

Mechanical work for step-to-step transitions is a major determinant of the metabolic cost of human walking

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Summary

In the single stance phase of walking, center of mass motion resembles that of an inverted pendulum. Theoretically, mechanical work is not necessary for producing the pendular motion, but work is needed to redirect the center of mass velocity from one pendular arc to the next during the transition between steps. A collision model predicts a rate of negative work proportional to the fourth power of step length. Positive work is required to restore the energy lost, potentially exacting a proportional metabolic cost. We tested these predictions with humans ($N=9$) walking over a range of step lengths (0.4–1.1 m) while keeping step frequency fixed at 1.8 Hz. We measured individual limb external mechanical work using force

plates, and metabolic rate using indirect calorimetry. As predicted, average negative and positive external mechanical work rates increased with the fourth power of step length (from 1 W to 38 W; $r^2=0.96$). Metabolic rate also increased with the fourth power of step length (from 7 W to 379 W; $r^2=0.95$), and linearly with mechanical work rate. Mechanical work for step-to-step transitions, rather than pendular motion itself, appears to be a major determinant of the metabolic cost of walking.

Key words: biomechanics, biped, energetics, locomotion, oxygen consumption, human.

Introduction

Why does walking require metabolic energy? One possible answer is for mechanical work performed by muscles. In studies on isolated muscle there is a proportional relationship between mechanical work and metabolic cost (Hill, 1938; Woledge, 1985). This has also been demonstrated in humans for tasks such as rowing or cycling, where the mechanical work performed on a load can be readily measured (Fukanaga et al., 1986; Pugh, 1974). For human walking, the clearest relationship between work and metabolic cost is observed during slope walking experiments. Efficiencies for walking on positive and negative slopes, defined as work performed against gravity divided by metabolic cost, approach 25% and –120%, respectively, and are similar to those found for performing positive and negative work in isolated muscle (Margarita, 1976).

For walking on level ground, however, it is unclear why mechanical work is required. There is no dissipative load external to the body as for rowing or cycling, nor is net work performed against gravity as for slope walking. Perhaps the body and limbs themselves act as a mechanical load. There are a variety of methods to quantify the mechanical work performed on the body and limbs (Burdett et al., 1983; Cavagna and Kaneko, 1977; Willems et al., 1995), but these neither predict nor explain where and why mechanical energy is dissipated.

Several inverted pendulum models of walking (Fig. 1) predict that work is not needed within each step, but rather between steps (McGeer, 1990; Alexander, 1995; Garcia et al., 1998; Kuo, 2002). In bipeds, single support can be modeled as an inverted pendulum, with the center of mass moving along an arc dictated by the stance limb (Fig. 2A). A pendulum conserves mechanical energy and requires no work to move along an arc, but the transition from one stance limb to the next does require work. Negative work is performed in the collision that redirects the center of mass velocity from one arc to the next (Fig. 2B), and positive work is required to restore the energy lost. These step-to-step transition costs will exact a proportional metabolic cost if muscle efficiency is constant.

These model predictions have been supported by previous experiments measuring mechanical and metabolic cost as a function of increasing step width (Donelan et al., 2001). A simple model (Kuo, 1999) predicted that collision costs would increase with the square of step width. Subsequent experimental measurements of mechanical work performed during step-to-step transitions (Donelan et al., 2001) showed a similar dependence ($r^2=0.91$), with a proportional increase in metabolic cost ($r^2=0.83$). This is, however, only a small part of the metabolic cost of normal walking because humans prefer to walk with a relatively narrow step width.

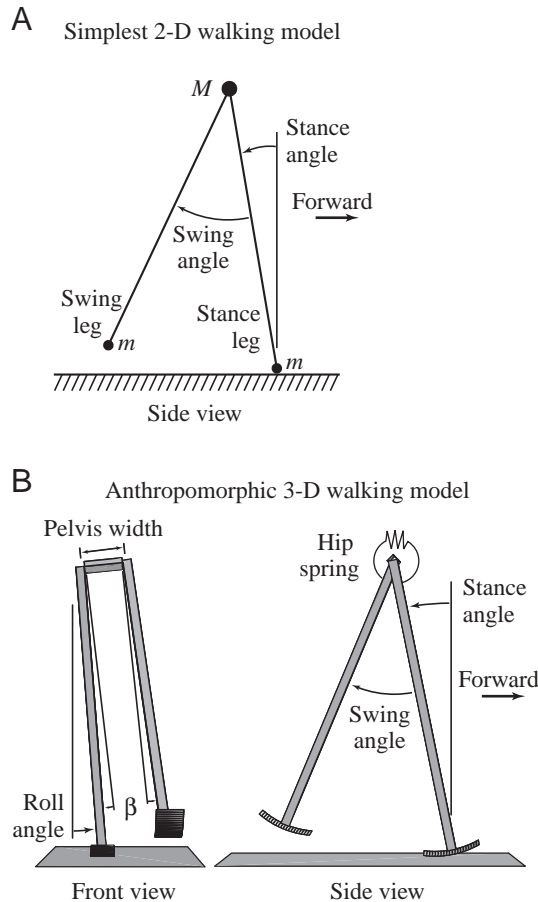


Fig. 1. (A) The simplest two-dimensional passive dynamic walking model has two degrees of freedom, stance leg angle and swing leg angle, and is restricted to motion in the sagittal plane. Mass is concentrated in points located at the pelvis (M) and feet (m), making it possible to compute step-to-step transition costs analytically (Garcia et al., 1998; Kuo, 2002) (B) The anthropomorphic three-dimensional passive dynamic walking model (Kuo, 1999) extends this model in two ways. First, it employs a torsional hip spring acting between the limbs, making it possible to explore the mechanics of walking at different step lengths or frequencies (after Kuo, 2002). Second, it includes an extra degree of freedom allowing for lateral motion and finite step widths. Step width is adjusted by changing the splay angle, β . The model has three degrees of freedom (stance, swing and roll angles).

Step-to-step transition costs associated with step length may comprise a much greater fraction of the metabolic cost of normal walking. Our models predict two important components to the cost of normal walking: a cost to increasing step length due to step-to-step transitions, and a cost to increasing step frequency due to moving the legs relative to the body (Kuo, 2001). The rate of mechanical work for step-to-step transitions is predicted to increase sharply with the fourth power of step length when walking speed increases proportionally with step length (Fig. 3A). The metabolic cost of moving the legs is predicted to depend more heavily on step frequency (Kuo, 2001) and to be isolated from the cost of step-

to-step transitions by keeping step frequency fixed. Several previous studies (e.g. Atzler and Herbst, 1927; Zarrugh et al., 1974; Elftman, 1966) indicate an increase in metabolic cost with step length, but because these studies provide few data points that specifically fix step frequency for a range of step lengths, we embarked on a new study designed for this purpose.

In the present study, we tested predictions regarding step-to-step transition costs in walking by measuring mechanical and metabolic costs in humans as a function of step length. A fixed step frequency was used to control for other potential metabolic costs such as for moving the legs. Based on our model's predictions (Fig. 3), and assuming constant muscular efficiency, we hypothesized that both the mechanical and metabolic power associated with step-to-step transitions would increase with the fourth power of step length.

Materials and methods

Model predictions

Models based on passive dynamic walking (McGeer, 1990; Alexander, 1995; Garcia et al., 1998; Kuo, 2002) lead to predicted mechanical costs as a function of step length. In these models, the legs move freely during a step, ending with an instantaneous and perfectly inelastic collision that produces initial conditions for the subsequent identical step. Energy is lost at each collision, even for models that have been adapted to walk on the level (Kuo, 2002; McGeer, 1990), and to walk at different step frequencies (Kuo, 2002).

We applied a previously developed model, the 'simplest two-dimensional passive dynamic walking model' (Fig. 1; briefly reviewed in Appendix), to predict how collision costs increase with step length (Kuo, 2002). During single support phases, the model behaves as an inverted pendulum (Fig. 2A). Each transition to a new stance limb (Fig. 2B) involves a collision, where the negative work per step, denoted $W_{\text{trans}}^{(-)}$, is performed by the leading limb on the center of mass, according to:

$$W_{\text{trans}}^{(-)} \propto f^2 \times l^4, \quad (1)$$

where f is step frequency and l is step length. Average rate of negative mechanical work $\dot{W}_{\text{trans}}^{(-)}$ is found by multiplying $W_{\text{trans}}^{(-)}$ by step frequency:

$$\dot{W}_{\text{trans}}^{(-)} \propto f^3 \times l^4. \quad (2)$$

To maintain a steady walking speed, an equal amount of positive work is required to restore the energy lost. Consequentially, positive work has the same dependence on step frequency and length as negative work, from Equation 2 (Kuo, 2002). We therefore predict that the collision cost, expressed in terms of average rate of mechanical work, increases with the fourth power of step length (Fig. 3). These predictions hold true even for a passive dynamic walking model with more anthropomorphic features (Figs 1B, 3) (Kuo, 1999).

Humans redirect the center of mass velocity during step-to-

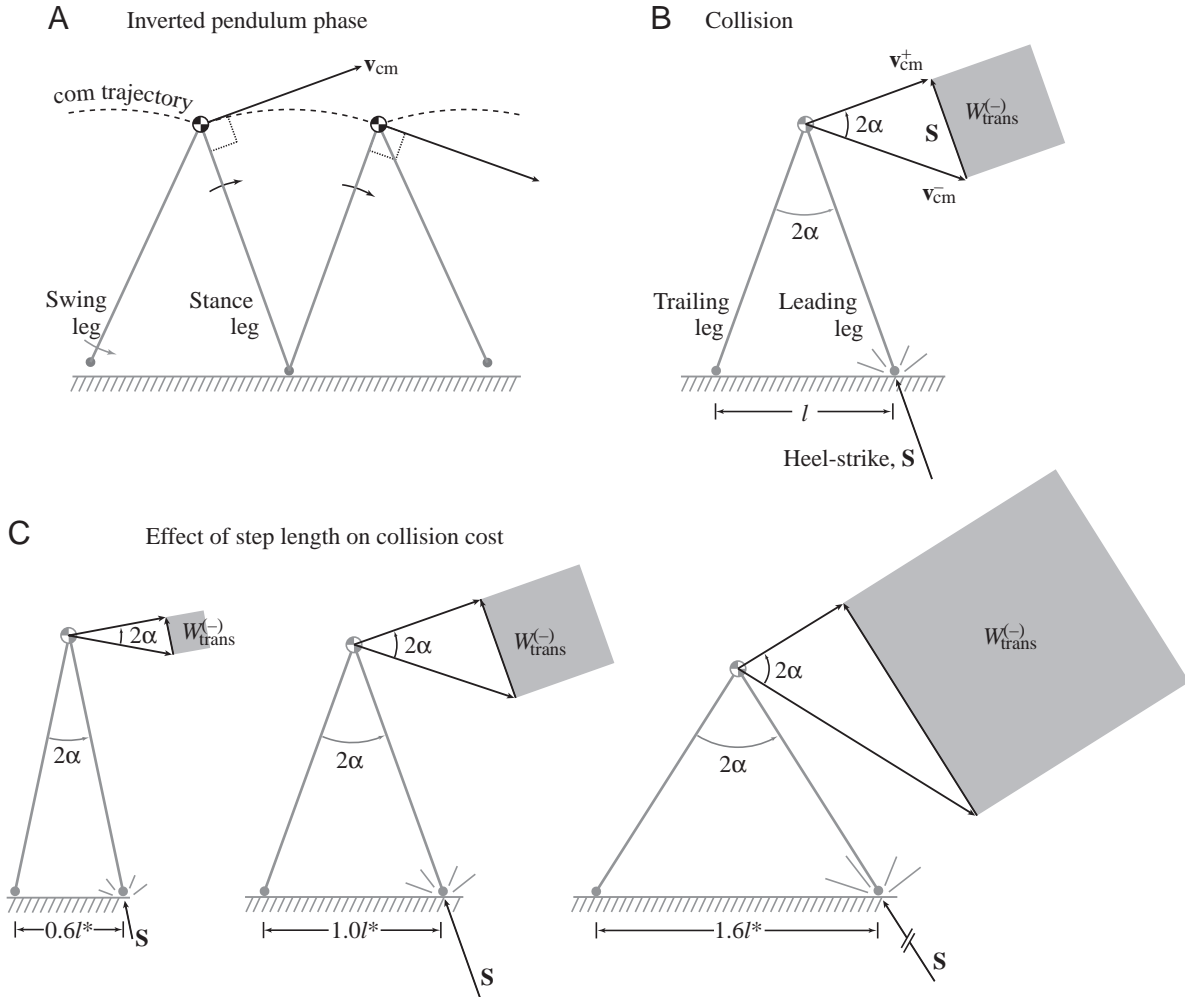


Fig. 2. (A) The direction of the center of mass velocity, \mathbf{v}_{cm} , is perpendicular to the stance limb during the single support inverted pendulum phase of the simplest two-dimensional passive dynamic walker. (B) Each transition to a new stance limb requires redirection of the center of mass velocity, from $\mathbf{v}_{cm}^{(-)}$ to $\mathbf{v}_{cm}^{(+)}$ (with the superscripts ‘-’ and ‘+’ denoting the instances immediately before and after impact, respectively), accomplished by an impulsive heel strike, \mathbf{S} , acting along the leading limb. \mathbf{S} also causes an instantaneous reduction in the magnitude of the center of mass velocity through negative work by the leading limb with $W_{trans}^{(-)} \propto |\mathbf{S}|^2$ (shaded square). To walk at steady speed, an equal amount of positive work is required (see Kuo, 2002; Donelan et al., 2002). The magnitude of $W_{trans}^{(-)}$, and thus the step-to-step transition cost, depends on $\mathbf{v}_{cm}^{(-)}$ and the angle between the legs, 2α (Equation 1). (C) When step frequency is kept fixed, $\mathbf{v}_{cm}^{(-)}$ and 2α are proportional to step length, l , so that $W_{trans}^{(-)}$ increases with l^4 (denoted by the differences in area of the shaded squares).

step transitions not with instantaneous collisions, but with negative work performed by the leading leg over a finite period of time (Donelan et al., 2001, 2002). The step-to-step transition costs are the negative external work performed to redirect the center of mass velocity from one inverted pendulum to the next, and the equal amount of positive external work performed to restore the energy lost. Equation 2 predicts that both of these quantities increase with step length raised to the fourth power.

In addition to these step-to-step transition costs, motion of the legs back and forth relative to the body contributes to external mechanical work, whether or not work is performed on the legs (see Appendix). Keeping step frequency fixed, this motion contributes a term increasing with the square of step length (Fig. 3B). Even though leg motion is not related to step-

to-step transition costs, it nevertheless affects the average external mechanical work rate.

Combining contributions from step-to-step transitions and limb motion, simple bipedal models predict that when walking faster by increasing only step length, the rate of external mechanical work \dot{W}_{mech} will be:

$$\dot{W}_{mech} = C_{trans}l^4 + C_{leg}l^2 + D, \quad (3)$$

where C_{trans} is a constant associated with step-to-step transition power, C_{leg} is a constant associated with leg motion, and D is a constant. The parameters C_{trans} , C_{leg} and D depend on gait parameters such as step width and step frequency, and on physical attributes such as inertial properties and musculoskeletal geometry.

Assuming constant muscular efficiency, the rate of

mechanical work for step-to-step transitions (Equation 3) translates directly into \dot{E}_{met} , a predicted metabolic rate:

$$\dot{E}_{\text{met}} = C'_{\text{trans}} l^4 + D', \quad (4)$$

where C'_{trans} and D' are parameters that depend on their counterparts in Equation 3 and on muscle efficiency (with the prime denoting metabolic rate). There is no term for leg motion in Equation 4, because our model predicts that the metabolic cost of moving the legs is determined by muscle force rather than muscle work (Kuo, 2001) (see also Appendix), with a cost that will be relatively constant at fixed step frequency, and which can therefore be subsumed within D' . In the present study, we tested these predictions with nonlinear regressions, quantifying the parameters from Equations 3 and 4 empirically.

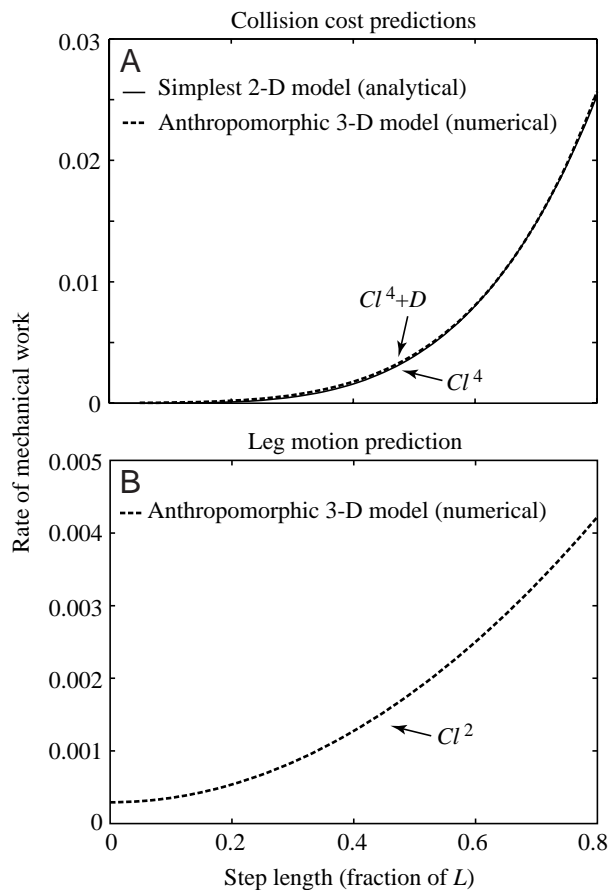


Fig. 3. (A) Walking models predict that the rate of external mechanical work dissipated in collisions is proportional to the fourth power of step length l (keeping step frequency fixed; Kuo, 2002). The simplest two-dimensional (Fig. 1A) and anthropomorphic three-dimensional passive dynamic walking models (Fig. 1B) both give similar predictions. (B) The anthropomorphic model predicts that leg motion also contributes to external work rate, with a term proportional to the square of step length. Step length is expressed as a fraction of leg length, L . Mechanical work rate shown is made dimensionless by dividing by $Mg\sqrt{gL}$, where M is body mass and g is the gravitational acceleration. C, D , constants. See Materials and methods for details.

Experimental procedures

We measured the mechanical and metabolic costs of walking as a function of step length in human adult subjects ($N=9$). All subjects (four male, five female, body mass 66.0 ± 8.4 kg; leg length 0.93 ± 0.05 m; means \pm s.d.) were healthy and exhibited no clinical gait abnormalities. Before the experiments began, volunteers gave their informed consent to participate, in accordance with university policy.

We first measured each subject's preferred step length, l^* , and step frequency, f^* , for walking at 1.25 m s^{-1} on a treadmill. After allowing each subject to acclimate to the treadmill for 10 min, we timed at least 100 steps at each speed to find the average step period, which is the reciprocal of f^* . We then found l^* by dividing speed by f^* . Average preferred step length was $l^* = 0.70 \pm 0.03$ m and average preferred step frequency was $f^* = 1.81 \pm 0.07$ Hz. Average step width, measured in the same manner as by Donelan et al. (2001), was 0.12 ± 0.03 m and did not change significantly with step length ($P=0.44$, ANOVA). For all remaining trials, subjects walked at their own f^* by stepping to a metronome.

We measured ground reaction forces for subjects walking overground at six different step lengths, keeping step frequency fixed. Subjects walked over two ground-embedded force platforms mounted in series (described in detail in Donelan et al., 2002), at target speeds within the range $0.75\text{--}2.00 \text{ m s}^{-1}$, presented in random order. These speeds were chosen so as to produce multiples of each subject's preferred step length: 0.6, 0.8, 1.0, 1.2, 1.4 and $1.6l^*$. The minimum step length was large enough to ensure that subjects could step on two separate force platforms, and the maximum was close to the largest that subjects could comfortably achieve. We discarded trials if the walking speed, measured with photocells, was not within 0.05 m s^{-1} of the target speed or if the individual feet did not fall cleanly on separate force platforms. We analyzed data for three acceptable trials from each subject at each of the step lengths. Reported values are averages from a single step, beginning and ending with successive heel strikes, from each of the three trials for each subject and condition.

In addition to the overground walking trials, we also conducted treadmill trials to measure the metabolic cost of walking at six step lengths. Metabolic cost was measured by indirect calorimetry using an open circuit respirometry system (Physio-Dyne Instrument Co., Quogue, NY, USA). After first measuring each subject's resting metabolic rate while standing, we then repeated the same walking trials as above, with the exception of a $1.5l^*$ condition (1.90 m s^{-1}) in place of $1.6l^*$ because subjects had difficulty maintaining the longer step length for a sufficient duration without switching into a run. Treadmill speed and metronome frequency were used to enforce step length and frequency. Following a 3 min period to allow subjects to reach steady state, we measured the average rates of oxygen consumption and carbon dioxide production over 3 min, and calculated metabolic rate (Brockway, 1987; described in detail in Donelan et al., 2001). We subtracted the metabolic rate for standing from all walking values and then

divided by body mass to derive normalized net metabolic rate, \dot{E}_{met} (W kg^{-1}).

Data analysis

We calculated mechanical step-to-step transition costs using the individual limbs method for quantifying external mechanical work (Donelan et al., 2001; reviewed in

Appendix). Briefly, the external mechanical power generated by a limb was found from the dot product of the limb's ground reaction force and the velocity of the center of mass (see Fig. 4 for intermediate results showing these quantities). The magnitude of negative external mechanical work per step was found from the time-integral of the negative portions of external mechanical power generated by the limb (Donelan et

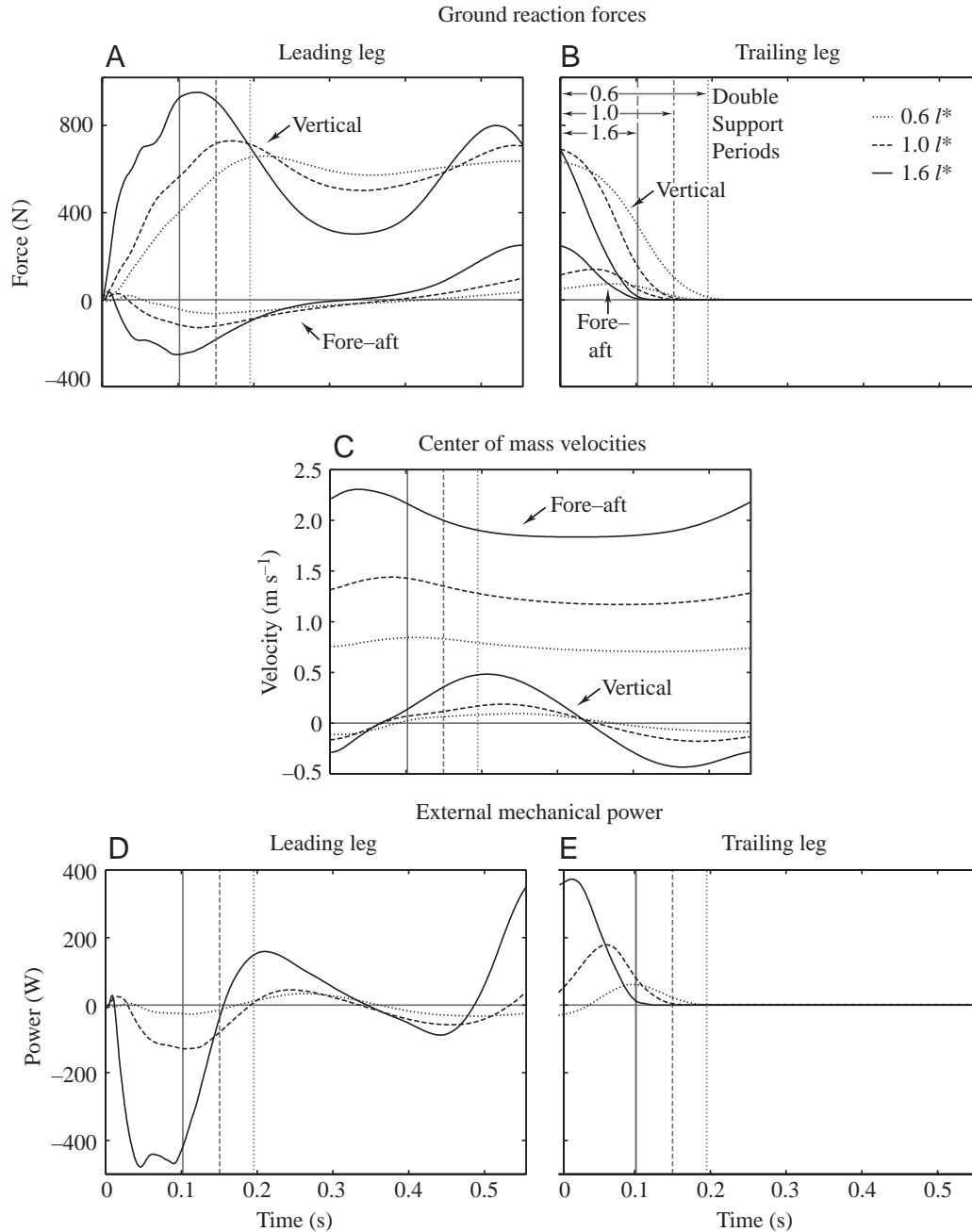


Fig. 4. Average ground reaction forces from two force plates during a single step of walking at three different step lengths ($N=9$). (A) Leading leg force plate, (B) trailing leg force plate. (C) Center of mass velocity for a single step, computed from ground reaction forces. The dot product of the ground reaction forces and center of mass velocity yields average external mechanical power produced by (D) the leading leg and (E) the trailing leg during a single step at different step lengths. As a result of the changes in ground reaction forces and center of mass velocities, the external mechanical power generated within a step increased at longer step lengths. Grey lines denote double support. Medio-lateral forces and velocities (not shown) are relatively small and change little with step length. They are, however, included in all calculations. l^* , preferred step length.

al., 2002). We determined the average normalized rate of negative external mechanical work, $W_{\text{trans}}^{(-)}$ (W kg^{-1}), by dividing the negative work for both limbs by body mass and step period.

The measures of step-to-step transition costs used here differ slightly from our previous estimates, described by Donelan et al. (2002). We previously estimated transition costs as a function of step width using the negative external mechanical work performed by the leading leg during double support alone. While some negative work continued beyond double support, it probably did not adversely affect our conclusions, as its magnitude was small. In the present study, however, the leading limb performed substantial negative work after double support during the longer step length conditions (Fig. 4D). Integrating negative power over the entire step therefore better quantifies step-to-step transition costs for the conditions presented here.

A trade-off to quantifying external work over an entire step, rather than the double support phase alone, is that motion of the legs can affect our measurements. We expect that including the term $C_{\text{leg}}l^2$ in Equation 3 will underestimate C_{trans} because external work from leg motion mathematically cancels some of the step-to-step transition costs (see Appendix). However, this estimate of the negative work of step-to-step transitions is sufficient to test the predicted relationship between step-to-step transition costs and step length given by Equation 3.

We used these data to test our predictions regarding step-to-step transitions. We first tested whether the measured rate of mechanical work increased with step length as predicted by Equation 3, and then tested whether measured metabolic rate increased as predicted by Equation 4. These tests were performed with a nonlinear regression to both equations, with r^2 and 95% confidence intervals (c.i.) indicating the degree and significance of fit. Because the offsets D and D' are purely empirical constants not predicted by the model, we performed the regressions with an individualized offset subtracted from each subject's data. To compare with previously reported data, we also calculated traditional combined limbs measures of external mechanical work (Cavagna, 1975) and percentage recovery (Cavagna et al., 1976).

Finally, we tested whether metabolic rate increased in proportion to mechanical work rate, as would be expected if muscle performed this work at constant efficiency. We used a linear regression for this comparison, with r^2 and 95% c.i. indicating the degree and significance of fit. The linear constant of proportionality was also used to estimate an efficiency, defined as negative external mechanical power divided by net metabolic power. We first estimated efficiency by performing a linear regression between total negative external mechanical power and net metabolic power. The result is probably an overestimate due to cancellation of swing leg work (see Appendix). To also estimate a lower bound on efficiency, we subtracted our estimated contribution of leg motion, $C_{\text{leg}}l^2$, from negative external mechanical power data (yielding a lower bound on negative step-to-step transition power), and

then performed a linear regression between this transition power and net metabolic power. Using these methods, we were restricted to step lengths for which we collected both mechanical and metabolic data, i.e. excluding the longest step length condition.

Results

In support of our hypothesis, the rate of mechanical work associated with step-to-step transitions increased with the fourth power of step length (Fig. 5A). A nonlinear regression to Equation 3 yielded coefficients $C_{\text{trans}}=0.087\pm 0.045 \text{ W kg}^{-1} \text{ m}^{-4}$ (mean \pm 95% c.i.), $C_{\text{swing}}=0.344\pm 0.135 \text{ W kg}^{-1} \text{ m}^{-4}$ (mean \pm 95% c.i.) and $D=0.122\pm 0.102 \text{ W kg}^{-1} \text{ m}^{-4}$ (mean \pm s.d.) ($r^2=0.98$). Our estimates for the mechanical step-to-step transition work rate therefore increased from 0.01 W kg^{-1} to 0.57 W kg^{-1} over the range of step lengths we employed.

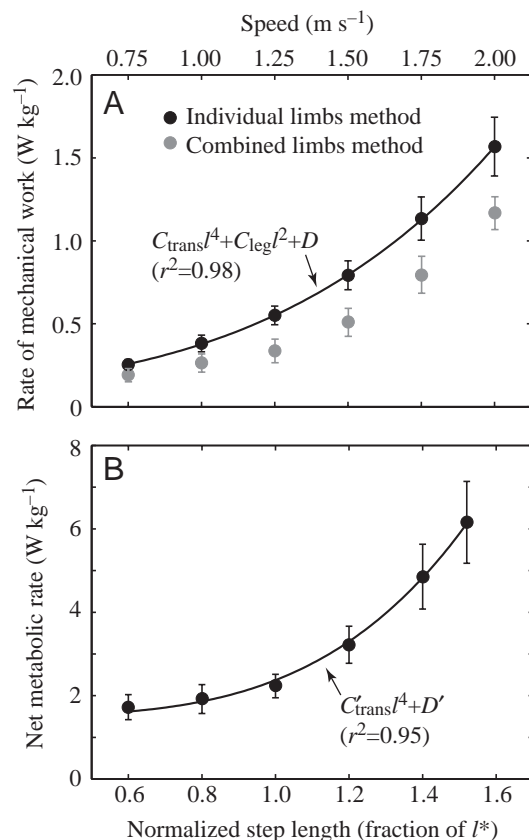


Fig. 5. (A) Increases in negative external mechanical work rate (black circles) and (B) net metabolic rate (black circles) were both dominated by the fourth power of step length l . External mechanical work rate (A) is compared against a nonlinear regression from Equation 3 (black line), and metabolic power (B) is compared against a regression from Equation 4 (black line). Note that traditional combined limbs measures of total negative external mechanical work rate (grey circles in A) underestimated the external work rate generated by the individual limbs. Values shown are means \pm s.d., $N=9$. l^* , preferred step length; C, C', D, D' , constants. See Materials and methods for details.

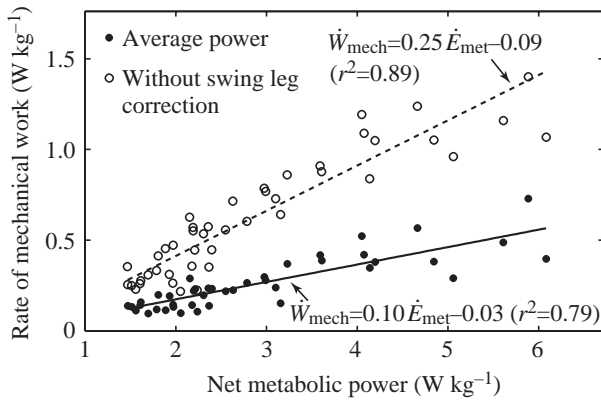


Fig. 6. Correlation between mechanical step-to-step transition costs and metabolic costs for varying step lengths. One estimate for step-to-step transition costs (open circles) is found from negative external mechanical work rate; a least-squares linear regression of these data exhibits linearity (broken line, $r^2=0.89$). This is probably an overestimate because it fails to attribute some of the increases in power to leg motion. A lower bound on step-to-step transition costs (solid circles) is found by correcting for the contribution due to leg motion, $C_{leg}l^2$ (Equation 3); a least-squares linear regression of these data also exhibits linearity (solid line, $r^2=0.79$). These data are for step lengths l^* in the range (0.6–1.4 l^*).

Also in support of our hypothesis, metabolic rate associated with step-to-step transitions increased with the fourth power of step length (Fig. 5B). A nonlinear regression to Equation 4 yielded the coefficients $C_{trans}=0.877\pm 0.060 \text{ W kg}^{-1} \text{ m}^{-4}$ (mean \pm 95% c.i.) and $D'=1.543\pm 0.363 \text{ W kg}^{-1} \text{ m}^{-4}$ (mean \pm s.d.) ($r^2=0.95$). The metabolic step-to-step transition rate therefore increased from 0.11 W kg^{-1} to 5.75 W kg^{-1} over the range of step lengths we used.

Our estimates of the efficiency of step-to-step transitions ranged from 10%–25% (Fig. 6). A linear regression between mechanical costs, correcting for swing leg work, and metabolic costs yielded a slope of 0.10 ± 0.02 (mean \pm 95% c.i.) ($r^2=0.79$), a lower bound on efficiency. Another regression, without the correction for swing leg work, yielded a slope of 0.25 ± 0.03 (mean \pm 95% c.i.) ($r^2=0.89$), likely to be an overestimate of efficiency.

Traditional combined-limbs measures of external mechanical work were on average 31% less than individual-limbs measures (Fig. 5A). The net metabolic cost observed here was substantially higher than that for unconstrained normal walking at the same speeds (e.g. by 87 W at 1.75 m s^{-1} ; Tolani and Kram, 1999; ANOVA, $P=0.0011$) but percentage recovery was not statistically different (ANOVA, $P=0.36$).

Discussion

Walking with longer steps requires considerable mechanical work and exacts a substantial and proportional metabolic cost. The mechanical cost is from energy lost in redirecting the center of mass velocity from step to step, and the positive work to restore that loss. The rate of work increases with the fourth

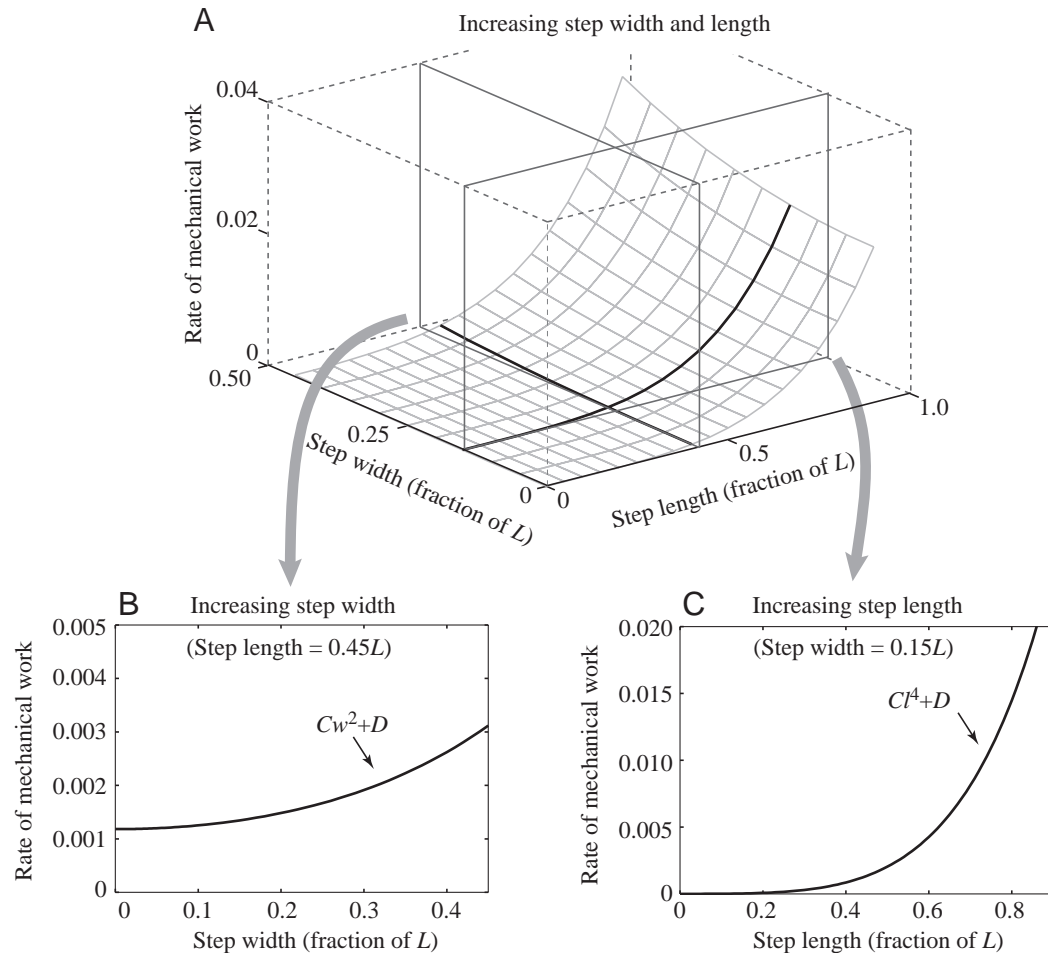
power of step length when step frequency is kept fixed. The proportional metabolic cost is probably due to the (positive) costs of performing both positive and negative mechanical work. Assuming efficiencies of 25% and -120% for positive and negative work, respectively (Margaria, 1976) we would expect a step-to-step transition efficiency of 21%, which falls within our range of estimates (10–25%, Fig. 6). The reasonable model fit ($r^2=0.79$ – 0.89) suggests that the mechanical work of step-to-step transitions does indeed determine the observed increases in metabolic cost, and the low values of estimated efficiencies suggest that elastic energy storage does not substantially contribute to step-to-step transitions over the step lengths tested.

Step-to-step transitions may also account for much of the overall metabolic cost of freely selected gait. The rate of work for these transitions increases sharply with step length, and to a lesser extent, step frequency (Equation 2). Humans typically walk faster by increasing step length and step frequency in almost equal proportion (for a review, see Kuo, 2001), rather than by increasing step length alone as in the present work. The preferred combination of step length and step frequency minimizes metabolic cost of transport (metabolic rate divided by speed, or energy per distance) at a given speed (e.g. Elftman, 1966), and is expected to result in slightly lower, but still substantial, step-to-step transition costs than were observed here.

In addition to step-to-step transitions, there appears to be another substantial component to the metabolic cost of walking that depends more heavily on step frequency (Atzler and Herbst, 1927; Zarrugh et al., 1974). If step-to-step transitions alone determined the metabolic cost of walking, they could be minimized by walking at high step frequencies and short step lengths. The preferred combination of step length and frequency (Elftman, 1966) may be a result of a trade-off between step-to-step transitions and a cost to increasing step frequency, such as for moving the legs back and forth. Indeed, our model of this trade-off predicts the preferred combination (Kuo, 2001). We aim to test the cost of moving the legs, its trade-off against step-to-step transitions, and the contribution of step frequency to step-to-step transitions (Equation 2) in future experiments.

The metabolic cost of high step frequencies does not, however, appear to be proportional to work performed on the legs. The external work originating from leg motion increases with the square of step length, corresponding to the term $C_{leg}l^2$ in our mechanical cost regression (Equation 3). But as predicted by our model, this work appears to contribute negligibly to metabolic cost; addition of a similar term to the metabolic cost regression (Equation 4) does not substantially improve the degree of fit (r^2 increases from 0.955 to 0.957). When walking faster by increasing only step length, metabolic costs associated with leg motion appear not to increase substantially. One possible explanation is that metabolic cost depends more on the cost of producing force, rather than work, to move the legs (Kuo, 2001). This would yield a large cost to high step frequencies that would be nearly constant when step frequency is kept fixed.

Fig. 7. (A) Walking models predict that the mechanical energy dissipated in collisions is a function of step length l and step width w (expressed as fractions of leg length, L). (B,C) Slices through the surface of A. (B) Collision costs increase with step width squared when walking with a fixed, substantial step length, as tested previously (Kuo, 1999; Donelan et al., 2001). (C) Collision costs increase with step length to the fourth power when walking at a fixed step width, as tested here. These predictions were constructed using a simple 3-D walking model (Fig. 1B; Donelan et al., 2001), walking at different step lengths or widths but constrained to walking with a fixed step frequency. C, D , constants. See text for details



Step-to-step transition costs depend not only on step length but also on step width (Fig. 7A). We previously studied transition costs as a function of step width while keeping step length and frequency fixed and found that, as predicted, they increased with the square of step width (Fig. 7B) (Donelan et al., 2001). The present study examined the effect of step length while keeping step width and frequency fixed, and found that transition costs increased with step length to the fourth power (Fig. 7C). These different relationships are predicted by a single model of redirecting of the center of mass between steps.

There are other costs of walking that are not explicitly represented in our models, as indicated by the y-intercept of the mechanical and metabolic power curves (Fig. 5). These offsets (D and D') are important in determining the magnitude of the minimum metabolic cost of transport and the speed at which it occurs (Schmidt-Nielsen, 1990). Metabolic cost of transport is the metabolic energy required to move a unit body weight or mass a unit distance, and animals prefer to move at speeds that minimize this cost (Alexander, 1989). A small part of the mechanical offset, D , may be explained by step-to-step transition costs due to the non-zero step width. There may be other mechanical work required of step-to-step transitions that is not accounted for in our rigid body model, such as to restore energy dissipated from flexible body deformations. It is also

probable that there are additional metabolic costs not attributable to step-to-step transitions or external mechanical work, such as for supporting body weight, moving the legs, moving other limbs, or controlling stability. However, our present data are insufficient to resolve their contributions.

Another limitation is that even though our experimental data are consistent with the proposed model, they also cannot preclude other possible explanations. Our tests were based on a power law relationship predicted by a simple model, in fact the simplest possible model based on mechanics (Garcia et al., 1998). The data fit of Equation 4 contains two coefficients, equivalent to a linear fit, treating l^4 as the independent variable. A linear fit can confirm the statistical significance of the linear coefficient, but cannot prove linearity. Our present results therefore do not prove that the l^4 term is exclusively superior to other possible terms. In addition, polynomials with additional statistical degrees of freedom would almost surely provide better fits. But a model capable of predicting such a polynomial would also probably be more complex than the simple model (Fig. 1A) proposed here. In fact, the predictions of the more complex anthropomorphic model (Fig. 1B) and our experimental data are fitted nearly as well with l^5 , rather than the l^4 of the simple model. We feel that the present analysis is a reasonable compromise between model

simplicity (which facilitates predictions made *a priori*) and goodness of fit. Not only is the model simple, but its physical manifestation (McGeer, 1990) can also walk down a slope with the same scaling of step-to-step transition costs as found here.

Our results are based on a measure of the external mechanical work performed by individual limbs. Traditional combined-limbs measures of external mechanical work (Cavagna et al., 1976) are prone to underestimating step-to-step transition costs because they ignore simultaneous positive and negative mechanical work by the trailing and leading legs (Donelan et al., 2001, 2002). Measures of the total mechanical work performed on the body and limbs (Burdett et al., 1983; Cavagna and Kaneko, 1977; Willems et al., 1995) include work performed both for step-to-step transitions and to swing the leg, of which the latter appears not to contribute to metabolic cost in a proportional relationship. Our measure of external work by individual limbs appears to better quantify step-to-step transitions than combined-limbs measures of external work. It cannot differentiate the effects of swing leg motion, but is less affected by this motion than measures of the overall mechanical work performed on the body and limbs. Still better estimates might result from a more complete separation of step-to-step transitions from swing leg motion, perhaps through a joint power approach to estimating the mechanical work performed by individual limbs (e.g. Winter, 1990) or through measuring muscle mechanical work directly (e.g. Prilutsky et al., 1996; Biewener and Roberts, 2000). The latter would assist in quantifying the degree to which transition work is apportioned between work performed by muscle fibers, elastic energy stored and returned by tendon, and energy dissipated in other structures (see Appendix).

Step-to-step transition costs help to relate the observed metabolic cost of walking with the inverted pendulum paradigm. An inverted pendulum by itself conserves energy while the center of mass moves in a pendular arc. Yet one of the enduring hypotheses of human walking is that it costs energy to produce vertical excursions of the center of mass (Saunders et al., 1953). The present model of step-to-step transition costs predicts that larger vertical excursions of the center of mass will indeed be correlated with, but do not themselves cause, increasing metabolic cost. The vertical motion of an inverted pendulum motion need not consume energy, but the transitions between steps require mechanical work, and it is this work that consumes metabolic energy. Longer steps result in greater vertical excursions of the inverted pendulum, but more importantly, they incur higher step-to-step transition costs. This theory is expected to apply not only to humans, but to any other animals whose walking can be likened to an inverted pendulum.

In summary, humans perform substantial mechanical work to redirect the center of mass velocity during step-to-step transitions. This work exacts a proportional metabolic cost, consistent with studies on slope walking, rowing, cycling and isolated muscle. Legged animals vary widely in size, shape,

and number of legs, but most walk with long steps and some walk with wide steps. The associated cost of step-to-step transitions may be a general and major determinant of the metabolic energy required for walking in all animals that make use of an inverted pendulum mechanism.

Appendix

Model details

Collision costs for the simplest passive walking model are derived as follows. At the end of each step, the transition to a new stance limb (Fig. 2B) requires redirection of the center of mass velocity, from \mathbf{v}_{cm}^- to \mathbf{v}_{cm}^+ (with the superscripts ‘-’ and ‘+’ denoting the instances immediately before and after impact, respectively), accomplished by instantaneous, inelastic collisions. The magnitude of \mathbf{v}_{cm}^+ is:

$$|\mathbf{v}_{\text{cm}}^+| = |\mathbf{v}_{\text{cm}}^-| \cos 2\alpha, \quad (\text{A1})$$

where 2α is the angle between the legs at the transition. This redirection of the center of mass velocity requires negative work by the leading limb. The magnitude of this negative work per step, $W_{\text{trans}}^{(-)}$, is:

$$W_{\text{trans}}^{(-)} = \frac{1}{2}M |\mathbf{v}_{\text{cm}}^-|^2 - \frac{1}{2}M |\mathbf{v}_{\text{cm}}^+|^2, \quad (\text{A2})$$

where M is the mass concentrated at the pelvis. Combining equations A1 and A2 yields:

$$\begin{aligned} W_{\text{trans}}^{(-)} &\propto |\mathbf{v}_{\text{cm}}^-|^2 (1 - \cos^2 2\alpha) \\ &\propto |\mathbf{v}_{\text{cm}}^-|^2 \sin^2 2\alpha \\ &\propto |\mathbf{v}_{\text{cm}}^-|^2 \alpha^2. \end{aligned} \quad (\text{A3})$$

We can restate Equation A3 as follows. First, α is nearly proportional to step length, l , for small angles. Second, \mathbf{v}_{cm}^- is proportional to walking velocity, v . Finally, v is the product of l and step frequency, f , yielding Equation 3 in the main text.

Experimental details

We used the individual-limbs method to calculate external mechanical work (Donelan et al., 2001, 2002). The external mechanical power (Fig. 4D,E), generated by a limb is equal to the dot product of the limb’s ground reaction force, \mathbf{F} , and the velocity of the center of mass, \mathbf{v}_{cm} . The magnitude of negative external mechanical work per step, $W^{(-)}$, performed by a limb is found from the time-integral of the external mechanical power generated by the limb, restricted to the intervals within each step over which the power is negative (denoted by the domain NEG). Total negative individual limb external mechanical work per step, $W_{\text{ILM}}^{(-)}$, is the summed magnitude of negative external mechanical work from each limb. For a biped,

$$\begin{aligned} W_{\text{ILM}}^{(-)} &= W_{\text{trail}}^{(-)} + W_{\text{lead}}^{(-)} \\ &= - \int_{\text{NEG}} (\mathbf{F}_{\text{trail}} \cdot \mathbf{v}_{\text{cm}}) dt - \int_{\text{NEG}} (\mathbf{F}_{\text{lead}} \cdot \mathbf{v}_{\text{cm}}) dt, \end{aligned} \quad (\text{A4})$$

where the subscripts ‘trail’ and ‘lead’ denote the double support trailing and leading limbs, respectively. We discuss

the assumptions and limitations of this method elsewhere (Donelan et al., 2001, 2002).

Analysis details

We use negative external mechanical power, averaged over an entire step, to estimate the mechanical costs of step-to-step transitions. However, average external mechanical work includes not only the work performed during step-to-step transitions, but also work performed to move the legs and perhaps energy fluctuations due to storage and return of elastic energy. Here we discuss briefly how these separate contributions may affect total external mechanical power and metabolic cost.

A large fraction of external mechanical work is due to the work required of step-to-step transitions (Fig. 4E,F). Most of this work occurs during the double support phase. But at longer step lengths, the stance leg performs some of the negative work extending beyond double support, into the beginning of single support (Fig. 4E; collision in Fig. A1). In addition, the stance leg performs some of the positive work prior to double support, at the end of single support (Fig. 4E; propulsion in Fig. A1).

While limb motion involves mostly internal work, it also contributes to the work done on the center of mass because movement of the legs also results in movement of the center

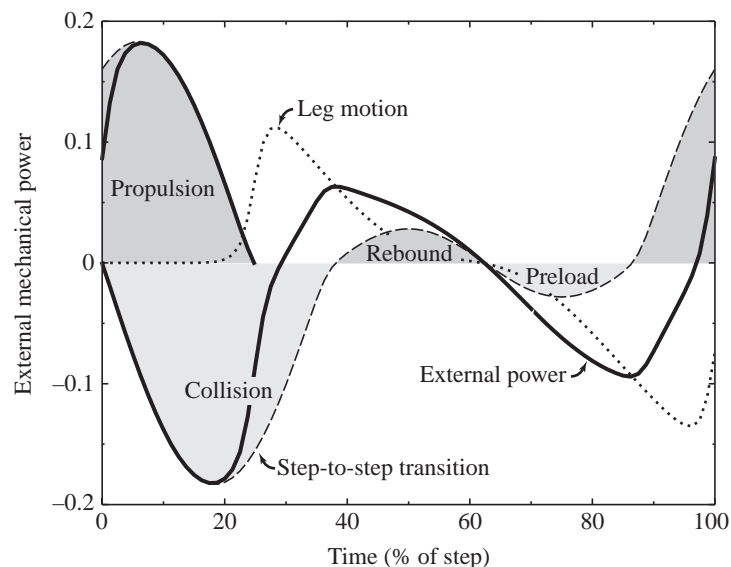


Fig. A1. (Appendix). Conceptual diagram of mathematical cancellation between different contributors to external mechanical power. Simultaneous positive and negative external mechanical power (broken line) is produced during double support due to propulsion and collision, respectively. But collision power in humans also extends beyond double support, and propulsion power also precedes double support. External power due to leg motion (dotted line) overlaps and mathematically cancels these quantities in measurements of external power during single support, even though they do not physically interact. The result is that total external mechanical power (solid line) tends to underestimate the positive and negative power associated with both step-to-step transitions and leg motion.

of mass. This is true even if the legs move passively or otherwise add no net mechanical energy over a step. In an anthropomorphic two-dimensional model with a hip spring acting between the legs (Kuo, 2001), motion of the legs generates positive and negative external mechanical power at the beginning and end of single support, respectively (Fig. A1). The internal mechanical power is equal and opposite, so that there is no net change in total mechanical energy. The magnitude of negative external power increases with the square of step length and the square of step frequency (Fig. 3B). Keeping step frequency fixed, moving the legs therefore contributes a term of the form $C_{leg}l^2$ to our external mechanical power regression model (Equation 3).

External mechanical power for moving the legs partially cancels power generated or dissipated during step-to-step transitions, making it impossible to separate the two contributions from force plate data alone (Fig. A1). This is a mathematical cancellation that is not representative of a physical cancellation, which would require a transfer of energy from one limb to the other. Inclusion of $C_{leg}l^2$ in a regression fit (Equation 3) will therefore underestimate C_{trans} (and C_{leg}), making our estimate a lower bound on step-to-step transition costs. An alternative method is to exclude the swing leg from the regression. But exclusion of $C_{leg}l^2$ from Equation 3 will attribute all increases in total external mechanical power to C_{trans} and none to C_{leg} . Though not a strict upper bound, the result is likely an overestimate of C_{trans} . The results of such a regression are coefficients $C_{trans}=0.200\pm 0.012 \text{ W kg}^{-1} \text{ m}^{-4}$ (95% c.i.) and $D=0.314\pm 0.087 \text{ W kg}^{-1} \text{ m}^{-4}$ ($r^2=0.96$).

External mechanical work measured within a step may have contributions from elastic energy storage and return. We consider three potential cases. First, the external mechanical work for moving the legs (Fig. A1; leg motion) could be due to storage and return of elastic energy by hip tendons rather than work performed by hip muscles (Alexander, 1990; Bennett, 1989). This is supported by previous theoretical work (Kuo, 2001) and by our current finding that metabolic cost is not proportional to work performed on the leg (see Discussion). Second, positive external mechanical work as the leg extends just prior to mid-stance (Fig. A1; rebound) may be due to stored elastic energy during the collision with ground (Fig. A1; collision). Third, negative external mechanical work by the stance limb just after mid-stance may reflect elastic energy being stored in tendon (Fig. A1; preload). The subsequent release of this stored energy would contribute to the positive external mechanical work performed to redirect the center of mass velocity (Fig. A1; propulsion). These potential uses for storage and return of elastic energy represent opportunities to save on work performed by muscle fibers and therefore to reduce metabolic cost. If this reduction is substantial, the measured metabolic cost could potentially differ from the prediction of Equation 4. The present study, however, is insufficient

to quantify elastic energy storage, which is best measured *in vivo* (Prilutsky et al., 1996; Biewener and Roberts, 2000).

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