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RESEARCH ARTICLE

Soft tissue deformations explain most of the mechanical work variations of human walking

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ABSTRACT

Humans perform mechanical work during walking, some by leg joints actuated by muscles, and some by passive, dissipative soft tissues. Dissipative losses must be restored by active muscle work, potentially in amounts sufficient to cost substantial metabolic energy. The most dissipative, and therefore costly, walking conditions might be predictable from the pendulum-like dynamics of the legs. If this behavior is systematic, it may also predict the work distribution between active joints and passive soft tissues. We therefore tested whether the overall negative work of walking, and the fraction owing to soft tissue dissipation, are both predictable by a simple dynamic walking model across a wide range of conditions. The model predicts whole-body negative work from the leading leg's impact with the ground (termed the collision), to increase with the squared product of walking speed and step length. We experimentally tested this in humans (N=9) walking in 26 different combinations of speed (0.7–2.0 m s^{-1}) and step length (0.5–1.1 m), with recorded motions and ground reaction forces. Whole-body negative collision work increased as predicted (R^2=0.73), with a consistent fraction of approximately 63% (R^2=0.88) owing to soft tissues. Soft tissue dissipation consistently accounted for approximately 56% of the variation in total whole-body negative work, across a wide range of speed and step length combinations. During typical walking, active work to restore dissipative losses could account for 31% of the net metabolic cost. Soft tissue dissipation, not included in most biomechanical studies, explains most of the variation in negative work of walking, and could account for a substantial fraction of the metabolic cost.

KEY WORDS: Inverse dynamics, Dissipation, Heel strike, Wobbling mass, Pendulum model, Metabolic cost

INTRODUCTION

Human walking incurs a metabolic energy cost in part because the muscles perform positive work to counter the negative work within each stride. There is currently no mechanistic prediction for how much work is performed, except that the positive and negative work of a steady stride cancel each other, so that one could be considered predictive of the other. Some of the negative work occurs actively when muscles act eccentrically to lengthen under load, and some occurs as passive dissipation from soft tissue deformations (Fig. 1A). Passive dissipation may account for 31% of the negative work of typical walking (Zelik and Kuo, 2010), but its distribution relative to active negative work is not known for more general walking conditions. However, walking patterns have been observed to scale quite consistently across a wide range of gait parameters (Grieve, 1968), with predictable total negative work (Adamczyk and Kuo, 2009). This suggests that the amount of passive dissipation and active negative work may be predictable across gait conditions. Such predictability could provide insight into when muscles actively perform both positive and negative work and thus consume metabolic energy (Abbott et al., 1952; Margaria, 1968).

One of the critical events of walking is the impact of the leg with the ground after the swing phase (termed heel strike). After heel strike, the leading leg performs negative work (during a phase termed collision) as the body center of mass (COM) velocity is redirected from a forward-and-downward direction from the previous stance phase, to a forward-and-upward direction at the beginning of the next (Adamczyk and Kuo, 2009; Kuo et al., 2005). For typical walking at 1.25 m s^{-1}, approximately 12.5 J of negative work is done during collision within the first 15% of the stride, with contributions from active muscle tendons and passive soft tissues (approximately 40% and 60%, respectively; Zelik and Kuo, 2010). The soft structures responsible for the dissipation are thought to include the foot and shoe (Honert and Zelik, 2019), particularly the heel pad (approximately 3.8 J; Baines et al., 2018), as well as the shank (Pain and Challis, 2001). Some passive dissipation may also occur with loading of articular cartilage (Hayes and Mockros, 1971) and intervertebral discs (Virgin, 1951), and from inertial loading of wobbling mass, for example muscle (Schmitt and Günther, 2011) and viscera (Minetti and Belli, 1994). Soft tissue dissipation appears to vary consistently with overall collision work, for example in obese and non-obese adults (Fu et al., 2015), and even for landing from a jump (Zelik and Kuo, 2012). The overall collision work accounts for most of the negative (and thereby positive) work of a stride (Zelik and Kuo, 2010), but it is unknown how it varies with gait conditions, and particularly how much of it is due to soft tissue dissipation.

The remainder of the stride appears to be systematically related to collision. Negative work during collision is followed by alternating phases of positive and negative work by the whole body. The work done during these phases (termed rebound, pre-load and push-off during stance; Donelan et al., 2002) increases in proportion to collision work during walking at preferred step length (Zelik and Kuo, 2010). These alternating phases resemble the oscillation of a purely elastic spring for each leg (Geyer et al., 2006), excited by ground contact. That action is not literally performed by springs, but by a combination of active muscle tendons and passive soft tissues. The oscillation-like behavior suggests that muscles are actively controlled as a function of dynamical state, so that the entire body acts like a consistent dynamical system. The negative work of an entire stride might therefore vary systematically with the magnitude of collision work, and across a variety of gait conditions.

The amount of collision work, and by extension of the entire stride, may actually be predictable (Fig. 1). A simple dynamic

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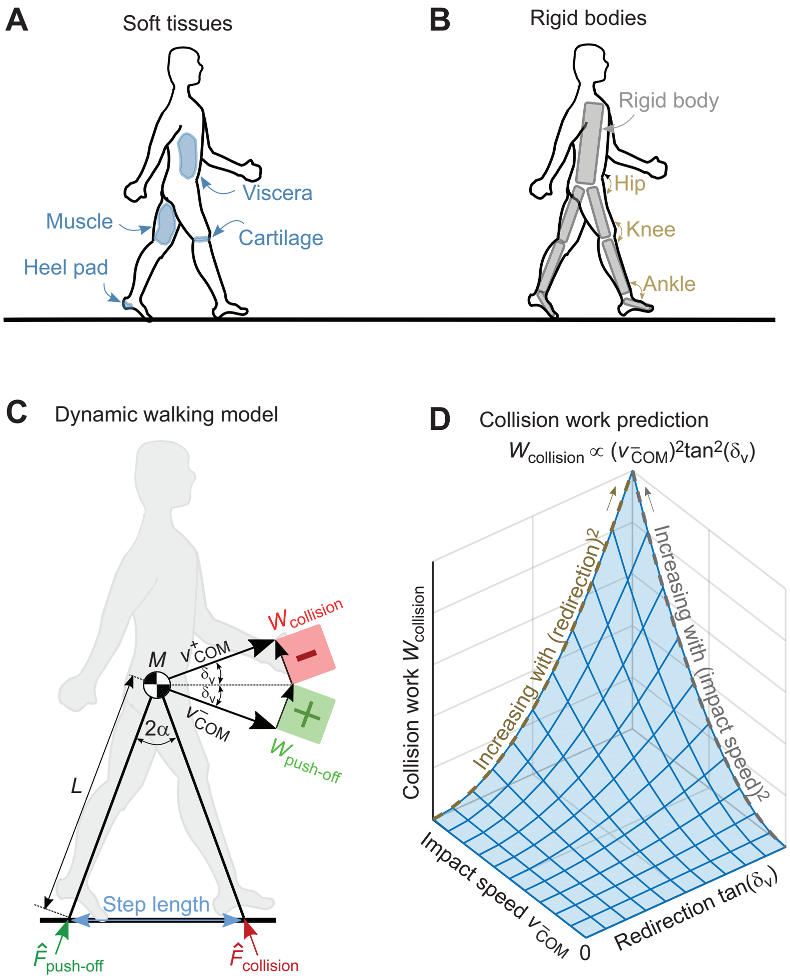

Fig. 1. Soft tissues, rigid bodies and negative work predicted by simple dynamic walking model. (A) Soft tissues such as viscera, muscle, cartilage and heel pad can dissipate energy by delivering force while deforming and/or displacing. (B) Rigid bodies are traditionally used for estimating joint torques and work (rates), using an approach referred to as inverse dynamics. (C) Dynamic walking model predicts negative collision work $W_{\text{collision}}$ at heel strike from center of mass (COM) velocity v_{COM}. A portion of this negative work may be due to soft tissue dissipation. (D) Predicted collision work $W_{\text{collision}}$ increases with impact speed v^{-}_{COM} squared multiplied by the squared tangent of COM velocity angular direction change δ_v. For a fixed speed, collision work should increase with redirection alone (dashed brown line), and for a fixed redirection, with impact speed alone (dashed grey line).

walking model predicts how work must be performed on the body COM to redirect its velocity between inverted pendulum stance phases (Kuo, 2001), forward-and-downward at the end of one arc, to forward-and-upward at the beginning of the next. This is achieved by negative collision work with the leading leg, and positive push-off work from the trailing leg. The collision work varies with gait parameters such as walking speed, step length and step frequency (Adamczyk and Kuo, 2009), as predicted by the simple model (Kuo, 2001). The work of the other phases may vary in proportion to the collision work, if part of a dynamical system. Similarly, the active and passive work may also vary in proportion to the collision work. The soft tissue dissipation during collision and the total negative work over a full stride might therefore be proportional to predictions from the simple dynamic walking model.

The purpose of the present study was to test whether negative work is systematically distributed between active and passive contributions, and across the entire stride for a wide range of walking conditions. The starting point for this inquiry is the whole-body collision work, as previously modeled and characterized across gait parameters such as step length and step frequency (Adamczyk and Kuo, 2009). For active versus passive contributions, we hypothesized that (passive) soft tissue dissipation during collision would remain a consistent fraction of the whole-body collision work predicted by model. And for the entire stride, we hypothesized that whole-body collision work would remain a consistent fraction of the negative work over a full stride. We tested these predictions with a human walking experiment, in which whole-body and soft tissue work were estimated for 26 different combinations of gait parameters, including a range of walking speeds while constraining step length and/or step frequency. The results may indicate whether simple dynamic walking models can predict both the amount and distribution of negative work during human walking.

MATERIALS AND METHODS

We used a simple dynamic walking model to predict the collision work during walking, and tested whether it was predictive of soft tissue dissipation during collision, as well as to overall negative work for the full stride. We tested predictions against experimental data on human subjects walking across a wide range of combinations of walking speed and step length. The testing data included rigid body mechanical work rate from inverse dynamics (see Fig. 1B), as well as whole-body and soft tissue mechanical work rates from a previously reported procedure based on COM work and motion capture (Zelik and Kuo, 2010, 2012). We next present the model predictions, followed by the experimental tests.

Model predictions

Predictions for negative collision work $W_{\text{collision}}$ were produced from a simple dynamic walking model (Adamczyk and Kuo, 2009; Kuo, 2001) (see Fig. 1C). The stance leg is treated as a simple inverted pendulum with length L and body mass M concentrated at the pelvis, and the swing leg as a simple pendulum with length L and an infinitesimal mass point foot. When the swing leg hits the ground, a collision impulse $\hat{F}_{\text{collision}}$ does negative collision work

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$W_{\mathrm{collision}}$ on the COM:

$$W_{\mathrm{collision}} \propto \frac{1}{2} M \cdot (v_{\mathrm{COM}}^{-})^2 \cdot \tan^2(\delta_v), \quad (1)$$

where M is the body mass, v_{COM}^{-} the pre-impact COM speed and δ_v the COM velocity angular direction change (Fig. 1C). The collision work $W_{\mathrm{collision}}$ in humans is hypothesized to increase similar to that of the simple model, with an empirical proportionality owing to unmodeled effects such as imperfectly rigid legs, distributed body mass and a finite-length (as opposed to point) foot (Adamczyk et al., 2006). The collision work may thus be regarded as a function of impact speed v_{COM}^{-} and COM velocity redirection $\tan(\delta_v)$ (Fig. 1D).

We hypothesize that the mechanical work of walking is distributed systematically between active joints and passive soft tissues, and across the time of a stride. Both soft tissues and joints (actuated by active muscles in series with tendons) contribute to whole-body collision work. If the distribution is systematic, the soft tissue negative work during collision $W_{\mathrm{soft,collision}}$ will be responsible for a consistent fraction of the collision work $W_{\mathrm{collision}}$:

$$W_{\mathrm{soft,collision}} \propto W_{\mathrm{collision}}. \quad (2)$$

Systematic distribution also means work should be distributed proportionately within a stride. This means that total negative work over the entire stride W_{stride} will change in proportion to collision work $W_{\mathrm{collision}}$:

$$W_{\mathrm{stride}} \propto W_{\mathrm{collision}}. \quad (3)$$

These hypotheses lead to several expectations for human experiments. For collision work $W_{\mathrm{collision}}$, we introduce an empirical coefficient $c_{\mathrm{collision}}$ for the proportionality Eqn 1:

$$W_{\mathrm{collision}} = c_{\mathrm{collision}} \cdot \frac{1}{2} M \cdot (v_{\mathrm{COM}}^{-})^2 \cdot \tan^2(\delta_v). \quad (4)$$

For soft tissue collision work $W_{\mathrm{soft,collision}}$, its proportionality to whole-body collision work $W_{\mathrm{collision}}$ (Eqn 2) results in the expectation:

$$W_{\mathrm{soft,collision}} = c_{\mathrm{soft}} \cdot \frac{1}{2} M \cdot (v_{\mathrm{COM}}^{-})^2 \cdot \tan^2(\delta_v), \quad (5)$$

with coefficient c_{soft}. The work of a stride may vary with collision (Eqn 3), but there may also be work within a full stride not related to collision. For example, the knee performs negative work to decelerate the swing leg, which has little effect on the COM. Such contributions are expected to have little or no dependency on the COM velocity, and are therefore lumped into a single constant offset d_{stride}:

$$W_{\mathrm{stride}} = c_{\mathrm{stride}} \cdot \frac{1}{2} M \cdot (v_{\mathrm{COM}}^{-})^2 \cdot \tan^2(\delta_v) + d_{\mathrm{stride}}. \quad (6)$$

Altogether, we expect that soft tissues contribute to collision work $W_{\mathrm{collision}}$, with a remainder explained by active joints. We expect that collision work $W_{\mathrm{collision}}$ contributes to full stride negative work W_{stride}, with a remainder due to negative work during other phases (e.g. pre-load, swing). We therefore expect soft tissue collision work $W_{\mathrm{soft,collision}}$ to be smaller than collision work $W_{\mathrm{collision}}$, which we expect to be smaller than full stride negative work W_{stride}, such that $c_{\mathrm{stride}}>c_{\mathrm{collision}}>c_{\mathrm{soft}}$. We test for c_{stride}, $c_{\mathrm{collision}}$ and c_{soft} using regression on experimental data. As this set of predictions depends entirely on COM velocity (i.e. v_{COM}^{-} and δ_v), we refer to it as velocity-based predictions.

In addition, we tested another set of gait-based predictions that do not require velocity data. Gait parameters such as average speed $\bar{v}$ and step length s are usually more readily available than instantaneous COM velocity data, and can also serve as predictors. This requires an additional set of assumptions, that average speed $\bar{v}$ and step length s are proportional to impact speed v_{COM}^{-} and COM velocity redirection $\tan(\delta_v)$, respectively. With a small angle approximation, step length is proportional to the inter-leg angle α (Fig. 1C), which should equal δ_v, and with another small angle approximation, $\tan(\delta_v)$. Thus, all gait-based predictions are:

$$W_{\mathrm{collision}} = c'_{\mathrm{collision}} \cdot \frac{1}{8} \frac{M}{L^2} \cdot \bar{v}^2 \cdot s^2, \quad (7)$$

$$W_{\mathrm{soft,collision}} = c'_{\mathrm{soft}} \cdot \frac{1}{8} \frac{M}{L^2} \cdot \bar{v}^2 \cdot s^2, \quad (8)$$

$$W_{\mathrm{stride}} = c'_{\mathrm{stride}} \cdot \frac{1}{8} \frac{M}{L^2} \cdot \bar{v}^2 \cdot s^2 + d'_{\mathrm{stride}}, \quad (9)$$

where the prime symbol (′) refers to gait-based predictors. As with the original coefficients, we expect that $c'_{\mathrm{stride}} > c'_{\mathrm{collision}} > c'_{\mathrm{soft}}$, tested using regression on experimental data. We also expect reduced accuracy with gait-based compared with velocity-based predictions, especially in gait conditions where the small angle approximation is less accurate.

Experimental procedures

Healthy adult subjects (N=9, body mass M=73.5±15 kg, leg length L=0.93±0.06 m, age 23.5±2.5 years, means±s.d.) walked on an instrumented treadmill at 26 different combinations of walking speed and step length. The combinations belonged to four experimental conditions: (1) preferred walking at varying walking speeds $\bar{v}$; (2) fixed frequency at varying step lengths s; (3) fixed step length at varying frequencies f; and (4) fixed average speed with inversely varying combinations of step length and step frequency (see Table 1). Step length s and step frequency f were varied relative to the preferred values s* and f*, determined from unconstrained walking at a nominal speed (v*=1.25 m s^{-1}). Walking speed $\bar{v}$ and step frequency f were manipulated by setting the treadmill belt speed and asking subjects to walk on the beat of an audio cue, respectively. Step length s was manipulated through both walking speed and step frequency from their ratio $s = \bar{v}/f$. The order of trials was randomized for each subject individually, who were earlier familiarized with each of the conditions during a 6-min practice trial. Subjects provided their written informed consent to participate in the experiment, which was approved by the Institutional Review

Table 1. Experimental walking conditions

Condition	Variable parameter	Constrained parameter	Negative work prediction
Preferred walking	$\bar{v}$: 0.56v*, 0.72v*, 0.88v*, 1.00v*, 1.12v*, 1.28v*, 1.44v*, 1.60v*	None	$W \propto \bar{v}^{2.84}$
Fixed step frequency	s: 0.56s*, 0.72s*, 0.88s*, 1.00s*, 1.12s*, 1.28s*, 1.44s*	f=f*	$W \propto s^4$
Fixed step length	$\bar{v}$: 0.56v*, 0.72v*, 0.88v*, 1.00v*, 1.12v*, 1.28v*, 1.44v*	s=s*	$W \propto \bar{v}^2$
Fixed speed	f: 0.70f*, 0.80f*, 0.90f*, 1.00f*, 1.10f*, 1.20f*, 1.30f*	$\bar{v}$=v*	$W \propto s^2$

Each of four experimental conditions including preferred walking with no constraint, and others constraining one of frequency f, step length s or average walking speed $\bar{v}$. These gait parameters yield a prediction of negative work W, according to a dynamic walking model. Asterisks indicate nominal/preferred.

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Board of the University of Michigan, where the experiment was performed.

We also used the gait-based coefficients c'_{stride}, $c'_{\text{collision}}$ and c'_{soft} to evaluate condition-specific predictions. For preferred and fixed step length walking, step length s is expected to increase with $\bar{v}^{0.42}$ (Grieve, 1968) and $\bar{v}^0$, respectively, so that the predicted negative work per stride increases with $\bar{v}^{2.84}$ and $\bar{v}^2$, respectively (Eqns 7–9; see Fig. 2 and Table 1). For fixed step frequency and fixed speed walking, average speed $\bar{v}$ increases with s^1 and s^0, respectively, so that the predicted negative work increases with s^4 and s^2, respectively (Eqns 7–9).

Human experiment

We used ground reaction forces and motion capture to estimate work performed by the body, including rigid body and soft tissue work. Ground reaction force F_{gr} was measured from treadmill force plates (Bertec, Columbus, OH, USA) at 1200 Hz and low-pass filtered at 25 Hz. Instantaneous COM velocity v_{COM} was determined from integrating the ground reaction force F_{gr} assuming periodicity of strides. In short, we linearly detrended the ground reaction force–time integral over an integer number of strides, assuming the average medio-lateral and vertical components of the COM velocity to be zero, and the average fore–aft component to equal the treadmill belt speed. Center of mass work rate ($\dot{W}_{\text{COM}}$) was determined from the dot product of each leg's ground reaction force F_{gr} and the detrended COM velocity v_{COM} (Donelan et al., 2002). In addition to ground reaction force measurements, motions of the lower limbs were captured at 120 Hz using a standard 3D motion capture system (Motion Analysis Corporation, Santa Rosa, CA, USA). Cluster markers were attached to the feet, shanks and thighs. Single markers were located at the head of the fifth metatarsus, left and right malleoli, left and right epicondyles, greater trochanter, left and right anterior superior iliac spine, and sacrum. Ankle, knee and hip joints were defined based on locations of malleoli, epicondyles and Helen Hayes (Davis) points, respectively (Davis et al., 1991). Ground reaction force and motion capture measurements were used in standard inverse dynamic analysis (Visual 3D, C-Motion, Germantown, MD, USA) for computing the joint angles, translational displacements, torques, forces and work rates in the ankle, knee and hip. The joint work rates were summed across joints to yield overall rigid body work rate $\dot{W}_{\text{rigid}}$ (also referred to as summed joint power using six-degree-of-freedom joints, e.g. Honert and Zelik, 2019). In addition, the segmental kinetic energies of the feet, shanks and thighs were computed assuming rigid bodies. At least five strides from each condition were analyzed per participant, selected to avoid motion capture occlusions and steps that landed on both force plates. Some of the trials could not be analyzed (five out of 324) owing to missing data (two), incorrect stepping (one) or synchronization error (two). These occasions all belonged to different subjects, and to different conditions. An additional (10th) subject was recorded in experiment but excluded from analysis owing to incorrect pelvis marker placement.

The resulting data were then used to estimate work quantities, as described previously (Zelik et al., 2015; Zelik and Kuo, 2010). Whole-body work rate $\dot{W}_{\text{body}}$ was defined as the COM work rate $\dot{W}_{\text{COM}}$ plus the peripheral work rate $\dot{W}_{\text{peri}}$, defined as the sum of all unilateral segmental kinetic energy fluctuations about the COM. The trunk and upper limbs contribute relatively little to walking (Vaughan et al., 1992), and so we limited our segmental analysis to the lower limbs (Fu et al., 2015). Whole-body work rate $\dot{W}_{\text{body}}$ typically becomes negative during collision starting at heel strike, then becomes positive during rebound until mid-stance, when it becomes negative during pre-load, before a final positive-work push-off at the end of stance (Donelan et al., 2002). The phases other than collision are mainly used for qualitative illustrative purposes, although pre-load and swing contribute to the overall negative work of a stride W_{stride}. Collision was defined as the interval between heel strike and the instant of the steepest upward COM velocity (Adamczyk and Kuo, 2009). Soft tissue work rate $\dot{W}_{\text{soft}}$ was determined from the discrepancy between rigid body work rate $\dot{W}_{\text{rigid}}$ and whole-body work rate $\dot{W}_{\text{body}}$ (Zelik et al., 2015; Zelik and Kuo, 2010). All work rates were calculated for each leg individually and then averaged between legs.

The primary work quantities of interest were collision work $W_{\text{collision}}$, soft tissue collision work $W_{\text{soft,collision}}$ and total negative work over the entire stride W_{stride}. Collision work $W_{\text{collision}}$ and soft tissue collision work $W_{\text{soft,collision}}$ were obtained by time-integrating whole-body work rate $\dot{W}_{\text{body}}$ and soft tissue work rate $\dot{W}_{\text{soft}}$, respectively, for the negative intervals of $\dot{W}_{\text{body}}$ during collision. Total negative work per stride W_{stride} was obtained from time-integrating whole-body work rate $\dot{W}_{\text{body}}$ during the intervals when it was negative. All of these work quantities were negative and are reported as magnitudes and computed as work per stride to facilitate comparison with the simple dynamic walking model. All kinetic

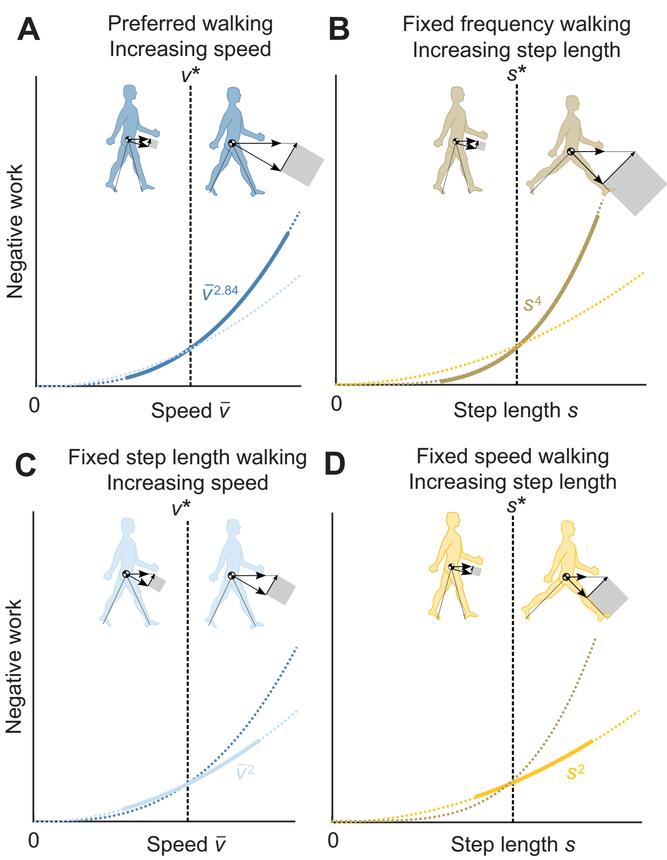

Fig. 2. Predictions of negative work during walking. (A) Preferred walking: assuming the empirical preferred step length relationship (Grieve, 1968), negative work increases with (speed)$^{2.84}$. (B) Fixed frequency: if speed increases linearly with step length, negative work increases with (step length)^4. (C) Fixed step length: if speed increases linearly with step frequency, negative work increases with (speed)^2. (D) Fixed speed: if step length and frequency vary inversely at fixed speed, negative work increases with (step length)^2. These relationships are predicted to apply to whole-body collision work, soft tissue collision work and total negative work over a full stride. Here, walking speed is treated as roughly proportional to impact speed, and step length proportional to redirection (Fig. 1).

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quantities were computed in normalized units, using base units of body mass M, leg length L and gravitational acceleration $\boldsymbol{g}$. Average normalized quantities were then plotted in terms of both dimensional units (left axes), and with base units shown (right axes).

RESULTS

The measured quantities generally exhibited qualitatively systematic variations with the gait conditions. For example, sagittal plane joint angle, torque and rotational work rate during walking at constant step frequency and increasing step length generally increased in amplitude with walking speed (see Fig. 3). Each joint's contribution may be inferred by comparing its work rate with the rigid body work rate (see Fig. 4A). Each joint contributed differently to rigid body work rate, with mainly positive contributions from the ankle, negative contributions from the knee and mixed contributions from the hip. Whole-body and rigid body work rates were similar in shape, but different in amplitude during preferred walking at 1.25 m s^{-1} (compare Fig. 4A and B) and other gait conditions (see Figs S1 and S2). These work rates and their difference were used to determine whole-body collision work $W_{\mathrm{collision}}$ and full stride negative work W_{stride} (see Fig. 4B), as well as soft tissue collision work $W_{\mathrm{soft,collision}}$ (see Fig. 4C).

Net rigid body work per stride was generally positive and appeared to increase with speed and step length (see Fig. 5). This is consistent with the expectation that soft tissues perform net dissipative work, not captured by rigid body inverse dynamics. In preferred walking and fixed step length walking, net rigid body work per stride appeared to increase with walking speed, with positive contributions from the ankle and hip and negative contributions from the knee (Fig. 5A,C). The effect of speed on hip and knee joint work was more pronounced in fixed step length walking (Fig. 5C), whereas the effect on ankle joint work was more pronounced in preferred walking (Fig. 5A). In fixed frequency walking, net rigid body work per stride appeared to increase with step length, with positive contributions from the ankle and nearly constant contributions from the hip (positive) and knee (negative) (Fig. 5B). In fixed speed walking, net rigid body work per stride appeared to increase with step length, with mainly positive contributions from the ankle and mixed contributions from the knee and hip. The latter two work terms showed a maximum and minimum at intermediate step lengths, respectively, increasing in amplitude towards the extremes (Fig. 5D).

Whereas all work-rate amplitudes generally increased with speed and step length, the increase was more pronounced for whole-body work rate than for rigid body work rate (see Figs S1, S2). This increase was most notable during collision and push-off. Rigid body work rate was similar in shape to whole-body work rate, but different in amplitude (upper panels versus middle panels Figs S1, S2). During collision specifically, whole-body work rate had a larger amplitude

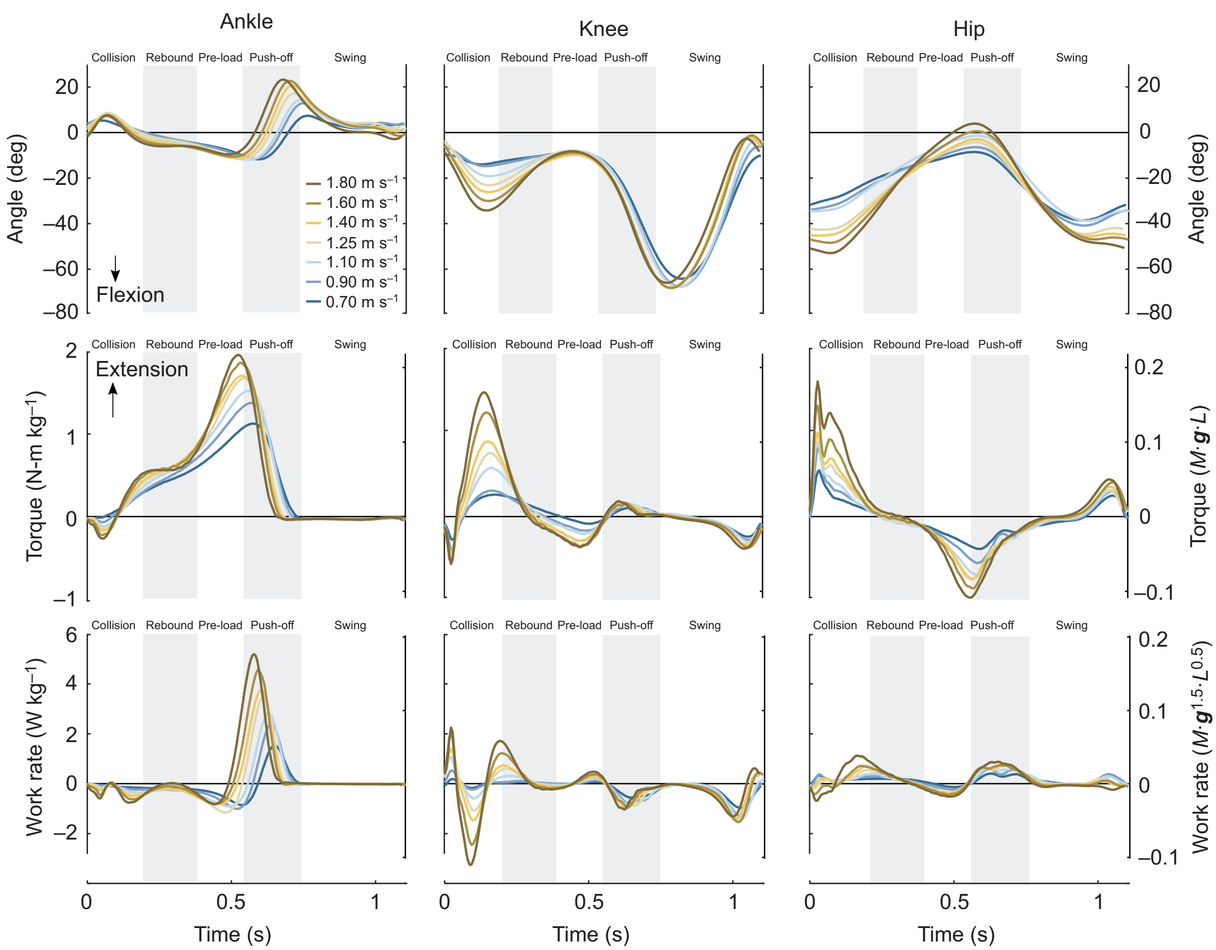

Fig. 3. Joint angle, torque and work rates during walking at constant step frequency. Amplitudes of sagittal plane joint angle, joint torque and joint work rate increased with walking speed (mean trajectories, N=9). Increases were most pronounced during collision (knee and hip) and push-off phases (ankle and hip). Each row of plots shares the same pair of vertical axes, with dimensional units on the left, and normalized units on the right (base units body mass M, leg length L and gravitational constant $\boldsymbol{g}$).

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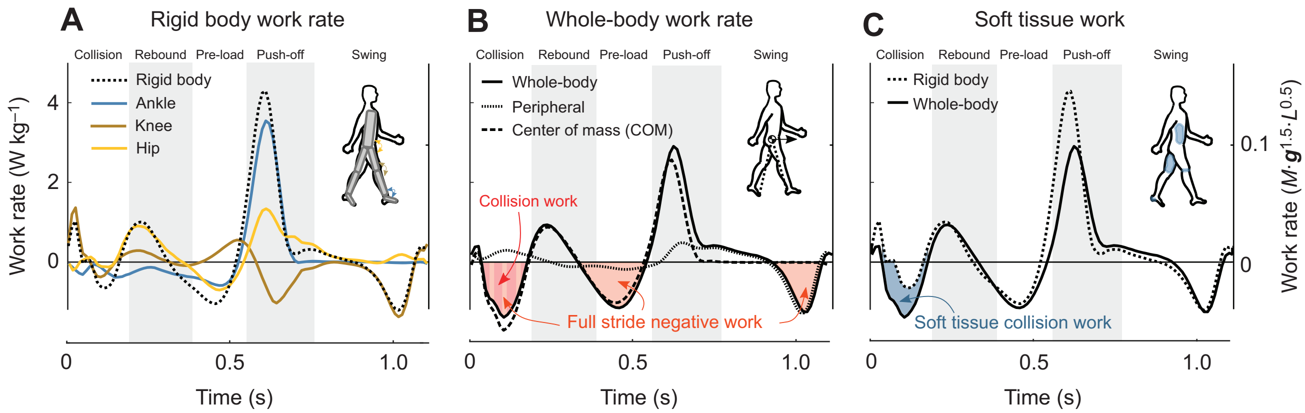

Fig. 4. Work rate versus time for three measures: rigid body, whole-body and soft tissue. Shown are representative data for preferred walking at 1.25 m s^{-1}. (A) Inverse dynamics yields rigid body work rate (dotted line), defined as the sum of work rates from ankle, knee and hip (solid, colored lines). (B) Whole-body work rate is the sum of center of mass (COM) work rate and peripheral work rate (Zelik and Kuo, 2010). Collision work (shaded red) and full stride negative work (shaded orange) are the negative whole-body work during collision and the entire stride, respectively. (C) Soft tissue work rate is the difference between whole-body work rate and rigid body work rate, also with soft tissue collision work quantified (shaded blue). Plots share the same pair of vertical axes, with dimensional units on the left, and normalized units on the right (base units body mass M, leg length L and gravitational constant $\boldsymbol{g}$). All lines indicate means across subjects (N=9).

than rigid body work rate, resulting in a substantial soft tissue work rate amplitude (lower panels Figs S1, S2). This soft tissue work rate amplitude seemed to increase with step length (lower panel Fig. S1) and with walking speed (lower panel Fig. S2), similarly as the amplitude of the whole-body work rate (upper panels Figs S1, S2). Altogether, whole-body and soft tissue work rate amplitudes during collision seemed to increase with walking speed and step length to a larger extent than rigid body work rate amplitudes. Soft tissue and rigid body work rates differed in the response immediately after collision. In nearly all conditions, soft tissue work rate returned to nearly zero at the end of collision, with little or no positive work. In contrast, the rigid body work typically became positive after collision, during rebound. Therefore, we interpret the soft tissue collision work as being largely passive and dissipative, whereas the rigid body collision work may have both active and passive contributions, possibly including a damped elastic oscillation.

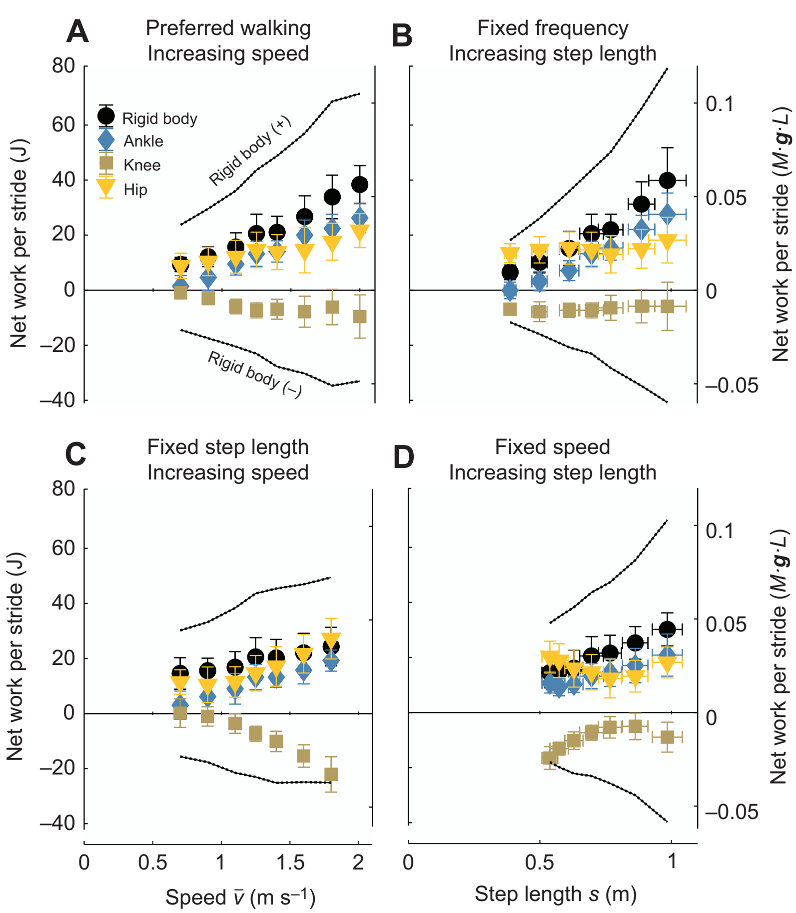

Fig. 5. Net joint work per stride during walking in four different experimental conditions. (A) Preferred walking at increasing speed. (B) Fixed frequency with increasing step length and speed. (C) Fixed step length with increasing speed and step frequency. (D) Fixed speed with increasing step length and decreasing step frequency. Shown are net rigid body work (black dots), which is the sum of net ankle (blue diamonds), net knee (brown squares) and net hip joint work per stride (yellow triangles). Envelopes (dashed lines) indicate total rigid body positive (+) and negative (−) work, defined as the sum of only the positive (negative) work intervals from each joint. For all conditions, net rigid body work per stride tended to increase with speed or step length, even though the whole body performs zero net work per stride during steady walking. Plots share the same pair of vertical axes, with dimensional units on the left, and normalized units on the right (base units body mass M, leg length L and gravitational constant $\boldsymbol{g}$). Symbols indicate means across subjects (N=9), error bars denote s.d.

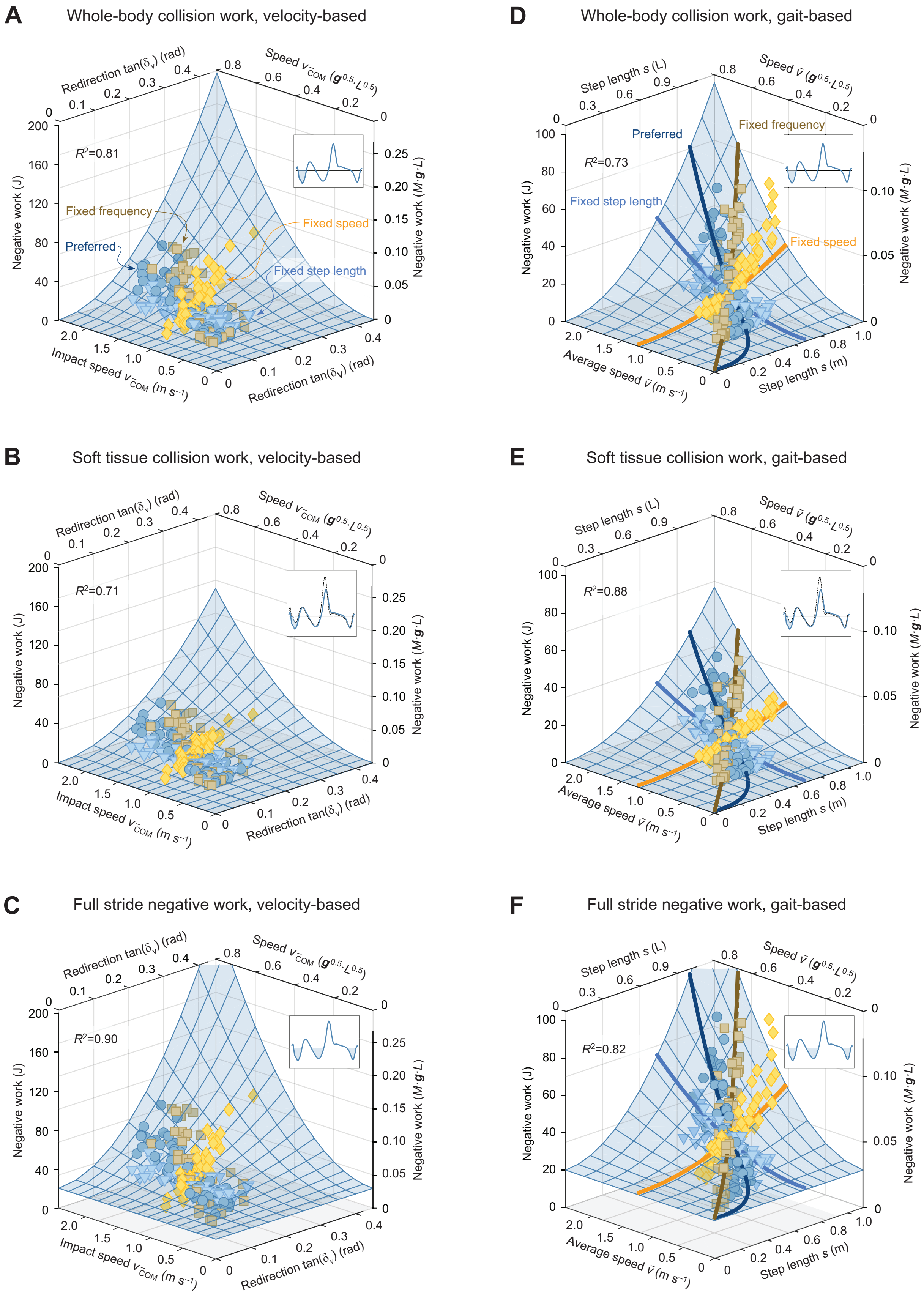

Fig. 6. See next page for legend.

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Fig. 6. Negative work done by the whole body and soft tissues during walking, with model prediction (mesh surface). Left column shows velocity-based predictors, right column shows gait-based predictors. Each column shows collision work, soft tissue collision work and full stride negative work. Velocity-based predictors impact speed v^-_{COM} and COM velocity redirection $\tan(\delta_\mathrm{v})$ for (A) whole-body collision (R^2=0.82), (B) soft tissue collision (R^2=0.71) and (C) whole-body full stride (R^2=0.90). Gait-based predictors average speed $\bar{v}$ and step length s for (D) whole-body collision (R^2=0.73), (E) soft tissue collision (R^2=0.88) and (F) whole-body full stride (R^2=0.82). Each prediction (A–F) was produced with one proportionality coefficient each, and tested with four walking conditions (indicated by different symbol–color combinations). Secondary axes (top and right axes) show normalized units, with base units of body mass M, leg length L and gravitational acceleration $\boldsymbol{g}$. Symbols indicate stride average for each individual subject (N=9).

Negative work increased across conditions according to the velocity-based predictions by the simple dynamic walking model (Fig. 6). As expected, the magnitudes of both collision work $W_{\mathrm{collision}}$ (Fig. 6A), soft tissue collision work $W_{\mathrm{soft,collision}}$ (Fig. 6B) and full stride negative work W_{stride} (Fig. 6C) increased with impact speed v^-_{COM} and the COM velocity redirection $\tan(\delta_\mathrm{v})$. All these cases were consistent with the same prediction proportional to $(v^-_{\mathrm{COM}})^2\tan^2(\delta_\mathrm{v})$ (Eqns 4–6), each with a single coefficient. For example, collision work $W_{\mathrm{collision}}$ increased with coefficient $c_{\mathrm{collision}}$=4.512±0.079 [estimate±95% confidence interval (CI); linear regression, R^2=0.81, P=4×10^{-147}; Fig. 6A]. Soft tissue collision work $W_{\mathrm{soft,collision}}$ also increased, with a smaller coefficient (c_{soft}=2.847±0.059, linear regression, R^2=0.71, P=6×10^{-130}; Fig. 6B). Full stride negative work W_{stride} increased with a larger coefficient (c_{stride}=5.083±0.108, linear regression, R^2=0.90, P=2×10^{-127}; Fig. 6C), and was accompanied by a significant offset in work (d_{stride}=20.87±0.44 J, mean±95% CI).

A comparison of the fitting coefficients reveals that soft tissues accounted for most of the collision work $W_{\mathrm{collision}}$, which in turn accounted for most of the full stride negative work W_{stride}. Quantified by the ratio between coefficients, collision work $W_{\mathrm{collision}}$ accounted for approximately 89% of the change in full stride negative work W_{stride} ($c_{\mathrm{collision}}$:c_{stride}=0.89±0.05; 95% confidence interval from Fieller's theorem; Fieller, 1954). The main difference was a constant amount of greater full stride negative work W_{stride} (20.9 J), not dependent on gait parameters. Similarly, soft tissues accounted for approximately 63% of the collision work $W_{\mathrm{collision}}$ (c_{soft}:$c_{\mathrm{collision}}$=0.63±0.04, Fieller's theorem) and approximately 56% of the change in full stride negative work W_{stride} (c_{soft}:c_{stride}=0.56±0.03) across conditions considered. Altogether, these results agree with the expectation that soft tissues dissipate substantial energy, mostly during collision, which can be quantitatively predicted from impact speed v^-_{COM} and COM velocity redirection $\tan(\delta_\mathrm{v})$ (Eqn 5).

Negative work increased across conditions according to the gait-based predictions by the simple dynamic walking model (Fig. 6). As expected, the magnitudes of collision work $W_{\mathrm{collision}}$ (Fig. 6D), soft tissue collision work $W_{\mathrm{soft,collision}}$ (Fig. 6E) and full stride negative work W_{stride} (Fig. 6F) increased with average speed $\bar{v}$ and step length s. All these cases were consistent with the same prediction proportional to $\bar{v}^2s^2$ (Eqns 7–9), albeit with different coefficients. For example, collision work $W_{\mathrm{collision}}$ increased as described by coefficient $c'_{\mathrm{collision}} = 1.250$±0.027 (estimate ±95% CI; linear regression, R^2=0.73, P=5×10^{-127}; Fig. 6D). Soft tissue collision work $W_{\mathrm{soft,collision}}$ also increased, with a smaller coefficient ($c'_{\mathrm{soft}} = 0.828$±0.011, linear regression, R^2=0.88, P=2×10^{-178}; Fig. 6E). Full stride negative work W_{stride} increased with a larger coefficient ($c'_{\mathrm{stride}} = 1.451$±0.042, linear regression, R^2=0.82, P=5×10^{-98}; Fig. 6F), accompanied by an offset (d'_{stride}=20.04±0.60 J; mean±95% CI). And as expected for zero net work per stride, full stride positive work yielded a comparable coefficient (1.468±0.042), offset (21.89±0.60 J) and overall fit to the same type of proportionality (R^2=0.83), meaning that negative and positive work were nearly equal in magnitude. Gait-based coefficients yield predictions for negative work during walking, given subject characteristics (mass M and leg length L) and gait parameters (speed $\bar{v}$ and step length s). For example (using Eqn 8), the predicted amount of negative work done by soft tissues during collision for the average subject walking at 1.25 m s^{-1} with a preferred step length of 0.70 m was 6.7 J.

These same fits were also examined on a condition-specific basis, and were found to agree reasonably well with predictions for most conditions (most R^2 values ≥0.5; see Fig. 7). The gait-based predictions (Fig. 6D–F) were evaluated for preferred walking (Fig. 7A), fixed step frequency (Fig. 7B), fixed step length (Fig. 7C) and fixed speed conditions (Fig. 7D), all using the same single coefficients reported above ($c'_{\mathrm{collision}}$, c'_{soft}, c'_{stride}). Soft tissue and whole-body negative work matched the predictions best in fixed frequency walking (R^2=0.91–0.95), as expected owing to the dominant effect of step length (see Fig. 7B). This was followed by preferred walking (R^2=0.83–0.90), which featured the largest increase in walking speed (see Fig. 7A). Negative work was predicted somewhat less well for fixed speed walking (R^2=0.39–0.66; see Fig. 7D). Soft tissue collision work $W_{\mathrm{soft,collision}}$ and full stride negative work W_{stride} were reasonably well predicted in fixed step length walking (R^2=0.52–0.68). The fits were relatively poor for whole-body collision work $W_{\mathrm{collision}}$ at fixed step lengths (R^2=0.13; see Fig. 7C), but this was because work changed little across this condition (9.9 J at most), and not because of substantial absolute error in the fit. Separate from these predictions, the rigid body collision work was small in all conditions, taking up only 28% of (whole-body) collision work $W_{\mathrm{collision}}$ (averaged across all conditions). Altogether, data agreed with predictions mainly for the preferred, fixed frequency and fixed speed predictions, where there was generally more change in dissipation across trials.

DISCUSSION

The present study aimed at testing whether negative work by the whole body or passive soft tissues varies systematically at various combinations of walking speed and step length. We tested whether the negative work done by soft tissues during collision ('soft tissue collision work') and the whole-body negative work over a full stride were both proportional to whole-body collision work. And in turn, we also tested whether collision work would increase as predicted by a simple model, with step length squared multiplied by walking speed squared. These quantities were found to agree reasonably well with the model. We next examine the results considering potential underlying mechanisms, as well as the implications for biomechanical analysis of human locomotion.

We found that soft tissues do substantial amounts of negative work over a wide range of walking conditions. Soft tissue work has previously been related to walking speed during preferred walking (Zelik and Kuo, 2010), but not for other conditions, and not relative to negative work done by the whole body. Here, we show that soft tissues account for most (approximately 63%) of the negative work done by the whole body during collision, over a variety of conditions quite different from preferred walking (Fig. 6). The negative collision work not performed by soft tissues may be performed by a combination of active dissipation by muscle, and

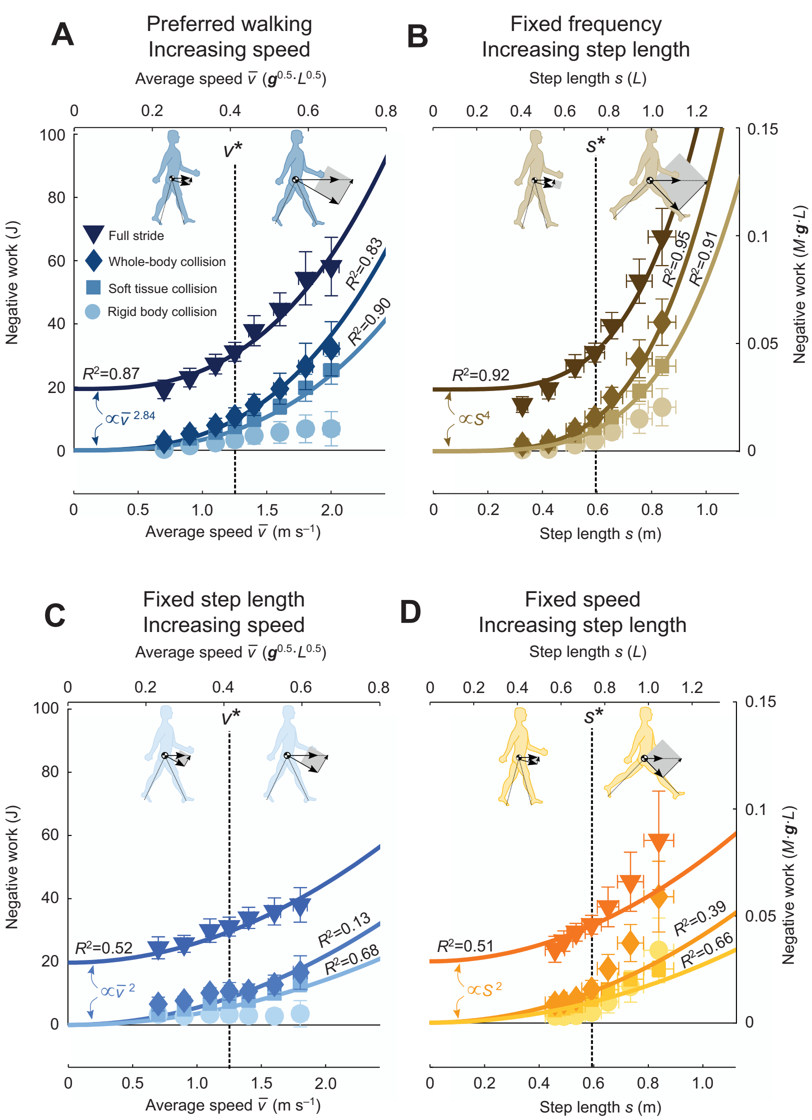

Fig. 7. Condition-specific effects of step length and speed on negative work during walking. (A) Negative work versus average speed for preferred walking (R^2=0.83–0.90). (B) Negative work versus step length for fixed frequency walking (R^2=0.91–0.95). (C) Negative work versus average speed for fixed step length walking (R^2=0.13–0.68). (D) Negative work versus step length for fixed speed walking, with poorer fit to predictions (R^2=0.39–0.66). All four conditions were tested against a single model with one proportionality coefficient (Fig. 6D–F) for each of three quantities: full stride negative work, total negative collision work and soft tissue collision work (c'_{stride}, $c'_{\mathrm{collision}}$, c'_{soft}). Secondary axes (top and right axes) show normalized units, with base units of body mass M, leg length L and gravitational acceleration $\boldsymbol{g}$. Lines indicate model prediction, symbols indicate experimental means across subjects (N=9), error bars denote s.d.

tendon passively storing some energy elastically, and perhaps returning during rebound (e.g. Fig. 4C). Our data are insufficient to quantify the actual amount of elastic return, which has been suggested to be quite substantial and attributable to the knee (Shamaei et al., 2013). But soft tissues appear to be well damped, with little indication of elastic return (see Figs S1, S2). If soft tissue collision losses (approximately 6.7 J at typical 1.25 m s^{-1}) were restored by active positive work at 25% efficiency (Margaria, 1968), it could account for approximately 31% of the net metabolic power of approximately 2.3 W kg^{-1} at that speed (Kuo et al., 2005). Soft tissue work is therefore an important dissipative contributor to negative work, and ultimately to the metabolic cost of walking.

We also found that the negative work of the entire stride is related to that performed during collision. Both quantities (W_{stride} and $W_{\mathrm{collision}}$) increased proportionately, with approximately the same power law with respect to either velocity- or gait-based predictors (Fig. 6). The collision accounted for approximately 89%, and soft tissues for approximately 56%, of the changes in negative work over an entire stride. This leaves a relatively small, 11% contribution from other phases to changes in overall negative work, albeit still in proportion to collision. There was also a substantial offset in the full stride negative work, accounting for as much as 87% of the total negative work at low speeds (below nominal). We interpret the offset as arising from other factors not considered here, such as the contribution of step width to collision (Donelan et al., 2001, 2002), and motion of the swing leg (Doke et al., 2005) and other parts of the body. The negative work of pre-load appears to be associated with elastic loading of the Achilles tendon, prior to subsequent release as part of push-off (Fukunaga et al., 2001; Zelik et al., 2014). That loading appears driven in part by the dynamical interactions triggered by collision, as is the overall positive work of the body over the full stride.

These changes are mechanistically predictable over a wide range of walking conditions. The mechanistic stimulus is the vector velocity of the COM, which is redirected during the step-to-step transition. Negative collision work was predicted from the velocity's magnitude v^{-}_{COM} and redirection $\tan(\delta_{\mathrm{v}})$ (Eqn 4), which both varied substantially across walking conditions. Despite a greater than two-fold variation in each of the gait parameters, the collision work was predicted reasonably well by a single empirical coefficient $c_{\mathrm{collision}}$ (R^2=0.81), and similarly for soft tissue collision work (R^2=0.71) and whole-body negative work over the stride (R^2=0.90). A drawback is that such predictions require the pre-impact COM velocity v^{-}_{COM}, which is not typically known prior to the experiment. Therefore, we also tested more convenient gait-based variables, namely, average speed $\bar{v}$ and step length s, that are more typically known or specified prior to the experiment. The gait-based predictions rely on assumptions such as the small-angle approximation, and that impact velocity is proportional to average speed. However, we found gait-based predictions of soft tissue collision work $W_{\mathrm{soft,collision}}$ to fit data about as well as velocity-based predictions (R^2=0.88 versus R^2=0.71). The exception was for large step lengths during fixed speed walking, which feature substantial redirection $\tan(\delta_v)$ but relatively less soft tissue collision work (see Fig. 7). Humans appear to behave less like inverted pendulums when walking with atypically high step lengths and low step frequencies. Although the fits for fixed speed walking (R^2 between 0.39 and 0.66) are not as good as for some other conditions, this is a consequence of performing a single fit for all conditions, some of which entailed much more work and therefore had greater influence on the proportionality coefficient. Better fits could be obtained with a separate coefficient for each specific condition, but our aim was to test a single model across all conditions. With the single coefficient limitation in mind, both soft tissue dissipation and whole-body negative work can be predicted reasonably well from a few gait parameters (i.e. walking speed and step length) and anthropometric parameters (see Eqns 7–9).

These predictions arise from a simple dynamic walking model that predicts the work needed to redirect the COM velocity during the step-to-step transition. It predicts general trends arising from inverted pendulum-like walking (Eqns 1–3), and not absolute work quantities, which required empirical proportionality coefficients. Here, we report reasonably accurate predictions of the negative work across a broad range of walking conditions, using a single proportionality coefficient for each work quantity (i.e. soft tissue collision, whole-body collision, full stride, c'_{soft}, $c'_{\mathrm{collision}}$, c'_{stride}). The model prediction does not distinguish between active and passive work, but we found that passive soft tissue dissipation was proportional to whole-body negative work. It appears that humans are quite systematic in distributing work between passive soft tissues and active muscle-tendons during walking. Thus, the combination of a simple model and only a few empirical coefficients unites the effects of multiple gait parameters on negative work.

These findings also help to reveal that traditional inverse dynamics analysis is least accurate during collision. Rigid body work accounted for only approximately 28% of total negative work following the impact at heel strike, across a wide range of walking conditions. The ratio of rigid body negative work to total negative work during collision was largest during fixed speed walking (36%) and smallest during preferred walking (21%). This is also corroborated by observed net rigid body work for a full stride not being zero as expected for periodic gait, but rather positive (Fig. 5) and increasing with greater speeds or step lengths. This can largely be explained by work done during collision, when soft tissues are most dissipative, and which rigid body work cannot capture (compare Fig. 4A and B). We used six-degree-of-freedom inverse dynamics, which can in principle capture some of the soft tissue work performed between neighboring segments or within the joints (Honert and Zelik, 2019). Even so, inverse dynamics seems quite inaccurate for quantifying the work performed during collision, which occurs within the first 200 ms or so after heel strike. The present study indicates the specific gait conditions and amount of work (Eqns 7–9, each with an empirical coefficient) not quantified by inverse dynamics.

There are also limitations to the quantification and interpretation of soft tissue dissipation. For example, we observed a large negative burst of soft tissue work during pre-load followed by a large positive burst during push-off (Figs S1 and S2). It is possible that this negative–positive sequence reflects subsequent energy storage and release by soft tissues, which may compress during pre-load and expand during push-off. The timing and magnitude of positive work seem consistent with that interpretation, but another possibility is that the work is not truly caused by soft tissues, but by unmodeled rigid body joints. In our analysis, we estimate soft tissue dissipation from the energy not accounted for by the rigid body model. For example, we did not measure the metatarsophalangeal joint, which may store and return energy during walking (Farris et al., 2019), and could potentially be included in a multi-segment (Farris et al., 2019) or deformable foot model (e.g. Takahashi et al., 2012) compatible with inverse dynamics. There remains the question whether such action is actively performed by muscle or passively by tendons, which may be addressed through techniques such as ultrasound imaging (Fukunaga et al., 2001). Thus, interpretation of soft tissue work can also depend on rigid body assumptions and on passive elasticity.

Soft tissue dissipation might superficially seem preferable to avoid. All negative work, whether by soft tissue dissipation or by active muscle, needs to be restored by an equal amount of positive work (Riddick and Kuo, 2020 preprint) in steady level locomotion, at the cost of metabolic energy. However, negative work is necessary during the step-to-step transition to redirect the COM velocity. Doing this necessary negative work with soft tissues instead of active muscles may be more economical, as muscles require metabolic energy even for negative work (Abbott et al., 1952). The possible economy of soft tissue dissipation is supported by the lower mass-normalized metabolic cost of walking for obese than healthy individuals (Fu et al., 2015). Soft tissues also enable a softer impact with the ground (Pain and Challis, 2006), which may help in avoiding damage or injury to other tissues. For example, high knee adduction moment impulse is considered a risk factor for knee osteoarthritis (Bennell et al., 2011), whereas high vertical loading rate is considered a risk factor for tibial stress syndrome (Milner et al., 2006). The human nervous system appears to apportion some negative work to soft tissues, and some to muscle tendons under active control. For example, humans prefer a jump landing that requires 37% more muscle–tendon dissipation than minimally necessary (Zelik and Kuo, 2012). The amount of soft tissue dissipation may also have other effects such as on the stability of walking (Masters and Challis, 2020). The distribution between active and passive dissipation may therefore be relevant to metabolic cost and a variety of additional mechanical effects.

Conclusions

Soft tissue dissipation during walking accounts for 56% of the variation in total negative work during walking. Both soft tissue and total negative work increase in consistent relative proportion, and with the square of walking speed and step length as predicted by a simple dynamic walking model. The model mechanistically explains how negative work is necessary to redirect the body's velocity between inverted pendulum-like steps. Across a variety of conditions, experimental data reveal substantial soft tissue dissipation during walking, in predictable amounts not captured by rigid body inverse dynamics analysis. In steady gait, negative and positive work are performed in equal magnitude, so that dissipative soft tissue work also requires active positive work that costs metabolic energy.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
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Data availability
All data are available on Figshare: https://doi.org/10.6084/m9.figshare.16530939.v3

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