

Mechanics and energetics of step-to-step transitions isolated from human walking

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SUMMARY

We isolated step-to-step transitions from other contributors to walking mechanics using a cyclical rocking task and then examined the contribution of individual joints to the total work required to redirect the velocity of the center of mass (COM). Nine participants were instructed to rock backward and forward in the sagittal plane, eliminating the need to swing the legs and progress forward. To systematically increase the required work, we increased step length from 60 to 100% of leg length, keeping rocking frequency constant. The individual limbs method quantified the COM work and the joint power method apportioned the COM work among its various sources. As predicted by a physics-based model, we found that work in rocking was performed mainly during the step-to-step transitions and increased strongly with step length. We also found that increases in the average COM work rate exacted a proportional metabolic cost. The similar patterns of COM work and COM work rate during rocking and walking support the use of rocking to isolate the mechanics of step-to-step transitions. We found that the ankle was the main joint contributing to the positive work required to redirect the COM velocity during forward rocking. At the longest length, it accounted for 88% of the work performed by the trailing leg joints. Interestingly, the summed contribution of ankle, knee and hip joint work accounted for only 39% of the front leg negative COM work during the forward transition, suggesting that most of the collision work is performed by passive tissue.

Key words: step-to-step transition, gait, biomechanics, mechanical work, metabolic cost.

INTRODUCTION

Step-to-step transitions are an important determinant of the mechanical work and metabolic cost of walking (Donelan et al., 2002a). The single support phase of walking is characterized by center of mass (COM) motion similar to that of an inverted pendulum (Cavagna et al., 1977), and each transition to a new stance limb requires redirection of the COM velocity from one inverted pendulum arc to the next (Adamczyk and Kuo, 2009; Donelan et al., 2002b). Because ground reaction forces are directed approximately along each leg (Biewener, 1990), redirection of the COM velocity during step-to-step transitions requires either negative collision work by the leading limb, positive push-off work by the trailing limb or some combination of the two (Ruina et al., 2005). Transition work depends strongly on step length during walking because the work required to redirect the COM velocity increases approximately quadratically with both the angle of redirection and the velocity of the COM (Donelan et al., 2002a). Transition work is an important determinant of the metabolic cost of walking, accounting for approximately two-thirds of net metabolic cost when walking at a moderate speed (Kuo et al., 2005).

Although step-to-step transitions appear to be important in walking, there are also other essential sub-tasks. For example, people actively swing their legs to modulate their step frequency (Doke et al., 2005b; Doke and Kuo, 2007). It can be difficult to attribute aspects of walking mechanics to any particular sub-task – both transitions and leg swing contribute to COM work and exact a metabolic cost (Doke et al., 2005a; Donelan et al., 2002a). To study mechanics in isolation, it is desirable to separate transitions from other contributors to walking mechanics. This approach has been used to gain insight into other aspects of gait. Hopping in place, for example, has proven to be a useful simplification to study muscle and joint coordination during running (Farley and Morgenroth, 1999;

Moritz and Farley, 2005; Moritz et al., 2004), and isolated leg swinging has been used to estimate the contribution of the swing phase to the total metabolic cost of walking (Doke et al., 2005b; Doke and Kuo, 2007).

The purpose of this study was to determine the contribution of individual joints to step-to-step transition work. We isolated transitions from other contributors to walking mechanics by instructing participants to rock back and forth from one leg to the other, restricting motion to the sagittal plane, thereby eliminating the need to swing the legs and progress forward (Fig. 1). We increased step length, keeping rocking frequency constant, to systematically increase the work required to redirect the COM during each transition. The individual limbs method quantified the work performed on the COM, and the joint power method apportioned the COM work among its various sources (Donelan et al., 2002b; Winter, 1990). We hypothesized that rocking would capture the following previously identified characteristics of step-to-step transitions in walking (Donelan et al., 2002a; Donelan et al., 2002b): (1) during each transition, the trailing leg would perform positive push-off work while the leading leg would perform negative collision work (the front and back legs have the opposite roles during the backward transition when compared to the forward transition, with the front leg acting as the trailing leg when transitioning backwards); (2) COM work would be performed mainly during the transition periods; (3) COM work would increase strongly with step length; and (4) metabolic power would increase proportional to increases in average COM work rate, defined as total positive COM work divided by rocking cycle duration. Before describing the experiments in more detail, we use a simple physics-based model to motivate our hypotheses and predict how rocking dynamics and transition work depend on step length and push-off work.

MATERIALS AND METHODS

Model

This rocking model consists of a point mass, located at the pelvis, and massless rigid legs of length L with point feet (Fig. 1). When one leg is in contact with the ground, the other leg does not swing but instead remains fixed to the stance leg. The system behaves as a conservative inverted pendulum during these single-support phases. During the transition between single-support phases, the COM velocity is redirected from one leg's pendular trajectory to the next using an impulsive push-off force acting along the trailing leg followed immediately by an impulsive dissipative collision force acting along the leading leg. A full rocking cycle consists of forward and backward half-cycles, defined by the direction of the COM velocity. Transitions between inverted pendulum phases occur in the middle of each half cycle, with the front leg leading during the forward transition and the back leg leading during the backward transition. The step length – the linear distance between the feet – is determined by the angle between the legs.

Rocking dynamics depend upon the relative contributions of forward and backward push-off work. Although the COM velocity has to be redirected during each transition, this can be accomplished by negative collision work by the leading leg, positive push-off work by the trailing leg or some combination of the two. Steady-state rocking requires that no net work is performed over a full rocking cycle; if the forward transition redirects the COM velocity with more positive push-off work than negative collision work, the subsequent backward transition must have more negative collision work than positive push-off work. We varied the work ratio n – the magnitude of backward push-off work relative to forward push-off work – to

understand how the coordination of the COM velocity redirection affects rocking dynamics. We varied n between 0 and 1 by making the backward transition push-off impulse a fraction of the forward transition push-off impulse. The COM velocity after each transition determines the duration of the subsequent inverted pendulum phase. Whenever forward push-off exceeded backward push-off ($n < 1$), the inverted pendulum moved faster after the forward transition when compared with the backward transition (Fig. 2A). To keep the duration of forward and backward half-cycles equal, we actuated the inverted pendulum phase of the front leg using a simple linear spring with stiffness k (right side of Fig. 1A) with rest length set at $\theta = 0$. There are many other ways to actuate the rocking motion and the specific predictions can depend upon the method. Our chosen actuation method appeared to simulate well the mechanism employed by our subjects to keep half-cycle durations equal (*cf.* Discussion). We simulated rocking cycles at different step lengths, l (0.6 – $1.0L$), and work ratios (0 – 1), adjusting k and the initial conditions to find steady-state cycles with equal half-cycle durations.

Underlying our four experimental hypotheses are three robust predictions that arose from analysis of this rocking model. The first prediction is that both forward and backward transitions will employ trailing leg push-off work and leading leg collision work to redirect the COM velocity. Although rocking could be powered with push-off work during only one transition ($n=0$), this results in a fivefold increase in the total positive work required to rock (Fig. 2D). This large penalty is due to: (1) the large increase in the positive push-off work required by the trailing limb to redirect the COM velocity when the redirection is not assisted by negative work by the leading limb (Ruina et al., 2005), which is only partially compensated by

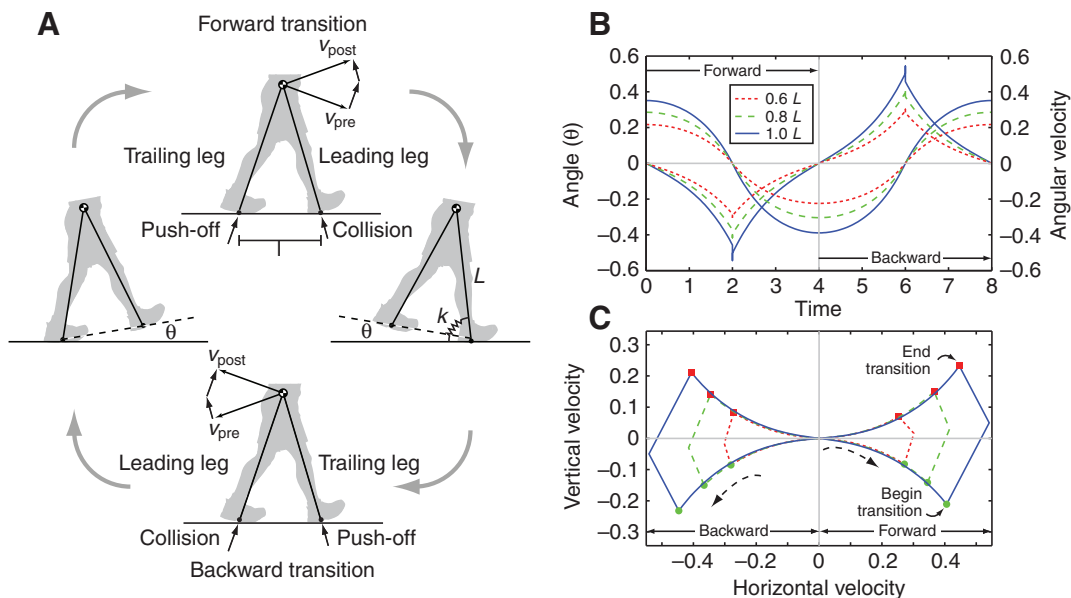


Fig. 1. (A) A physics-based model of sagittal plane rocking consisting of massless rigid legs of length L fixed rigidly to a point-mass pelvis. During single-support phases, the system behaves as an inverted pendulum with one degree of freedom, θ . During the transition between single-support phases, the COM velocity is redirected from the pre-transition velocity, v_{pre} , to the post-transition velocity, v_{post} , using an impulsive push-off force acting along the trailing leg followed immediately by an impulsive collision force acting along the leading leg. A full rocking cycle consists of forward and backward half-cycles, defined by the direction of the COM velocity. Transitions between inverted pendulum phases occur in the middle of each half cycle, with the front leg leading during the forward transition and the back leg leading during the backward transition. The step length, l , is determined by the angle between the legs. To keep the duration of forward and backward half-cycles equal, the front leg is actuated using a simple linear spring, k . (B) Example steady-state rocking mechanics for three different step lengths, all at a work ratio of 0.5. (C) Example model hodographs illustrating the COM velocity changes during the same rocking cycles presented in B. Note how the COM velocity changes from upward to downward during the pendulum phase, and then from downward to upward, owing to push-off and collision forces, during the step-to-step transition. Axes for time and angular, vertical and horizontal velocity are in dimensionless units.

a reduction in the positive work required during the subsequent transition; (2) the backward pre-transition velocity increasing with a reduction in work ratio (Fig. 2A) requiring more work to complete the COM velocity redirection; and (3) the front leg actuation by the spring, required during single-support phases when the work ratio is less than unity, contributing to the total positive work required to rock. The second prediction is that the majority of COM work will be performed during the transition, a pattern that is insensitive to work ratio and its dependence on step length (Fig. 2C). Finally, the third prediction is that average COM work rate will increase with step length (Fig. 2D). This is valid even if work ratio were to change with step length as long as work ratio consistently decreased or increased with length. Our final experimental hypothesis, that metabolic power would increase proportional to increases in average COM work rate, follows from the predicted increase in COM work with length and an assumption of constant muscle efficiency (Donelan et al., 2002a).

Experimental procedures

We determined the COM work, joint work and metabolic costs of rocking as a function of step length in nine healthy participants (eight males and one female; age=28.7±3.7 years, mass=75.1±10.0 kg, $L=0.92\pm0.04$ m, mean ± s.d.). Participants rocked at five different step lengths (0.6–1.0 L), enforced by asking participants to contact two appropriately spaced markers using the heel of their front foot and toe of their back foot. Although rocking removed the need to swing the legs, thereby eliminating its contribution to COM and joint work, there was certainly a metabolic cost associated with supporting

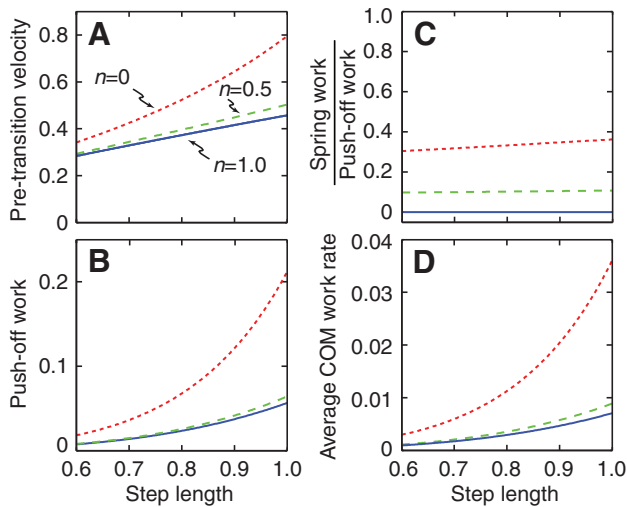


Fig. 2. Modelling results. (A) At longer step lengths, the inverted pendulum phase sweeps through a larger angular displacement, causing the pre-transition COM velocity to increase with length. Although forward pre-transition velocity has a linear dependence on length for all work ratios (solid line), backward pre-transition velocity increases more strongly with length as work ratio decreases. (B) The increase in pre-transition velocity, combined with the effect of step length on the angle through which the COM velocity has to be redirected, causes the sum of the forward and backward push-off work to increase strongly with length. (C) Although the actuation of the front leg contributes to COM work when $n < 1$, the relative contribution of positive COM work performed by the spring to that performed during push-off is relatively small at all work ratios and nearly constant across step length. (D) Consequently, the dependence of average COM work rate on step length is determined mainly by total push-off work at all work ratios. All axes are in dimensionless units.

the leg that was off the ground during the single-support phase. We randomized the step length order and had participants switch front legs after each trial. We enforced a constant dimensionless rocking frequency of 0.50 (25 cycles min^{-1} , on average) by asking participants to match both their front and back foot ground contacts to a metronome beat. This frequency produced large amplitude rocks without requiring the participants to be stationary during single-support phases. *Post hoc* analyses demonstrated that participants rocked at the desired step lengths and frequencies and that rocking half-cycles were of equal duration. Participants were instructed to keep their hands on their hips and restrict their motion to the sagittal plane. We familiarized the participants with the rocking task on the day prior to testing. Simon Fraser University's Office of Research Ethics approved the protocol and participants gave their written informed consent prior to experimentation.

We measured the ground reaction forces, joint kinematics and metabolic cost during each rocking trial. Force plates (Bertec Corporation, Columbus, OH, USA) measured the individual limb ground reaction forces and moments at 960 Hz and these signals were then low-pass filtered (fourth order, zero-lag, 25 Hz cut-off, Butterworth filter). An eight-camera motion capture system (Vicon Motion Systems, Los Angeles, CA, USA) recorded the kinematics of reflective markers placed bilaterally on the fifth metatarsal of the feet, the lateral malleoli, the lateral epicondyles of the knees, the greater trochanters and the sacrum. Marker data were captured at 120 Hz and then low-pass filtered (fourth order, zero-lag, 6 Hz cut-off, Butterworth filter). We measured oxygen consumption and carbon dioxide production (Vmax Encore, SensorMedics Corp., Yorba Linda, CA, USA) to estimate metabolic power (Brockway, 1987; Donelan et al., 2002a). To ensure that participants reached steady state within each 6-min trial, we analyzed respiratory gases over the final 3 min and ground reaction forces and kinematic data over the final 1 min. Prior to beginning the rocking trials, we determined each participant's resting metabolic cost during standing and subtracted this cost from all other metabolic measurements.

Data analyses

We calculated the work performed on the COM using the individual limbs method (Donelan et al., 2002b). Briefly, the rate of work performed on the COM by each leg is defined as the dot product of the individual limb ground reaction force and the COM velocity. To determine COM velocity, we first calculated the acceleration of the COM from the vector sum of ground reaction and gravitational forces and then integrated this acceleration with respect to time. On average, there is zero COM displacement during rocking; we determined the integration constants by forcing the average COM velocity to zero for each rocking cycle. We used inverse dynamics and standard anthropometric tables to determine the ankle, knee and hip joint powers from the measured ground reaction forces and joint kinematics (i.e. joint power method) (de Leva, 1996; Winter, 1990). Because rocking motion occurs primarily in the sagittal plane, we restricted our inverse dynamics analysis to this plane. We defined each rocking cycle as beginning when the COM reversed direction from moving backward to moving forward, and averaged the COM velocity, COM work rate and joint powers across rocking cycles within each trial. After Adamczyk et al., we defined the forward and backward transitions as beginning when the vertical COM velocity reached a minimum and started to be redirected upwards (Fig. 3A) (Adamczyk et al., 2009). The endings of the transitions were defined as occurring when the vertical COM velocity reached its maximum, indicating that the velocity redirection was completed.

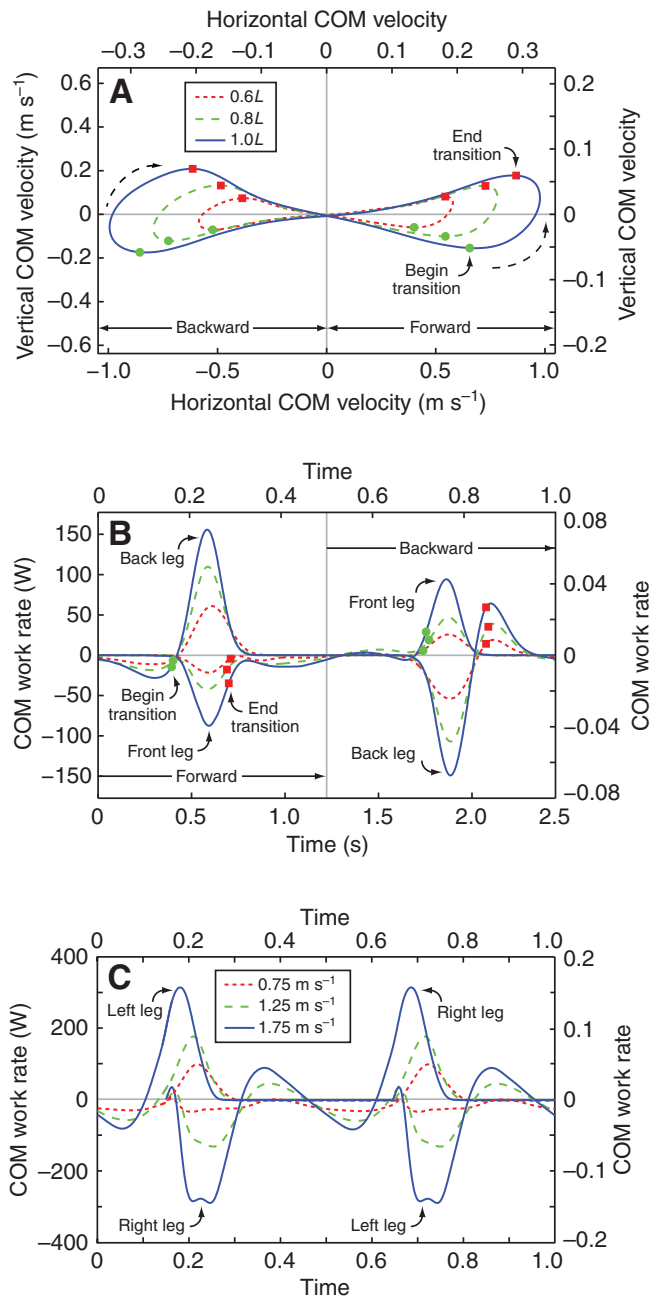


Fig. 3. (A) Rocking COM hodographs illustrate the sagittal plane COM velocity components. The forward and backward transitions began when the vertical COM velocity reached a minimum and it started to be redirected upwards (green circles). The transitions ended when the vertical COM velocity reached its maximum, indicating that the velocity redirection was completed (red squares). (B) Rocking COM work rate. During the forward rocking transition, the front leg performed mainly negative COM work whereas the back leg performed mainly positive work. The role of the front and back legs switched during backward rocking. The data presented in A and B are the means across all participants ($N=9$) at the shortest, intermediate and longest rocking lengths. (C) Walking COM work rate. Comparing B with C illustrates that the patterns of COM work rate performed during walking and rocking are similar, especially during the push-off and collision phases. In walking, one stride is comprised of left and right steps, whereas one rocking cycle is comprised of a forward and a backward half-cycle. The walking COM work rate was adapted from Donelan et al. (Donelan et al., 2002b). Where appropriate, the left and bottom axes are in SI units and the right and top axes are in dimensionless units.

The various measures of work were calculated from cumulative time-integrals of the COM work rate or individual joint powers, restricting the integrations to appropriate phases of the rocking cycle (e.g. forward transition). We defined the average COM work rate as total positive COM work divided by rocking cycle duration.

Where appropriate, statistical comparisons were performed using paired t -tests and repeated-measures ANOVA, with a level of significance of $P < 0.05$. We used regression to determine the dependence of COM work rate and metabolic power on step length, and their dependence on each other, with r^2 and 95% confidence intervals indicating the degree and significance of fit. To account for inter-participant variability, we computed the offset in each relationship separately for each participant and then averaged the offsets across participants (Donelan et al., 2002a). To account for differences in body size, we analyzed all variables in dimensionless form using base units of participant mass, M , gravitational acceleration, g , and leg length, L (Adamczyk and Kuo, 2009; Donelan et al., 2002a). We used mean mass and leg length to re-dimensionalize variables and report results in SI units. All analyses were performed using MATLAB (MathWorks, Natick, MA, USA).

RESULTS

COM work was performed mainly during the step-to-step transitions and increased strongly with step length (Figs 3, 4). During forward rocking, back leg positive COM work (push-off work) increased by 140% from 12 ± 5 J (mean \pm s.d.) at $0.6L$ to 28 ± 8 J at $1.0L$ ($P=1.3E-14$, $N=9$). The magnitude of front leg negative COM work (collision work) also increased strongly from -4 ± 4 to -16 ± 8 J, a 287% increase ($P=1.3E-14$, $N=9$). We observed similar patterns during backwards rocking; front leg push-off work increased by 186% from 6 ± 5 J at $0.6L$ to 16 ± 8 J at $1.0L$ ($P=3.9E-11$, $N=9$) and back leg collision work increased by 120% from -12 ± 4 to -26 ± 6 J ($P=7.6E-12$, $N=9$). The mean work ratio – the relative magnitude of backward push-off work to forward push-off work – was 0.55 ± 0.46 and was independent of step length ($P=0.57$). Most of the COM work during rocking was performed during transitions; participants spent only $25 \pm 2\%$ of the rocking cycle inside of transitions but performed $66 \pm 9\%$ of the COM work during this time (Fig. 3B, Fig. 4).

The ankle was the main joint contributing to the work required to redirect the COM velocity during forward rocking (Figs 4, 5). During the forward transition push-off phase, the back ankle positive work equalled or exceeded the back leg positive COM work. At $0.6L$, for example, the 11 ± 2 J of back ankle work was not significantly different than the 12 ± 4 J of back leg COM work ($P=0.65$). At $1.0L$, the back ankle performed 33 ± 5 J of positive work, 19% greater than the 27 ± 6 J of back leg COM work ($P=3.6E-3$, $N=9$). The knee and hip joints made small contributions to push-off relative to the ankle joint, accounting for a mean of 10 and 2% of the back leg positive COM work, respectively. During the forward transition collision phase, joint work could not explain the negative COM work performed by the front leg. The summed contribution of ankle, knee and hip joint work was only 39% of the front leg COM negative work at $1.0L$ ($P=8.3E-5$, $N=9$), suggesting that more than half of the collision work was performed by sources other than these leg joints. Of the joints, the knee made the greatest contributions to collision work, including -3 ± 1 J of the -16 ± 8 J of front leg COM work at $1.0L$.

Although the legs performed similar functions during forward and backward transitions, the contributions of the individual joints were quite different (Figs 4, 5). Rather than having a dominant

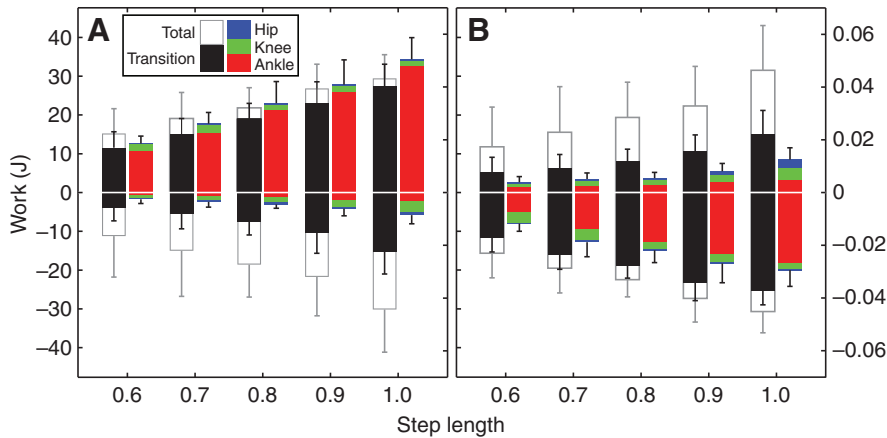


Fig. 4. Average COM work and individual joint work at different step lengths during the forward (A) and backward (B) rocking half-cycles. White bars illustrate the total positive and negative COM work performed by both legs over the full half-cycle. Black bars show the positive COM work performed by the trailing leg during the transition (push-off work) and the negative COM work performed by the leading leg during the transition (collision work). The adjacent coloured bars illustrate the contribution of the trailing and leading leg individual joints to the push-off and collision work with blue, green and red bars illustrating hip, knee and ankle work, respectively. In some cases, the contribution from the hip is too small to be seen clearly. Error bars are \pm s.d. ($N=9$). For clarity, we have shown the error bars for the summed positive and negative joint work rather than for each joint individually. The left axes are in SI units and the right and bottom axes are in dimensionless units.

contribution from the ankle joint, the ankle, knee and hip contributed nearly equal amounts of work during backward push-off. Of the 16 ± 8 J of COM work attributed to front leg push-off, the ankle performed 26%, the knee performed 16% and the hip performed 16% at $1.0L$. Averaged across the measured step lengths, 45% of the front leg COM work was performed by sources other than these leg joints. Whereas the front ankle joint played a small roll during the forward transition, the back ankle was responsible for most of the negative work performed during the backward transition. Of the -26 ± 6 J of COM work attributed to the back leg, the ankle performed 73% at $1.0L$, with much smaller contributions from the knee and hip (5 and 1%, respectively). Averaged across the measured step lengths, 19% of the back leg COM work was performed by sources other than these back leg joints.

The average COM work rate increased strongly with step length and exacted a proportional metabolic cost (Fig. 6). The average COM work rate increased from 0.15 ± 0.03 W kg^{-1} at $0.6L$ to 0.33 ± 0.05 W kg^{-1} at $1.0L$, equating to a 126% increase in work rate over a 67% increase in step length ($P=9.9E-15$, $N=9$). The best-fit power-law relationship between step length and average COM work rate had an exponent of 1.9 ± 1.4 ($R^2=0.95$). Similar to average COM work rate, metabolic cost increased by 101% over the lengths tested – from 1.80 ± 0.24 W kg^{-1} at $0.6L$ to 3.62 ± 0.55 W kg^{-1} at $1.0L$ ($P=3.7E-15$, $N=9$). A power-law equation with the same exponent as for average COM work rate (1.9) also described well the dependence of metabolic cost on step length ($R^2=0.92$). There was a strong positive correlation between metabolic cost and average COM work rate ($R^2=0.92$; Fig. 6C). The dimensionless slope of the best-fit line, 0.09 ± 0.01 , is a measure of the efficiency of transition work in rocking.

DISCUSSION

Rocking appears to isolate the mechanics of step-to-step transitions. Although rocking eliminated the need to swing the legs and progress forward, the COM work-rate patterns exhibited during the transitions of rocking and walking are similar (Fig. 3B,C). As predicted by a physics-based model (Figs 1, 2), the trailing leg performed positive push-off work while the leading leg performed negative collision work during both forward and backward transitions, work was performed mainly during the transition periods and the COM work rate increased strongly with step length (Fig. 3B and Fig. 4). We also found that increases in average COM work rate in rocking

exacted a proportional metabolic cost (Fig. 6). These characteristics of rocking transitions match those observed during walking (Donelan et al., 2002a; Donelan et al., 2002b).

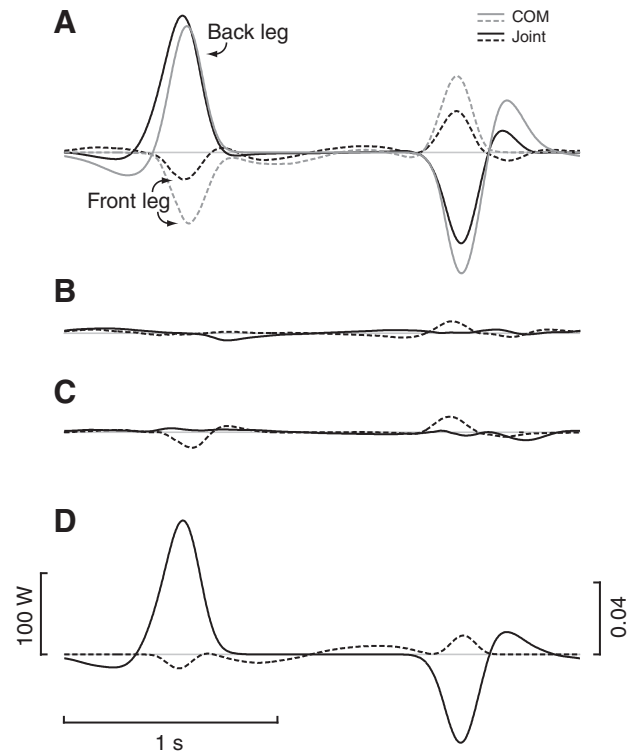


Fig. 5. (A) A comparison of the sum of the individual joint powers (black lines) with the COM work rate (grey lines) illustrates that some of the COM work is performed by sources other than the leg joints, particularly during the forward transition collision phase. The hip (B) and knee (C) joint powers are modest when compared to the contributions from the ankle joints (D). The sagittal plane joint power data are the average across all participants ($N=9$) for a full rocking cycle at the longest step length ($1.0L$). The back and front legs are represented by solid and dashed lines, respectively. The horizontal grey lines indicate zero power, with positive and negative power above and below the line, respectively. The left and bottom scale bars are in SI units and the right scale bar is in dimensionless units. These scale bars apply to all data.

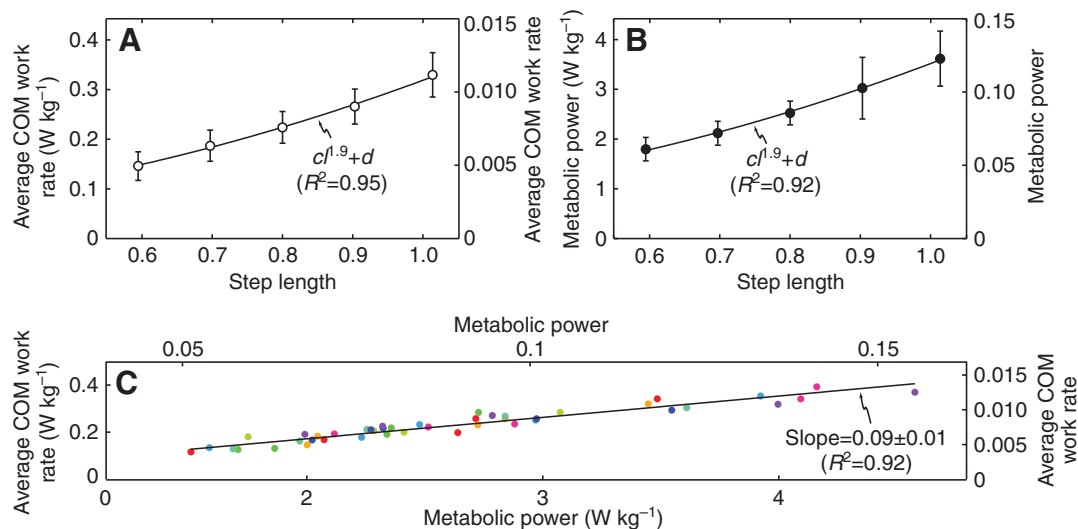


Fig. 6. (A) Average COM work rate increased strongly with step length (l). The dimensionless coefficients for the best-fit power-law relationship illustrated were $c=0.009\pm 0.001$ and $d=0.002\pm 0.001$. (B) Metabolic power also increased strongly with step length. A power-law equation with the same exponent as for average COM work rate also described well the dependence of metabolic cost on step length, but with dimensionless coefficients of $c=0.09\pm 0.01$ and $d=0.04\pm 0.01$. In A and B, the illustrated data points are means \pm s.d. ($N=9$). (C) There was a strong positive correlation between metabolic cost and average COM work rate. Each colour represents a single participant and all step lengths from all participants are included. Where appropriate, the left and bottom axes are in SI units and the right and top axes are in dimensionless units.

Although rocking appears to capture the essential characteristics of walking transitions, there are fundamental differences between the two tasks. First, the COM in rocking does not continuously progress forward as in walking, but reverses directions twice for each rocking cycle. As a result, the COM velocity at the beginning of each transition is lower in rocking than walking when comparing the two at the same step length and frequency, thus requiring less work to redirect the COM velocity (Fig. 3B,C). Second, our estimate of the efficiency of step-to-step transition work ($9\pm 1\%$) is likely lower than that actually used during walking. It is reasonable to assume that backward transitions are considerably less practiced than forward transitions and poor coordination may have contributed to the relatively low measured efficiency. Another likely contributor to the low measured efficiency is a metabolic cost for supporting the gravitational torque of the leg that was off the ground during single-support phases. Previous estimates of transition work efficiency have ranged from 10 to 25% (Donelan et al., 2002a).

Emphasizing the importance of coordinating the COM velocity redirection, the front and back legs used different patterns of joint work to accomplish similar overall leg function during forward and backward transitions. It appears possible to rock with leg functions that differ greatly. When the work ratio is zero in our rocking model, only the forward transition trailing leg performs push-off work (Fig. 2B). This is not the optimal coordination – total work is minimized when positive work is shared equally between forward and backward transitions (Fig. 2D) (Kuo, 2002; Ruina et al., 2005). Correspondingly, our participants performed positive push-off work during each transition, irrespective of transition direction. This similar leg function was accomplished with a dominant contribution from the back ankle joint during the forward push-off but nearly equal contributions from the front leg ankle, knee and hip during the backward push-off (Figs 4, 5). Although overall coordination of leg function was similar, our participants performed significantly more positive work during forward transitions than during backward transitions (Figs 3, 4). The penalty for the preferred work ratio, 0.55, is likely not severe; this work ratio increased total work by 17%

over the optimal coordination in our rocking model. We suspect that participants preferred this manner of rocking because the forward-pointing foot allows the ankle to push off effectively during the forward transition, but little ankle joint displacement is available for pushing off when moving backward. Although the knee joint could perform backward push-off work, it would necessitate that participants keep their knee bent during the previous inverted pendulum phase – an energetically expensive strategy (Gordon et al., 2009; Ortega and Farley, 2005). In addition to performing work to straighten the leg, participants needed to actuate the rocking motion outside of the transitions in order to meet the experimental requirement of equal forward and backward half-cycle durations while preferring unequal division of work between forward and backward transitions (Fig. 2C). This equal timing appeared to be accomplished by the front leg ankle extensors. The ankle performed negative work followed by positive work during front leg single-support phases in a manner similar to the function of the linear spring in our physics-based model (Fig. 5).

The major contributors to push-off and collision work during forward transitions appear to be the ankle joint and soft tissue, respectively. Positive work by the trailing leg ankle met or exceeded the trailing leg push-off work and accounted for nearly all the joint work performed during this phase (Figs 4, 5). This is consistent with the literature that regards the ankle joint as the major contributor to push-off during walking (Sawicki et al., 2009; Winter, 1983). The extra joint work may act to move the body parts relative to the COM, it may do work against other tissues located elsewhere in the body or it may be an artefact of the assumptions required in a two-dimensional inverse dynamics analysis. Interestingly, most of the negative work performed by the leading leg during the transition cannot be attributed to the joints of the leading leg (Fig. 4). Although it is possible that muscles crossing unmodeled joints performed some of the missing work, we suspect that most of it is performed by soft tissue in the legs and torso (Gruber et al., 1998; Pain and Challis, 2006; Zatsiorsky and Prilutsky, 1987). Similarly, Zelik and Kuo found that soft tissue plays a major role in redirecting the COM

velocity using the same comparison of COM work with joint work that we use here, but applied directly to human walking (Zelik and Kuo, 2010). Devita and colleagues have demonstrated that, although the joint power method may overlook work done by soft tissue, it does accurately account for both positive and negative work done by muscle (DeVita et al., 2007).

Performing negative work with passive tissue reduces the negative work required from muscle; however, the direct energy savings is minor. At 1.0L, for example, passive tissue appears to perform approximately -9.4 J of negative work during the forward collision. Assuming an efficiency of -120% (Margaria, 1968), this equates to a 0.04 W kg^{-1} savings – only 1.2% of the total metabolic cost. The indirect benefits may be more meaningful. If participants were to perform forward collision work with the muscles that cross the knee, for example, they would have to flex the knee joint. Participants would then need to either keep the knee bent during single-support phases or do positive knee work timed too early to benefit COM redirection. In either case, there is an associated metabolic cost that is probably substantial. More generally, humans may use negative work by passive tissue to avoid energetically unfavourable leg configurations, a potentially useful mechanism for reducing metabolic cost.

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