing because the (physiological) source of the work is unclear, and the ground reaction forces are not acting directly on the COM. As COM power is equal to the time derivative of the body's kinetic and potential energy (Eqn 2), the integral of COM power also represents the change in energy. In contrast, joint and foot segment power are integrated over time and are reported as mechanical work (also in units of J), as these reflect specific forces/moments acting over specific displacements/angles (e.g. ankle moment acting over measured angular rotation).

In summary, this study poses the question: can the net work performed at or about the lower limb joints and in the foot segment explain the observed changes in the energy state of the body during gait? An alternative phrasing, which may be less clear to some readers but is more consistent with published biomechanics literature, is: can Joint+Segment work account for the Total work performed by the body? Throughout the manuscript, we will use the former phrasing and terminology.

RESULTS

Total rate of energy change versus Joint+Segment power

We observed qualitative similarities between the Total rate of energy change, and 3DOF+Foot and 6DOF+Foot power. Each time-varying profile displayed corresponding fluctuations of negative and positive work/energy (Fig. 2A). However, magnitudes varied with phase of gait. 3DOF+Foot and 6DOF+Foot power were in strong agreement with each other during phases that involved principally negative power (Collision, Preload and Swing), but greater differences were observed during periods of positive power (Rebound and Push-off). During Push-off, the 6DOF+Foot power was similar to the Total rate of energy change, but 3DOF+Foot power was smaller in magnitude. During Collision, 3DOF+Foot and 6DOF+Foot power exhibited smaller magnitudes than the Total rate of energy change.

3DOF versus 6DOF joint power

Joint-level differences between 3DOF and 6DOF power were observed mainly at the hip and knee (Fig. 2C). 6DOF hip power was, on average, higher in magnitude than 3DOF estimates, an effect most pronounced during Preload and Push-off. 6DOF knee power displayed a shift towards positive power during Collision, Preload and Push-off. Small differences in ankle power were also observed during Preload and Push-off.

Comparison with prior literature

Our biomechanical estimates were in good qualitative agreement with prior literature reporting 3DOF joint (Eng and Winter, 1995), 6DOF ankle (Buczek et al., 1994), Foot (Takahashi et al., 2012) and COM power (Donelan et al., 2002a). To our knowledge, 6DOF knee and hip power and Peripheral rate of energy change have not been published for level-ground walking.

Push-off work and energy change

Total energy change during Push-off was comparable to 6DOF+Foot work, but not to 3DOF+Foot work (Fig. 3). At 1.4 m s^{-1}, we found 23.7±3.4 J (mean±s.d.) of Total energy change during Push-off (Table 1) and a similar amount of 6DOF+Foot work (22.1±2.5 J, P=0.07), but significantly less 3DOF+Foot work (15.8±2.1 J, P<0.0001). The 6DOF+Foot work was 6.3 J higher than the 3DOF+Foot work, which accounted for the majority of the missing work at nominal speed (7.9 J). The larger magnitude of the 6DOF+Foot work could be attributed to increased contributions from each lower-limb joint (Fig. 4A), most notably a 55% increase in hip work from 6.0±2.0 to 9.3±1.8 J (3DOF+Foot versus 6DOF+Foot, P=0.0002). Knee work during Push-off also changed by ~30% from −6.7±2.3 to −4.8±2.5 J (P=0.0008). The ankle displayed a smaller 5% increase from 22.4±3.7 to 23.6±3.7 J (P=0.006).

Positive work and energy change over stride

At 1.4 m s^{-1}, the total positive energy change over the stride (39.4±4.4 J; Table 1, Fig. 3) was comparable to the 6DOF+Foot work (40.5±

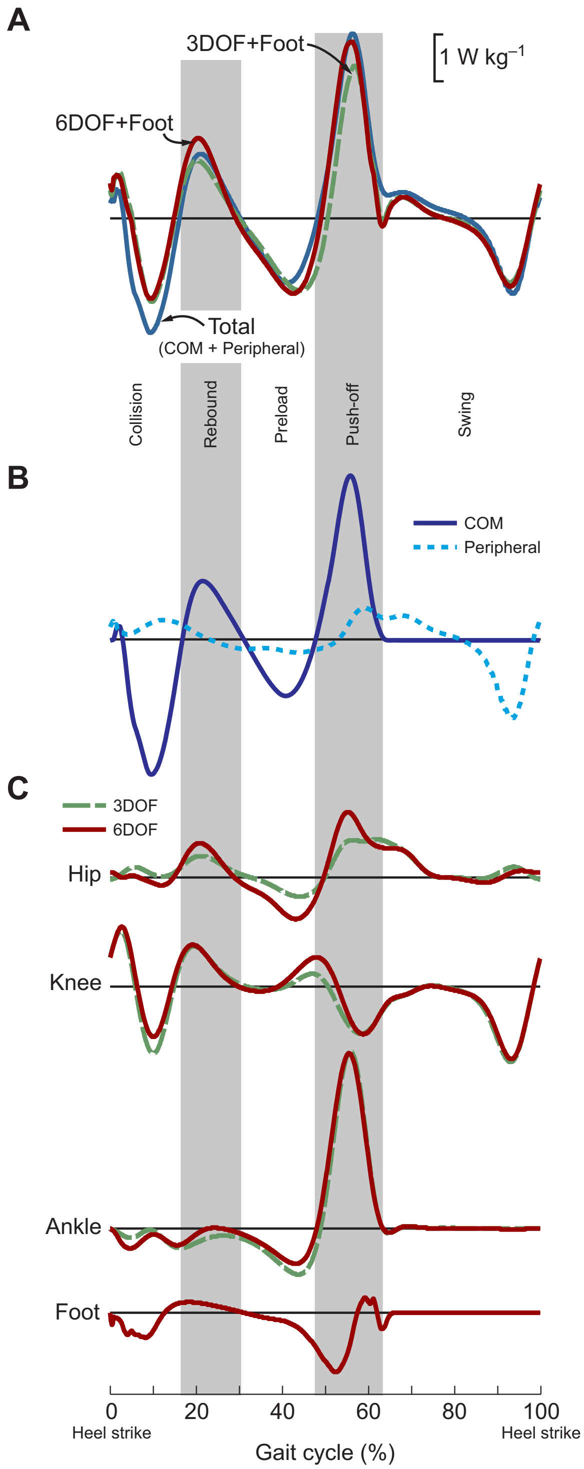

Fig. 2. Mechanical power and rate of energy change. (A) Summed power and rate of energy change. Three estimates are depicted: 3DOF+Foot power (rotational hip, knee and ankle power+deformable foot power, green dashed line), 6DOF+Foot power (rotational and translational power for all joints and the foot, red solid line), and Total rate of energy change (COM+Peripheral, blue solid line). (B) COM and Peripheral rates of energy change, due to motion of and about the body's COM, respectively, are depicted. (C) Power contributions from individual joints and the foot segment. Conventional 3DOF rotational joint power and full 6DOF joint power are shown. Foot power estimates were only calculated based on a 6DOF deformable body model. Individual-limb results are shown for subjects walking at 1.4 m s^{-1} (N=9). Phases of gait – Collision, Rebound, Preload, Push-off and Swing – are depicted by alternating regions of shading.

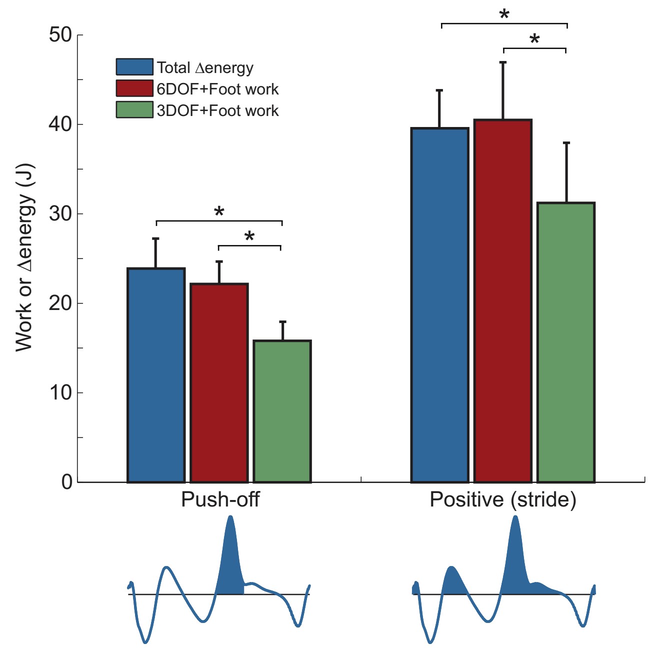

Fig. 3. Mechanical work and energy change. 6DOF+Foot work estimates explain Total positive energy changes (Δenergy) during Push-off and positive energy changes across the entire stride cycle; work that is missed by conventional 3DOF+Foot estimates. Results (means and s.d.) are shown for subjects walking at 1.4 m s^{-1} (N=9). *P<0.05. At the bottom, the shaded areas depict regions of integrated positive power and rate of energy change.

6.5 J, P=0.53), whereas 3DOF+Foot work was about 25% less (31.2±6.7 J, P=0.0002). On average, 6DOF work magnitudes were larger than 3DOF work at each lower-limb joint: 3.6 J at the hip, 3.2 J at the knee and 1.5 J at the ankle (Fig. 4B), although only ankle and knee differences reached statistical significance. We observed subject-specific hip work differences: five of nine subjects exhibited 6DOF hip work that was >7 J higher than the 3DOF estimate, while the other four subjects exhibited >2 J less hip work at 1.4 m s^{-1}.

Other phases of gait

Joint+Segment work was in good agreement with Total energy change during other phases of gait, with the exception of Collision. No significant differences were found during Rebound or Preload for Total energy change versus 3DOF+Foot

Table 1. Mechanical work and energy change

	Total (J)	3DOF+Foot (J)	6DOF+Foot (J)
Collision	−13.1±3.4	−5.8±4.1*	−5.7±2.2*
Rebound	9.4±3.0	7.1±5.2	10.4±3.4
Preload	−14.4±1.7	−15.1±3.2	−15.5±2.0
Push-off	**23.7±3.4**	**15.8±2.1*,‡**	**22.1±2.5‡**
Swing	−4.8±1.1	−6.8±0.9*	−7.0±1.2*
Positive (stride)	**39.4±4.4**	**31.2±6.7*,‡**	**40.5±6.5‡**
Negative (stride)	−38.5±4.8	−36.0±5.9	−36.5±6.0
Net (stride)	0.8±0.5	−4.8±9.8‡	4.0±2.3‡

Results are reported as means±s.d. (in J) for a single limb, for individuals walking at 1.4 m s^{-1} (N=9). Positive and negative energy change and work over the stride were computed by integrating the Total rate of energy change, and 3 degree-of-freedom (DOF)+Foot and 6DOF+Foot power curves directly, as opposed to calculating work/energy for each source (e.g. joint, segment, center-of-mass) individually and then summing those values.
Asterisks indicate statistically significant differences compared with Total energy change, and double daggers indicate differences between 3DOF+Foot and 6DOF+Foot work. Bold indicates values depicted in Fig. 3.

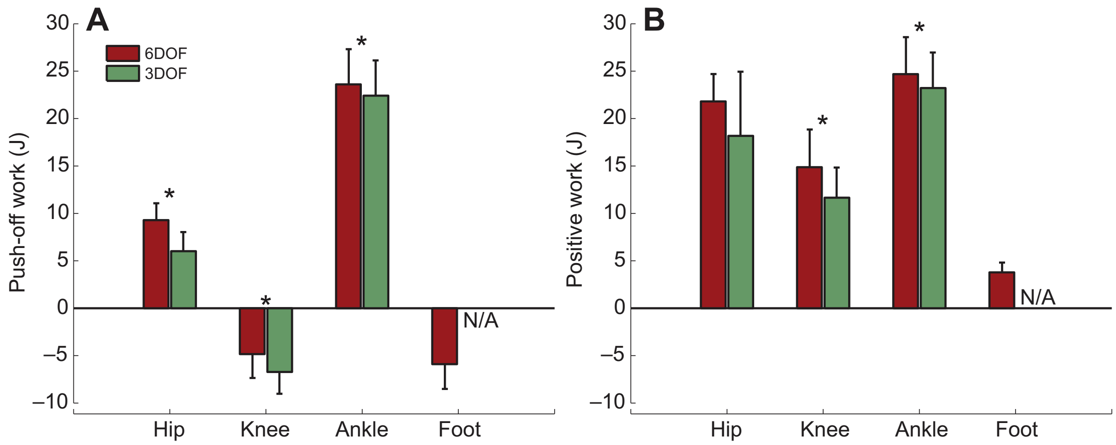

Fig. 4. Joint and foot segment work. On average, 6DOF calculations yielded more positive work than 3DOF estimates at each joint for (A) Push-off work and (B) positive work across the stride. In particular, 6DOF estimates indicate that hip work may, on average, perform >50% more Push-off than conventionally estimated at 1.4 m s^{-1} (N=9). Foot power was estimated based on a 6DOF deformable body model and is thus not applicable (N/A) to 3DOF analysis. Data are means and s.d. (*P<0.05).

work or Total energy change versus 6DOF+Foot work (P>0.08, Table 1). Differences in work during Swing phase were small, on average less than 2 J, although they reached statistical significance. Significant differences were also found during Collision. In terms of the magnitude of negative work, we observed 55% less Joint+Segment Collision work (−5.8±4.1 J of 3DOF+Foot work, −5.7±2.2 J of 6DOF+Foot work) than Total energy change during Collision (−13.1±3.4 J).

Net work and energy change over stride

The net Total energy change (sum of positive and negative) over the stride was close to zero (<1 J), as expected for steady gait (Table 1). However, Joint+Segment work over the stride was net negative for 3DOF+Foot (approximately −5 J) and net positive for 6DOF+Foot estimates (+4 J).

Effect of gait speed

Work/energy results were qualitatively consistent across a broad range of speeds, from 0.9 to 2 m s^{-1} (Fig. 5). Total positive energy change across the gait cycle and during Push-off was always significantly higher than 3DOF+Foot work estimates. 6DOF+Foot work consistently provided a better estimate for Total energy change. Total energy change and 6DOF+Foot work were generally not significantly different for Push-off or for positive contributions

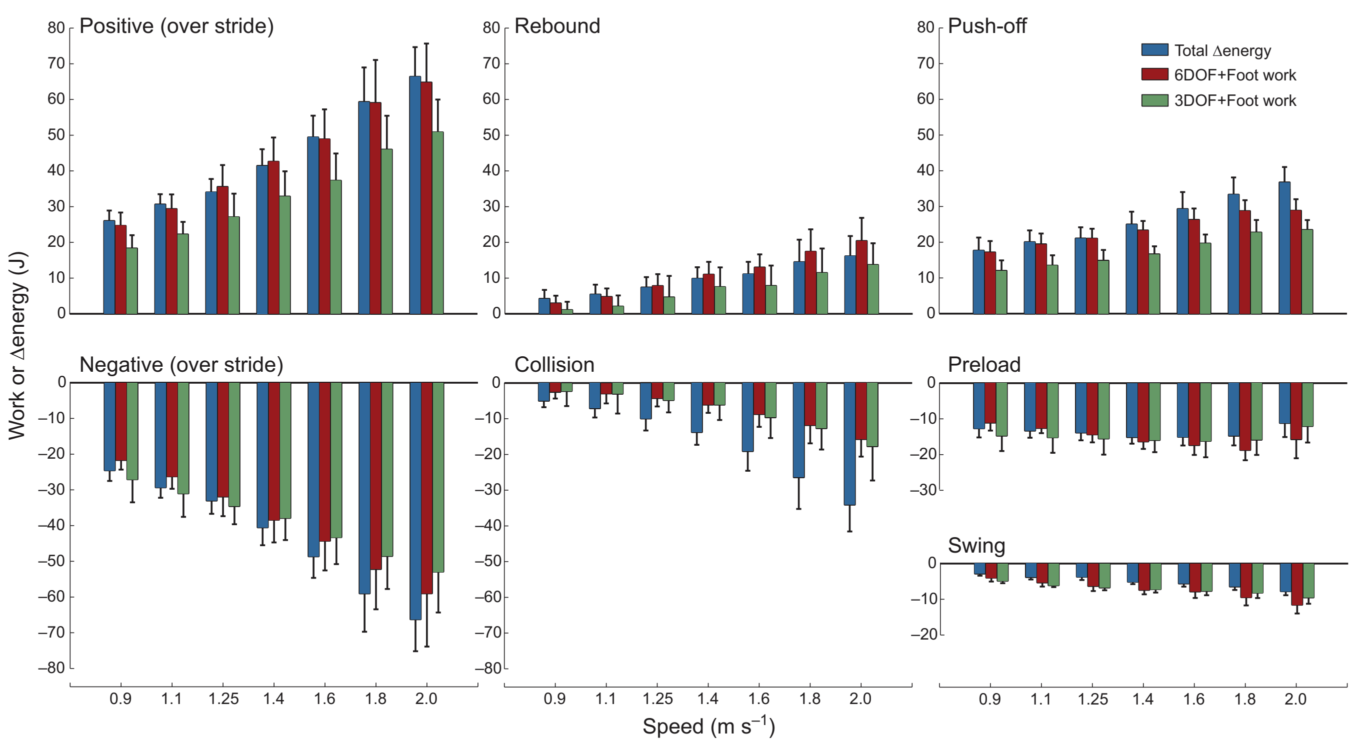

Fig. 5. Mechanical work and energy change across walking speed. Summary measures (means and s.d.) are reported for each phase of gait, and for positive and negative work and Total energy change of a single leg over the entire gait cycle for gait speeds from 0.9 to 2 m s^{-1} (N=9).

across the stride, especially at slower speeds. However, a slight degradation in the correspondence of Push-off was observed at higher speeds (>1.4 m s^{-1}). For example, during Push-off, Total energy change and 6DOF+Foot work were in strong agreement at 1.25 m s^{-1} (21.1±3.1 versus 20.5±2.7 J, P=0.51), but less so at 1.6 m s^{-1} (28.5±4.7 versus 25.7±3.1 J, P=0.01).

DISCUSSION

We integrated various biomechanical analyses to investigate unmeasured positive work during walking. We discovered that the missing work could be explained by extending 3DOF inverse dynamics to 6DOF analysis of the hip, knee, ankle and foot (6DOF+Foot). Our results reaffirm the importance of foot contributions to gait, and revealed that hip Push-off work may be >50% higher than conventionally estimated by 3DOF inverse dynamics. Below, we discuss how these findings advance our biomechanical understanding of human walking, and the implications for experimental and computational research, clinical gait analysis and assistive technology development.

Accounting for the unmeasured positive work

6DOF+Foot work explained the positive energy changes of/about the body's COM during walking, specifically during gait phases when conventional 3DOF estimates failed to capture much of the body's kinetics (Fig. 3). To our knowledge, this is the first experimental study to reconcile joint- and segment-level positive work generation with the overall energy changes of the body. Previous attempts have demonstrated partial agreement in these estimates, but only during limited portions of the gait cycle (e.g. Winter, 1979). Our findings provide novel and compelling evidence that the 6DOF+Foot approach gives a more accurate and complete estimate of how work is distributed amongst various physiological sources. These improved estimates of biomechanical work advance our empirical knowledge of gait and have potential implications for: (1) assistive technologies (e.g. prostheses, orthoses) that are frequently designed to mimic biological function (Au et al., 2007; Dollar and Herr, 2008; Goldfarb et al., 2013; Lenzi et al., 2013), (2) musculoskeletal simulations of locomotion that are optimized based on empirical biomechanical estimates (Delp et al., 2007; Neptune et al., 2001; Umberger, 2010) and (3) surgical decision-making that relies, in part, on clinical gait analysis and the calculation of joint kinetics to prescribe a surgical plan (e.g. for children with cerebral palsy; Gage, 1994; Wren et al., 2011).

The 6DOF+Foot work estimates were generally in strong agreement with positive changes in Total energy, across subjects and gait speeds (Fig. 5); however, at the highest speeds, we did find that 6DOF+Foot Push-off work corresponded slightly less well (Fig. 5). Differences between Total energy change and 6DOF+Foot work at higher speeds might be due to skin motion artifacts, or larger contributions from the swing limb or from (unmeasured) trunk/arm movement (e.g. a 3 cm vertical excursion of a single arm's COM would contribute about 1 J to raising the body's COM, based on standard anthropometric tables; Winter, 2005). Nevertheless, 6DOF+Foot estimates were consistently found to outperform 3DOF+Foot estimates across all speeds, with the best correspondence to Total energy change at low to moderate speed (Fig. 5).

Key scientific implications

6DOF+Foot results indicated that hip muscles and tendons may play a larger role in positive work production than previously estimated (Figs 2 and 4). Much of this hip work is likely due to active muscle contractions, based on the following observations. First, over the gait cycle, we calculated substantially more positive hip work than negative, suggestive of work generated by muscle (although not conclusive because of unknown biarticular muscle–tendon contributions). Second, there was no negative hip work (from either the ipsilateral or contralateral side) immediately preceding the positive Rebound work, which might have been indicative of tendinous energy storage followed by elastic energy return. In contrast, during Push-off, positive hip work might be partially due to elastic tissues (given the preceding negative hip work during Preload). Given the morphology of the hip socket (Cereatti et al., 2010), the intra-joint forces (Ren et al., 2008) and the cartilage thickness (Shepherd and Seedhom, 1999), it is unlikely that substantial work is performed in compression of the hip joint. The underestimate of hip work by 3DOF inverse dynamics may result from methodological limitations (e.g. related to tracking of thigh or pelvic segments). Of all the joints, the hip is perhaps most susceptible to inaccuracies from joint center mislocation, in part due to the inability to place anatomical markers both laterally and medially. Techniques such as functional joint center estimation (Schwartz and Rozumalski, 2005) have been developed to aid joint localization and might improve 3DOF hip work estimates, but this requires future study.

Increased hip work has potential implications for how we think about economy of locomotion. Elasticity of the Achilles tendon is typically credited as an energy-saving mechanism (Farris and Sawicki, 2012b; Lichtwark et al., 2007) that acts as the primary source of Push-off work at low to moderate walking speeds (Fukunaga et al., 2002; Ishikawa et al., 2005). Hip powering is often considered a less economical strategy because of the hip's muscle–tendon architecture (Sawicki and Ferris, 2009) and inability to effectively redirect the body during the step-to-step transition (Kuo, 2002; Zelik et al., 2014). However, we found ~9 J of hip Push-off work, which was significantly higher than previously estimated, and a non-negligible fraction of the simultaneous ankle work (~23 J). This distribution of Push-off work, along with the positive hip work observed during Rebound, motivates us to reconsider the apparent near-optimality of human walking economy (Elftman, 1966; Zarrugh et al., 1974), and re-emphasizes the opportunity for metabolic energy savings with assistive devices that augment hip work.

Our results highlight the important contributions of the foot during gait, but also expose questions about the functional role of the negative work performed. Negative Foot work during Push-off (approximately −6 J at 1.4 m s^{-1}) was comparable to the simultaneous work performed about the knee joint (Fig. 4), indicating that foot contributions should not be neglected in understanding whole-body gait dynamics. However, our 6DOF Foot analysis was unable to identify the specific physiological tissues performing the work. The foot appears to dissipate substantial energy during Push-off (Fig. 2), consistent with previous studies (e.g. Siegel et al., 1996; Takahashi and Stanhope, 2013), which may undermine the energy-saving benefits of the Achilles tendon elastic recoil (Ishikawa et al., 2005; Sawicki and Ferris, 2008; Zelik et al., 2014). One possibility is that the foot absorbs substantial energy in rotation of the metatarsophalangeal joints (Bruening et al., 2012; MacWilliams et al., 2003), and that this dissipation is not beneficial to walking economy (Song and Geyer, 2011; Song et al., 2013). Perhaps this foot behavior is useful for other reasons (e.g. balance, conforming to non-level terrains), and it would be interesting to explore functional trade-offs. Another possibility is that the foot may not absorb as much energy as it presently appears. Current methodological limitations (e.g. not accounting for biarticular muscle function; Prilutsky et al., 1996; Sasaki et al., 2009) might result in systematic

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over-estimation of the magnitude of negative work, and thus fail to capture positive work performed by foot muscles and tendons (Kelly et al., 2015). Yet another possibility is that the foot absorption is beneficial to locomotor economy, albeit indirectly; for example, by serving as a gearing mechanism that facilitates economical force production of the calf muscles (Carrier et al., 1994) or contributing to arch support (Kelly et al., 2014). Additional studies are needed to more accurately measure foot contributions and discern these versus other possible explanations of function.

6DOF inverse dynamics

6DOF inverse dynamics has not been widely adopted by basic science or clinical research communities. This may be due to limited experimental evidence assessing the practical significance of the 6DOF approach. Few studies have sought to compare 3DOF versus 6DOF analysis of biological joints. Two studies found relatively small (∼5–7%) differences in ankle Push-off work (Buczek et al., 1994; Takahashi et al., 2014), similar to 3DOF versus 6DOF ankle differences observed here (Fig. 4). Duncan et al. (1997) found larger differences for 3DOF versus 6DOF work when summing across hip, knee and ankle joints during stair ascent/descent. They found that 6DOF joint work estimates were more consistent with the work done to raise/lower the body's COM; however, their 6DOF work estimates still did not completely explain the net work performed against gravity, perhaps because of neglected foot contributions. Here, we build upon these prior studies and present evidence that 6DOF+Foot estimates can account for the Total positive energy changes of the body during walking. We found 6DOF versus 3DOF joint work differences to be of the order of a few joules (Fig. 4), which may be clinically and/or scientifically relevant. For example, in hemiparetic gait, the measured differences in hip work between the affected versus unaffected limb are about 2–3 J (Olney and Richards, 1996), and similar joint work differences have been observed when comparing the gait of younger versus older adults (Winter et al., 1990).

6DOF inverse dynamics may also provide practical benefits over more traditional 3DOF estimates. Unlike 3DOF analysis (Holden and Stanhope, 1998; Stagni et al., 2000; Zelik and Kuo, 2010), 6DOF analysis is not sensitive to the estimated joint center location (Buczek et al., 1994). Interpretation of the translational terms of 6DOF analysis may nevertheless be challenging because of the multiple possible sources of work (e.g. compression of joint cartilage, inaccurate rigid-body assumptions, rotational dynamics missed as a result of joint center mislocation that then appear in the translational work term). These interpretations may require further analysis or additional experiments to be distinguished. As conventional 3DOF rotational joint estimates are contained within the 6DOF analysis, no information or interpretative capabilities are lost. 6DOF analysis simply provides a more complete picture. There continues to be a need to improve methodologies that link our empirical joint- and segment-level biomechanical work estimates to specific physiological sources (e.g. muscle fascicles).

Current versus previous analysis of work during walking

We re-analyzed walking data from Zelik and Kuo (2010), and thus it is worth briefly summarizing the similarities and differences observed in the previous versus current study. The previous investigation compared 3DOF hip–knee–ankle joint work with COM energy change (previously referred to as COM work) during the Stance phase of walking, and thus did not include estimates of Peripheral work or Foot work, both of which were estimated in this current study. The main finding of the previous study was that 3DOF hip, knee and ankle work estimates failed to capture substantial negative work during the Collision phase of walking, and that this unmeasured work might be due to soft tissue deformations in the body. The 6DOF+Foot results presented here corroborate this finding (Fig. 2A), and recent studies have begun to tease out specific contributions from visceral bouncing (Cazzola, 2010; Daley et al., 2013) and heel pad compression (Pain and Challis, 2001). Further research is needed to identify spatiotemporal contributions from other soft tissues.

We did observe some differences in the Rebound phase. Missing positive work was previously observed during Rebound, and considered as a possible indication of elastic recoil of soft tissues after Collision. In the current study, we discovered that this missing work was mostly or completely reduced for each subject when we used 6DOF+Foot estimates, due principally to increased hip work contributions (Fig. 2). This suggests that passive tissues may not contribute substantial positive work during Rebound in walking (i.e. the viscously damped response of soft tissues may be relatively small at slow to moderate speed; Fu et al., 2014), although this conclusion would benefit from more direct empirical validation. Our updated interpretation highlights that using the 6DOF+Foot methodology is not simply about improving the accuracy of measurement but can impact our scientific understanding and conclusions.

3DOF joint work and COM energy change were previously observed to be in relatively good agreement during Push-off (Zelik and Kuo, 2010); however, in retrospect it is unclear why these work values corresponded so well, or whether this was simply coincidental. Here, we present a more complete estimate of lower-limb contributions by including the foot segment, which performs substantial negative work during Push-off. We demonstrated that 3DOF+Foot Push-off work was significantly lower than the positive changes in Total energy of the body, and also significantly lower than COM energy changes alone (i.e. even when Peripheral energy was ignored). 6DOF+Foot work was necessary to account for Total Push-off.

Energy-Accounting analysis

Energy-Accounting analysis compares Total energy change estimates with Joint+Segment work estimates as a way of evaluating the completeness of our empirical biomechanical measures. This Energy-Accounting approach provides a unified framework for understanding biomechanical work at the level of joints and body segments, whether in humans or in other animals. Each individual power and rate of energy change estimate – COM, Peripheral, 3DOF, 6DOF and Foot – has its own limitations, some of which are described during equation derivations in Materials and methods. Below, we expand upon these methodological considerations. This section is not intended to be an exhaustive analytical discussion of methodological assumptions/limitations; rather, it summarizes what these empirical estimates capture (and miss) in practice.

Joint+Segment work and Total energy change estimates both capture much of the body's dynamics; however, there are several limitations and differences to acknowledge. Inverse dynamics assumes rigid-body segments and thus misses (or incorrectly estimates) work to some degree because of non-rigid segment deformations and imperfect estimates of segmental mass, inertia and kinematics (and joint center mislocation for 3DOF analysis). The Joint+Segment approach, in general, fails to measure work done elsewhere in the body – for example, due to passive wobbling of viscera, or the motion of unmeasured joints/segments (e.g. trunk and arms in this study). However, the soft tissue deformations (outside the foot) are expected to contribute little during phases of positive work production in walking (e.g. Push-off), given their viscoelastic

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properties and inability to perform net positive work (Zelik and Kuo, 2010). COM energy and Foot work estimates do not rely on the same rigid-body assumptions and therefore capture contributions from muscles and tendons about the joints as well as by other soft tissues in the body and foot, respectively. Peripheral energy changes reflect body movements relative to the COM, assuming rigid-body segments, but this estimate fails to capture energy changes due to non-rigid-body motion relative to each individual body segment's COM (e.g. deformation of the thigh segment that does not contribute to motion of the thigh's COM). Despite these limitations, if the body joints and segments analyzed reflect the primary contributors to movement, then we expect Joint+Segment work to agree strongly with the body's Total energy change. The key exception is during periods of substantial soft tissue work (e.g. after impacts), as this work would be largely captured by the Total estimates but largely uncaptured by the Joint+Segment approach.

We interpret discrepancies between Total energy change and Joint+Segment work as work that is not captured by inverse-dynamics-based estimates (as opposed to simply an over-estimate of the Total energy change). The magnitude of Total energy change is treated as more accurate for the following reasons. First, it has been previously demonstrated that net Total energy change is close to zero for tasks that are known to involve zero net work (e.g. jump-landing task; Zelik and Kuo, 2012). This is also supported by findings here on steady-state walking (mean net Total energy change: 0.8 J, Table 1; subject range: 0.08–1.7 J at 1.4 m s^{-1}). By contrast, neither 3DOF (hip–knee–ankle) work (DeVita et al., 2007; Zelik and Kuo, 2010) nor 3DOF+Foot work (mean: −4.8 J, Table 1; subject range: −18 to +8 J) sum to zero, indicating that some of the work performed by the body is not being captured accurately by these measures. Second, Joint+Segment estimates only reflect work from explicitly modeled/measured joints and segments, and thus miss contributions from soft tissues and other body segments; contributions that are largely captured by the Total estimate, specifically as they contribute to COM energy changes. Finally, we demonstrated that 6DOF+Foot analysis yielded results that were similar to the Total energy change, which provided additional *post hoc* support for the fidelity of this latter estimate.

We computed biomechanical work and energy measures for each limb individually in order to separately analyze the major phases of positive and negative work and energy change (Push-off and Collision, respectively), which temporally overlap and therefore largely cancel each other out for the trailing and leading limb. Various other locomotor tasks (e.g. running, hopping, jump landing) do not exhibit this simultaneous, opposing limb work and thus combined-limb analysis may be appropriate for these activities. To perform the individual-limb analysis here, we assumed that Peripheral contributions from the ipsilateral body segments (thigh, shank, foot) could be summed with ipsilateral COM energy changes, and then compared with work performed by the ipsilateral joints and foot segment. Below, we discuss this assumption during Swing and Stance phases.

During Swing phase, the ipsilateral COM energy changes (derived from ground reaction forces) are by definition zero (Fig. 2B); thus, ipsilateral Total energy change is simply equal to Peripheral contributions (due to motion relative to the body's moving COM). Meanwhile, Joint+Segment work represents swing limb contributions, which act both on and about the body's COM. Thus, these two estimates are not capturing precisely the same dynamics (i.e. they differ by the magnitude of work the swinging leg performs on the body's COM); however, in practice, this difference is relatively small for walking, as the swinging leg primarily contributes to Peripheral work (Donelan et al., 2002b). Because Peripheral energy change and Joint+Segment work estimates are based on the same segmental mass and inertia assumptions and the same estimated kinematics, we can approximate from our data the swing leg contributions to contralateral stance limb COM energy change. Subtracting Total energy change from Joint+Segment work during Swing, we can confirm that the swing limb has a relatively small influence on contralateral COM work (∼2 J at 1.4 m s^{-1}, Table 1). Nevertheless, the absolute accuracy of both Total and Joint+Segment measures is limited by non-individualized anthropometric assumptions (i.e. segmental mass and inertia).

During Stance phase, Total energy change is dominated by energy fluctuations of the COM (Fig. 2B). These energy changes are principally due to stance-limb Joint+Segment work, but are also affected by the contralateral swing leg (as discussed above) and other upper-body sources. As swing limb contributions were small compared with work performed on the body's COM, we chose to ignore them in this study. We also expected passive tissue and upper-body contributions to be minimal during most of the gait cycle. During Push-off, non-rigid-body deformations (e.g. bouncing of the viscera) are expected to be relatively small compared with the wobbling of soft tissues after footstrike impacts. We therefore expected both the ipsilateral Joint+ Segment work and the ipsilateral Total energy change measures to reflect stance limb contributions during most of Stance, except immediately after heelstrike. In summary, we considered individual-limb Energy-Accounting analysis to be a reasonable and useful approach to assess biomechanical work production during Stance and Swing in walking.

Conclusions

A well-known, but vexing issue in experimental biomechanics is that mechanical work measurements rarely (if ever) add up properly. While successful research can and has been performed by observing relative changes/trends in biomechanical estimates, the issue of unmeasured body kinetics is nonetheless restrictive and problematic for many scientific questions, as well as for clinical assessment and assistive technology development. Here, we present a unified Energy-Accounting framework for measuring and understanding biomechanical work in humans and other animals. We discovered that in order to fully account for the positive energy changes of the body during human walking, we must extend commonly used 3DOF inverse dynamics estimates to 6DOF analysis of the hip, knee, ankle and foot. This 6DOF+Foot analysis provides an improved biomechanical estimate of work production during human walking, and reveals that muscles acting about the hip may play a larger role in positive work production than previously estimated. Improved empirical estimates may inform assistive technology development, biomechanical simulations and clinical decision-making. With regards to 3DOF inverse dynamics, we conclude that it may be time to expand our biomechanical toolbox.

MATERIALS AND METHODS

Data collection

We studied mechanical work, power, energy and rate of energy change during shod, level-ground human walking. We re-analyzed data (Zelik and Kuo, 2010) for 10 healthy subjects (seven males, three females, 24± 2.5 years old, 73.5±15 kg, 1.76±0.11 m) over a range of speeds (0.9, 1.1, 1.25, 1.4, 1.6, 1.8 and 2.0 m s^{-1}). Ground reaction forces were recorded using a custom-built instrumented treadmill, which independently measured forces under each foot at 1200 Hz. Lower-limb kinematics were recorded at 120 Hz using an 8-camera motion capture system (Motion Analysis, Santa Rosa, CA, USA). Reflective markers were placed on the pelvis (sacrum and iliac spines), and bilaterally on the hip (greater trochanter), thigh (segmental triad), knee (lateral and medial epicondyles), shank (segmental triad), ankle

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(lateral and medial malleoli), heel (calcaneus) and foot (fifth metatarsal). Force data were low-pass filtered at 25 Hz and marker motion at 6 Hz (zero-lag, 3rd order Butterworth). We analyzed 40 s of data for each walking speed. Of the 70 total trials (10 subjects, seven speeds), three trials were excluded because of data acquisition issues. The study was approved by the University of Michigan Institutional Review Board and subjects provided written consent.

Energy-Accounting analysis

We performed an Energy-Accounting analysis (as summarized in the Introduction), which investigates specific sources of power and work within the body by comparing their contributions to the Total energy changes of the body (of/about the COM). The specific purpose of this analysis was to determine whether and when summed joint and foot segment power (and work) estimates account for the body's Total rate of energy change (and magnitude of energy change). Below, we define the various biomechanical estimates computed. Equations are presented in generalized form, followed by additional study-specific details.

COM power (P_{com}) reflects the rate of work done on the body's COM (Donelan et al., 2002a). It can be calculated from the 3-dimensional dot product of all ground reaction forces with COM velocity [$\sum(\vec{\mathrm{F}}_i)\cdot\vec{\mathrm{v}}_{\mathrm{com}}$; combined-limb analysis], or from the sum of the dot product of each force (e.g. ground reaction force under each individual foot) with COM velocity [$\sum(\vec{\mathrm{F}}_i\cdot\vec{\mathrm{v}}_{\mathrm{com}})$; individual-limb analysis]:

$$P_{\mathrm{com}}=\sum_{i}^{N_i}(\vec{\mathrm{F}}_i)\cdot\vec{\mathrm{v}}_{\mathrm{com}}=\sum_{i}^{N_i}(\vec{\mathrm{F}}_i\cdot\vec{\mathrm{v}}_{\mathrm{com}}). \tag{1}$$

In this study, COM velocity was integrated from the ground reaction forces, assuming steady-state, periodic strides and no energetic losses to the environment (i.e. negligible air resistance and ground deformation). COM power is also equal to the rate of energy change of the COM ($\dot{E}_{\mathrm{com}}$), as calculated by the time derivative of COM kinetic plus potential energy:

$$P_{\mathrm{com}}=\dot{E}_{\mathrm{com}}=\frac{\mathrm{d}}{\mathrm{d}t}\left(\frac{1}{2}m_{\mathrm{com}}\vec{\mathrm{v}}^{2}_{\mathrm{com}}+m_{\mathrm{com}}\boldsymbol{g}h_{\mathrm{com}}\right), \tag{2}$$

where $\boldsymbol{g}$ is gravitational acceleration and h_{com} is the height of the COM. The benefit of using Eqn 1 is discussed below.

The Peripheral rate of energy change ($\dot{E}_{\mathrm{per}}$) is due to the motion of segments relative to the body's COM. We estimated Peripheral contributions as the time derivative of changes in rotational and translational segment energy, the latter with respect to the COM (Cavagna and Kaneko, 1977; Willems et al., 1995):

$$\dot{E}_{\mathrm{per}}=\frac{\mathrm{d}}{\mathrm{d}t}\left(\sum_{\mathrm{s}}^{N_{\mathrm{s}}}\frac{1}{2}\vec{\mathrm{I}}_{\mathrm{s}}\cdot\vec{\omega}^{2}_{\mathrm{s}}+\frac{1}{2}m_{\mathrm{s}}(\vec{\mathrm{v}}_{\mathrm{s}}-\vec{\mathrm{v}}_{\mathrm{com}})^{2}\right). \tag{3}$$

3-Dimensional segmental velocity ($\vec{\mathrm{v}}_{\mathrm{s}}$) and squared angular velocity ($\vec{\omega}^{2}_{\mathrm{s}}$) were estimated from kinematics, assuming rigid-body segments (s). Segmental mass (m_{s}) and inertia ($\vec{\mathrm{I}}_{\mathrm{s}}$) were based on a standard rigid-body anthropomorphic model (Hanavan, 1964) in Visual3D software (C-Motion, Germantown, MD, USA). The Peripheral rate of energy change was computed from the sum of foot, shank and thigh segments (N_{s}=3 for each limb in this study). We then estimated the body's Total rate of energy change as the sum of COM and Peripheral terms:

$$\dot{E}_{\mathrm{total}}=\dot{E}_{\mathrm{com}}+\dot{E}_{\mathrm{per}}. \tag{4}$$

The terms external and internal power/work were avoided because of their inconsistent definitions in literature (e.g. Cavagna et al., 1963; Fenn, 1930).

We computed 3DOF joint power (i.e. rotational power in sagittal, frontal and transverse planes) using conventional inverse dynamics. Calculations were performed for hip, knee and ankle using standard commercial software (Visual3D) and its anthropometric model. Joint centers of rotation were estimated based on regression from anatomical landmarks: the ankle from medial and lateral malleoli, the knee from medial and lateral femoral epicondyles, and the hip from the Helen Hayes pelvic marker set (Davis et al., 1991). Rotational power of the trunk and arms is relatively small at typical walking speeds (Cavagna and Kaneko, 1977; Willems et al., 1995; Winter, 1979) and was ignored in our analysis (nominally performed on walking at 1.4 m s^{-1}). We summed across hip, knee and ankle joints (j; N_{j}=3 for each limb in this study) to calculate the 3DOF joint power (P_{3d}).

$$P_{\mathrm{3d}}=\sum_{\mathrm{j}}^{N_{\mathrm{j}}}\vec{\mathrm{M}}_{\mathrm{j}}\cdot\vec{\omega}_{\mathrm{j}}, \tag{5}$$

where $\vec{\mathrm{M}}_{\mathrm{j}}$ and $\vec{\omega}_{\mathrm{j}}$ signify 3DOF external joint moments and angular velocities, respectively. This calculation assumes that all mechanical power originates from articulation of segments about fixed joint centers.

Foot power (P_{foot}) was estimated from a deformable body model because of the foot's many internal degrees of freedom (e.g. metatarsophalangeal joints, heel pad, arches). Here, the term Foot refers to everything distal to the ankle (including the shoe). This estimates 6DOF power due to compression and rotation of the Foot. As this Foot power (sometimes called 'distal foot power' in the literature) calculation has been explained in prior work (Takahashi et al., 2012), we only briefly summarize it here:

$$P_{\mathrm{foot}}=\vec{\mathrm{F}}_i\cdot\vec{\mathrm{v}}_{\mathrm{ftd}}+\vec{\mathrm{M}}_{\mathrm{free}}\cdot\vec{\omega}_{\mathrm{ft}}, \tag{6}$$

where $\vec{\mathrm{M}}_{\mathrm{free}}$ is the free moment (i.e. a vector with two columns of zeros and a then a third column representing the ground reaction moment about the vertical axis), $\vec{\omega}_{\mathrm{ft}}$ is the angular velocity of the foot, $\vec{\mathrm{F}}_i$ is the ground reaction force under the foot and $\vec{\mathrm{v}}_{\mathrm{ftd}}$, the velocity of the center-of-pressure in the foot's reference frame, is approximated as the velocity of the foot's center-of-mass plus the cross product of $\vec{\omega}_{\mathrm{ft}}$ with the vector from the foot's center-of-mass to the center-of-pressure underneath.

We defined conventional Joint+Segment power (also written as 3DOF+Foot power) as the summation of commonly used power estimates:

$$P_{\mathrm{3d+foot}}=P_{\mathrm{3d}}+P_{\mathrm{foot}}. \tag{7}$$

6DOF inverse dynamics, which includes independent estimates of both 3DOF rotational joint power and 3DOF translational joint power (i.e. accounting for linear motion along each orthogonal Cartesian direction), was also computed for the hip, knee and ankle joints. 6DOF joint power (P_{6d}) is relatively uncommon in the biomechanics literature compared with 3DOF; however, two technical publications (Buczek et al., 1994; Duncan et al., 1997) summarize the theoretical basis and benefits:

$$P_{\mathrm{6d}}=P_{\mathrm{3d}}+\sum_{\mathrm{j}}^{N_{\mathrm{j}}}\vec{\mathrm{F}}_{\mathrm{j}}\cdot(\vec{\mathrm{v}}_{\mathrm{dist}}-\vec{\mathrm{v}}_{\mathrm{prox}}), \tag{8}$$

where $\vec{\mathrm{F}}_{\mathrm{j}}$ is the internal joint force (as estimated from inverse dynamics), and $\vec{\mathrm{v}}_{\mathrm{dist}}$ and $\vec{\mathrm{v}}_{\mathrm{prox}}$ are estimates of the joint center velocity based on the distal and proximal segment motions, respectively. This 6DOF joint power relaxes the assumption in 3DOF inverse dynamics that the joint center corresponds precisely to the instantaneous center of rotation (Duncan et al., 1997). This additional translational term might be due to physical translation within the physiological joint, but might also be due to methodological limitations in estimating joint center location or movement of non-rigid-body segments (Buczek et al., 1994).

Finally, we define 6DOF Joint+Segment power (denoted 6DOF+Foot power):

$$P_{\mathrm{6d+foot}}=P_{\mathrm{6d}}+P_{\mathrm{foot}}. \tag{9}$$

We produced summary measures of mechanical work and energy change by integrating each power and rate of energy change waveform over the gait cycle, and over individual phases of gait. The gait cycle was defined as one stride from heelstrike to subsequent ipsilateral heelstrike, and phases of gait – Collision, Rebound, Preload, Push-off and Swing – were defined for each limb based on fluctuating regions of positive and negative individual-limb COM power (Zelik and Kuo, 2010). We performed individual-limb analysis, so each power/rate of energy change and each work/energy measure was computed individually for each limb. For the right leg, work/energy was computed for each individual stride. Then we found the average right leg work/energy by calculating the mean across all strides. Similar computations were performed for the left leg. We then averaged across both legs to compute subject-specific work/energy. Finally, we averaged across subjects. All 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. Average power/rate of energy change and work/energy normalization constants were $mg^{3/2}L^{1/2}$=2357 W and mgL=727 J, respectively.

We note two additional methodological considerations. First, we performed individual-limb analysis in this study, which has benefits and drawbacks. The benefit of individual-limb analysis is that it enables us to separately assess Push-off and Collision, the two major phases of positive and negative power during human walking. This cannot be accomplished using a combined-limbs approach (Donelan et al., 2002a). The drawback to individual-limb analysis is that we had to partition energy change contributions between limbs. To do so, we assumed that ipsilateral Peripheral rate of energy change could be added to ipsilateral individual-limb COM power [$(\vec{F}_i \cdot \vec{v}_{com})$ in Eqn 1, where $\vec{F}_i$ represents the ground reaction force under a single foot], to reflect contributions to changes in the energy state of the body. We then compared this ipsilateral COM+Peripheral rate of energy change with summed ipsilateral Joint+Segment power. The implications of performing individual-limb analysis are addressed further in the Discussion.

Second, we computed 6DOF inverse dynamics as an extension of the 3DOF approach, and thus used segmental motion estimates that were not fully independent. In 3DOF inverse dynamics, it is common to track segmental motions using marker sets that may share markers with an adjacent segment. Of the seven markers used in this study to track the shank and six markers used to track the thigh, two markers at the knee were shared between the two segments. Technically, for 6DOF inverse dynamics, each segmental motion should be computed from independent marker clusters (Buczek et al., 1994). However, this is incompatible with various commonly used marker sets (e.g. Helen Hayes) that do not include three independent tracking markers per segment. To maintain broad applicability to clinical gait research, we performed 6DOF analysis based on the standard 3DOF segmental motion-tracking techniques, similar to Duncan et al. (1997).

In summary, while there are limitations to each biomechanical calculation, they provide complementary estimates that allow us to assess the completeness of our empirical measures. Specifically, they allow us to determine whether and when the joint- and segment-level work sources in the body can explain whole-body energy changes. Identifying discrepancies between these estimates is useful regardless of whether they are due to methodological limitations, measurement inaccuracy or unmeasured physiological sources.

Statistics

Statistical comparisons for Total energy change versus 3DOF+Foot work versus 6DOF+Foot work, and for 3DOF versus 6DOF joint work were performed using repeated measures analysis of variance with Holm–Sidak correction and a significance level of 0.05. Primary analysis was performed for a nominal gait speed of 1.4 m s^{-1}.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
All authors contributed to the conception and design of the research, data interpretation and manuscript preparation. In addition K.E.Z. and K.Z.T. contributed to data analysis.

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