

Energetic cost of producing cyclic muscle force, rather than work, to swing the human leg

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Summary

We compared two hypothesized energetic costs for swinging the human leg quickly. The first cost is to perform mechanical work on the leg, and the second is to produce muscle force cyclically at high frequencies. Substantial metabolic energy is expended to perform isolated leg swinging, especially at rates greater than the leg's natural pendular frequency. To determine whether the production of muscle force contributes to this cost, we measured oxygen consumption in human subjects ($N=6$) performing isolated swinging of the leg at frequencies 0.7–1.1 Hz. Amplitude of swing was varied as a function of frequency so that the rate of positive mechanical work performed on the leg remained fixed. We expected that the cost of producing force would increase, in contrast to the cost of performing work. The results showed that average rate of positive mechanical work performed on the leg remained nearly constant as a function of frequency, at

$0.073 \pm 0.014 \text{ W kg}^{-1}$. Net metabolic rate, however, increased by 53%, from 0.66 W kg^{-1} to 1.01 W kg^{-1} . Work may be performed on the leg and with a proportional metabolic cost, but it cannot explain the substantial increases observed here. Metabolic energy expenditure appears to increase in proportion with muscle force or torque, and in inverse proportion to duration of force. This energetic cost may be associated with cyclical calcium transport, where rate-limiting of crossbridge attachments may require greater sarcoplasmic calcium concentration at high frequencies of leg swinging to produce the same amplitude of muscle force. It may also be relevant to moving the legs back and forth relative to the body during walking.

Key words: metabolic energy, locomotion, biomechanics, isometric force, calcium transport.

Introduction

Muscles consume metabolic energy both when performing mechanical work and when simply producing force without work. Most straightforward is the energetic cost of performing work, which occurs at an efficiency of up to 25% (Woledge et al., 1985). Less straightforward is the cost of producing force. Although this cost increases with the magnitude of force, it also appears to increase with cycle frequency when force is produced periodically (Chasiotis et al., 1987). Many rhythmic limb movements involve some combination of work performed on the limb and short, periodic production of force. The cost of producing force may therefore be a substantial component of the overall metabolic cost of these movements.

The cost of producing force cyclically has been demonstrated most directly with electrically stimulated muscle under isometric conditions. Human quadriceps muscle hydrolyzes more adenosine triphosphate (ATP) when stimulated intermittently rather than continuously (Chasiotis et al., 1987), and this cost increases when the stimulation durations are shorter, even when the total stimulation duration is kept the same (Bergstrom and Hultman, 1988). Canine gastrocnemius muscle has been shown to consume 70% more

ATP relative to developed force for shorter durations (0.25 s vs 0.75 s), also keeping the proportion of rest and total stimulation duration constant (Hogan et al., 1998). Intermittently stimulated muscle also appears to fatigue faster (Bergstrom and Hultman, 1988) and produce more lactate (Hogan et al., 1998). The increased energy cost may be associated with activation–deactivation dynamics, and the cost of calcium transport (Verburg et al., 2001) into the sarcoplasmic reticulum (SR).

This cost may also contribute to functional, non-isometric movements. Taylor et al. (Taylor et al., 1980) proposed that the energetic cost of running is dominated by the cost of producing force for short durations. Quantitatively expressed as a cost proportional to body weight and inversely proportional to the duration of ground contact, the cost was found to fit well with data from humans and birds (Roberts et al., 1998). In a study of isolated swinging of the human leg (Doke et al., 2005), we found the net rate of metabolic energy expenditure to increase by about fivefold, from 0.41 to 2.10 W kg^{-1} , as the frequency of swinging increased from 0.5 to 1.1 Hz. The metabolic cost per swing was approximately proportional to hip torque and inversely proportional to swing frequency. We had proposed

that such a cost could explain one of the trade-offs determining the optimum combination of step length and step frequency for walking at a given speed (Kuo, 2001).

Although metabolic cost correlates inversely with force duration, the relationship is not necessarily causal. Mechanical work, of unknown amount, is also performed in the movements listed above. Work therefore also provides an alternative explanation for the observed energetic costs. We cannot definitively attribute the costs of these movements to the production of force without controlling for the production of work.

There is nonetheless reason to expect that the production of force might have substantial cost, particularly in rhythmic movements (Kuo, 2002). A rhythmic movement such as swinging of the leg requires no net mechanical work over a complete cycle. The leg can be swung faster than its pendular natural frequency by applying bursts of force to reverse the motion. This force may perform mechanical work on the leg within a cycle, if it is applied when the leg is moving. However, if force is applied at the extremes of motion, when the leg is moving slowly, there need be little within-cycle work. In fact, human leg swinging is produced with hip torques (proportional to muscle force) that are greatest at the extremes of motion, and at relatively high frequency (Doke et al., 2005). These conditions suggest the possibility of relatively little within-cycle mechanical work and a substantial cost of producing force.

The purpose of the present study was to partially isolate the cost of performing work from that of producing force. These costs can be partially separated by experimentally controlling for the amount of work performed. The rate at which within-cycle work is performed on the leg may be kept constant by swinging the leg at decreasing amplitudes with increasing swing frequency. Cycling rate for force production would, however, be expected to increase with swing frequency. The metabolic rate for producing force would therefore be expected to increase, whereas that for performing work would remain constant.

Materials and methods

We measured the mechanics and energetics of swinging a single human leg at different frequencies but with a constant rate of mechanical work. These conditions are predicted to have different metabolic costs depending on whether production of work or force dominates the energetics of forced leg motion. We devised a theoretical model of leg dynamics to determine the appropriate frequencies and amplitudes of motion and to predict trends in metabolic cost. This model was then tested by measuring energy expenditure of human subjects under conditions determined by the model. A mechanical frame was constructed to hold subjects upright as they performed leg swinging at a variety of frequencies (see Fig. 1), with amplitude controlled through visual feedback. We measured joint torque and leg displacement angle, and used these variables to estimate the work performed on the leg. We also measured

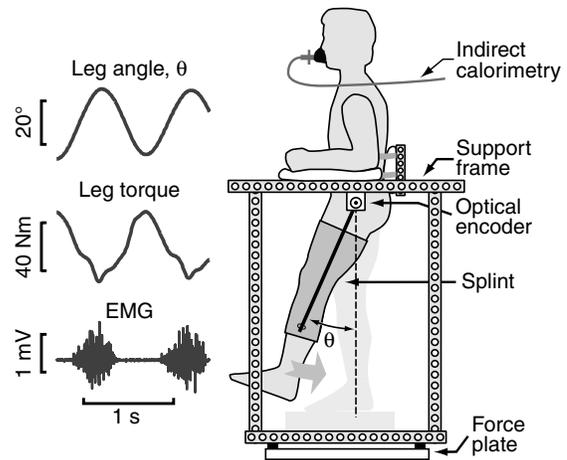


Fig. 1. Experimental apparatus. Subject performed swinging of one leg while securely strapped to a rigid frame. Leg angle θ was measured using an optical encoder. Subjects attempted to swing at a target amplitude, displayed through visual feedback. The target amplitude was varied with frequency to maintain a constant average rate of positive mechanical work on the leg. A force plate measured ground reaction forces, which were used with θ to calculate the leg torque about the hip. Electromyographic (EMG) activity of the medial hamstring was also recorded to assess duration of muscle force production. Oxygen consumption was measured to provide indirect calorimetry of metabolic energy expenditure.

oxygen consumption, and compared these measurements with model predictions to determine how work and force contribute to metabolic energy expenditure.

Model

We modeled two potential explanations for metabolic cost. The work hypothesis predicts that metabolic rate of energy expenditure (hereafter referred to simply as 'metabolic rate') is proportional to the average rate at which positive mechanical work is performed on the leg. The energetic cost may be attributed primarily to cross-bridge cycling (actomyosin ATPase) as work is performed. The cyclic force hypothesis predicts that when muscular force is generated over short periodic intervals, metabolic cost increases with the peak force and inversely with force duration (Doke et al., 2005; Kuo, 2001). This cost may be associated with calcium transport (SR ATPase) after each burst of force (Hogan et al., 1998), rather than cross-bridge cycling. We introduce a simple model of leg swinging, to form quantitative descriptions of how the two competing explanations will predict different energetic costs.

A simple pendulum model of leg swinging predicts how the mechanical work and force acting on the leg depend on amplitude and frequency conditions. The model is identical to one previously presented (Doke et al., 2005). Details of its application to the present study are given in the Appendix. The relevant quantities in the model are the leg angle $\theta(t)$ and torque $T(t)$ applied to the hip (both functions of time t). Both quantities vary approximately as sinusoids, with zero-to-peak amplitudes

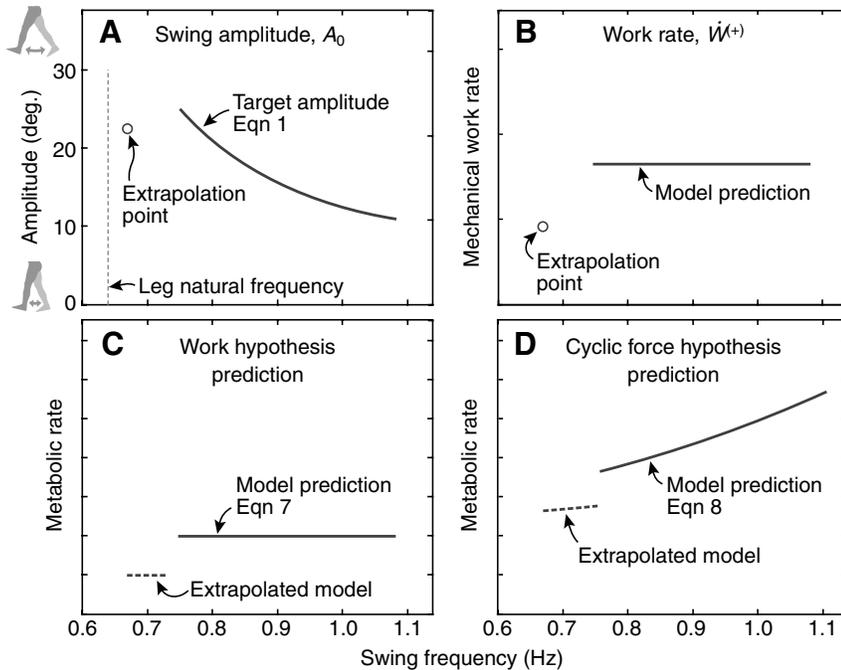


Fig. 2. Model predictions of metabolic energy expenditure as a function of frequency of leg swinging. A simple pendulum model shows that (A) setting target amplitudes to decrease with swing frequency (according to Eqn 1) will result in (B) a constant rate of positive work performed on the leg. (C) The work hypothesis predicts that a constant rate of work will result in a constant rate of metabolic energy expenditure (Eqn 6). (D) In contrast, the cyclic work hypothesis, where energy is expended to produce force for short durations, predicts that metabolic rate will increase with swing frequency (Eqn 7). Both hypotheses predict trends (rather than absolute metabolic rates) that are to be tested against experimental data with least-squares fits. The ability to predict energy expenditure may independently be tested at a different combination of swing frequency and amplitude (extrapolation point, denoted by open circles). The extrapolated model, fitted from the original data, may be compared against the extrapolation data. All predictions apply to swing frequencies at least as fast as the natural frequency, labeled in A, of the leg swinging freely under gravity, as computed from leg inertial properties.

A_0 and T_0 , respectively. The model shows that the average rate of positive work $\dot{W}^{(+)}$ increases approximately with $A_0^2 \times f$, where f is the frequency of swinging (in Hz). If the amplitude changes approximately as $f^{-1.5}$, the work rate $\dot{W}^{(+)}$ will be kept constant. The actual relationship is:

$$\text{Constant work rate: } A_0(f) \propto |f_n^2 f - f^3|^{-0.5}, \quad (1)$$

where f_n is the natural frequency of the leg swinging freely as a pendulum.

Another potential energetic cost is for the cyclic production of force. This is a proposed cost that increases in proportion to force or torque, and inversely with the duration of force (Kuo, 2002; Doke et al., 2005), to explain the substantial metabolic cost of moving the leg back and forth. In mechanical terms, we define a ‘force/time’ quantity, F_τ , to be:

$$F_\tau \propto T_0/\tau \propto T_0 f, \quad (2)$$

where τ is the duration of force. We assume that muscle force at the hip is proportional to torque, and τ is proportional to swing

period (and therefore inversely proportional with f). The metabolic cost per contraction is expected to increase in direct proportion to F_τ for frequencies greater than f_n .

This cost for producing force may potentially be explained by calcium transport energetics. Calcium must be actively pumped into the SR following each burst of muscle force, at a fixed energetic cost of one ATP per two calcium ions (e.g. Ma and Zahalak, 1991). The rate of crossbridge attachment – and therefore the rate of force production – increases with free calcium concentration in the sarcoplasm. When produced cyclically at high frequencies, muscle force may be rate-limited by crossbridge attachment dynamics, unless the calcium concentration is increased. More calcium must therefore be transported at high frequencies, without resulting in more force or a greater number of attached crossbridges. This would explain why the energetic cost per contraction could increase with F_τ , even if force were kept fixed.

We express both predictions in terms of metabolic rate, as can be estimated from rate of oxygen consumption. The work hypothesis predicts that metabolic rate \dot{E} increases with the average rate at which positive work is performed within each cycle, $\dot{W}^{(+)}$, expressed as the proportion:

$$\text{Work hypothesis: } \dot{E} \propto \dot{W}^{(+)} \quad (3)$$

In contrast, the cost of cyclic force production is predicted to increase with the rate of the force/time quantity:

$$\text{Cyclic force hypothesis: } \dot{E} \propto \dot{F}_\tau \quad (4)$$

Applying decreasing amplitude of leg swinging as a function of frequency (Eqn 1; Fig. 2A) will result in a constant rate of positive work (Fig. 2B). The work hypothesis therefore predicts a roughly constant metabolic rate (Fig. 2C), whereas the cyclic force hypothesis predicts an increasing metabolic rate (Fig. 2D), by combining Eqn 1, Eqn 2 and Eqn 4. These predictions only apply to swinging movements that are faster than the leg’s natural frequency f_n . At frequencies lower than f_n , work must be performed on the leg and would be expected to dominate over force.

Experimental procedure

We tested the two potential costs on six male subjects (aged 29.8 ± 4.9 years, mean \pm s.d.) performing swinging of a single leg in the sagittal plane at a range of frequencies, keeping rate of work approximately fixed (see Fig. 1). All subjects were healthy, had similar stature (body mass 69.0 ± 4.3 kg, leg length 0.95 ± 0.05 m), and had no clinical gait abnormalities. They gave their informed consent to participate in the study. We

measured mechanical and metabolic costs of swinging the leg at six frequencies ranging from 0.67 Hz to 1.08 Hz. The lower bound was close to the estimated pendular natural frequency of subjects' legs (Doke et al., 2005). Each subject was instructed to stand on one leg and swing the other leg at the specified amplitude and frequency for 6 min at a time, with the first 3 min of energy expenditure data discarded to allow subjects to reach steady state. Visual feedback of the subject's swing leg angle was displayed in real time on a computer screen, with two lines indicating the target amplitudes. Frequency was controlled with audible feedback from a metronome. Trial order was randomized to reduce fatigue and ordering effects, and subjects were allowed to rest for at least 1 min between trials.

The rate of mechanical work was kept fixed by selecting swing amplitudes as a function of frequency (see Fig. 2). We selected a frequency of 0.75 Hz and amplitude of 25° as the base condition, from which the smaller amplitudes at the higher frequencies were derived according to Eqn 1. A single additional trial was conducted at an amplitude of 22.5° and frequency of 0.67 Hz to match our previous study of leg swinging at fixed amplitude (Doke et al., 2005). This condition was not included in subsequent model fits, but did serve as a basis for comparison against previous results and also as a test of the model's ability to extrapolate predictions of metabolic cost.

We measured ground reaction forces and swing leg displacement as each subject swung their left leg. Subjects stood within a metal frame with a foot platform for the supporting leg, with the body supported and stabilized through padded back and arm rests. An optical encoder placed at hip height on the frame measured the swing leg displacement. A force platform underneath the frame measured the ground reaction forces and moments in three axes, at a sampling rate of 120 Hz. The upper body was strapped securely to the frame, and each subject wore a lightweight knee splint on their swing leg to prevent the knee from bending. We used anthropometric measurements to estimate the inertial properties of the leg (Yeadon and Morlock, 1989), and applied these parameters with recorded data in inverse dynamics equations (Kuo, 1998) to calculate the hip reaction torque. The average rate of positive mechanical work performed on the leg was calculated by integrating the positive intervals of the product of hip reaction torque and angular velocity of the swing leg, and dividing by the duration of the whole trial.

We measured metabolic energy expenditure using an open circuit respirometry system (VMax29, Sensory Medics Corp., Yorba Linda, CA, USA). We collected a baseline measurement of the subject standing still inside the ergometer on one leg and subtracted it from the other data to yield net metabolic rate. We calculated net metabolic rate, \dot{E} , based on the average rate of oxygen consumption subtracted by resting baseline during quiet standing. We assumed a rate of 20.96 W for 1 ml O₂ s⁻¹. We monitored the respiratory exchange ratio (RER) during the experiment, and we confirmed that the whole experiment was conducted under aerobic conditions.

To account for subject differences in body size, we analyzed mechanics and metabolic data using dimensionless variables. Body mass M , gravity g , and leg length l served as the base units. Some subjects also tended to swing the leg at above or below the target amplitude. To account for these differences, we included each subject's actual amplitude divided by the target amplitude, denoting the ratio \tilde{A}_0 , in the normalization. Hip torque was therefore normalized by $\tilde{A}_0 M g^{0.5} l^{0.5}$ (mean value 157.38 N m), and rates of mechanical work and metabolic rate were both normalized by $\tilde{A}_0^2 M g^{1.5} l^{0.5}$ (mean value 1729.45 W). For the reader's convenience, data are also reported in dimensional units such as N m and W kg⁻¹, found by multiplying dimensionless quantities by the mean normalization factors.

Simple surface electromyographic (EMG) measurements were taken to verify whether durations of muscle activity were decreasing with swing frequency, as was assumed for the cyclic force hypothesis (Eqn 4). The EMG signals were taken from the medial hamstring (MH; electrode placed over semitendinosus) and rectus femoris (RF) of the swing leg using a custom-made EMG preamp system. Data were recorded from all subjects for MH, but only three subjects for RF. Electrodes were placed underneath the leg splint. Data were recorded over a 1 min interval during each trial, at a sampling rate of 1 kHz. These data were first high-pass filtered at 20 Hz, then rectified, and then separated into bursts using a minimum threshold of 0.04 mV. Average burst durations were determined from these data, which were then low-pass filtered at 25 Hz before calculating average root-mean-square (RMS) values. Both burst duration and RMS were calculated from at least 15 bursts per trial.

Model fits

Mechanics and metabolic rate data were compared against the predictions for work and cyclic force. We tested whether subjects produced the target amplitudes as a function of frequency, and whether this yielded the expected relationships in rate of work $\dot{W}^{(+)}$, torque amplitude T_0 , and duration of EMG bursts τ . Finally, the measured rate of metabolic energy expenditure, \dot{E} , was compared against the predictions from the work and cyclic force hypotheses.

We performed regression tests on our data using the pendulum model described above. The previous study has shown a good fit to this model (Doke et al., 2005), and here, we further support the model using the constant mechanical work rate condition. We tested the predictability of the model on torque amplitude T_0 , average rate of positive mechanical work $\dot{W}^{(+)}$, and metabolic rate \dot{E} . A regression formed from a leading term approximation of hip torque (see Appendix) has the form:

$$T_0 = C_T \times f^{0.5} + D_T, \quad (5)$$

where f is frequency in Hz. The offset D_T was included because subjects use a small amount of torque to control the leg even when swinging at the natural frequency (Doke et al., 2005). All other fits also included constants C and D determined by

regression, with subscripts T, W, E or F, denoting torque, work, energy or force, respectively.

EMG patterns were also examined as a function of swing frequency. We tested whether burst duration τ was proportional to f^{-1} , as would be expected if muscles were cyclically activated with constant duty factor. We also examined RMS EMG to determine whether it increased with swing frequency in a manner similar to the predicted hip torque amplitude (Eqn 5).

We then tested the metabolic rate predictions. Because of our experimental condition, we expect the rate of mechanical work to be constant. The work hypothesis would therefore predict constant metabolic rate (Eqn 1 and Eqn 3):

$$\dot{E} = C_W, \quad (6)$$

where C_W is a constant. In contrast, the cyclic force hypothesis predicts that metabolic rate will increase with the frequency raised to the 2.5 power for frequencies above f_n . We therefore tested the regression (based on Eqn 1 and Eqn 4):

$$\dot{E} = C_E \times f^{2.5} + D_E. \quad (7)$$

We also tested for a linear relationship between metabolic rate and the empirically measured force/time:

$$\dot{E} = C_F \times \dot{F}_\tau + D_F. \quad (8)$$

Offsets D_E and D_F allow for constant costs associated with supporting body weight on one leg and stabilizing against the support frame. Different subjects expended differing amounts of metabolic energy even under the same conditions. As with hip torque, energy is expended even when swinging at the leg's natural frequency, to overcome small friction losses and perhaps to provide small corrective torques in order to follow the target amplitude and frequency. We therefore allowed for different individual offsets, D_T , D_E and D_F in the regressions above.

Results

The leg swinging data and associated energy expenditure data compared well with the pendulum model. Subjects performed leg swinging at approximately the target amplitudes we specified, yielding the expected trends in hip torque and rate of work. Subjects produced decreasing amplitudes of leg swing (Fig. 3A) that matched well ($R^2=0.98$) with the specified values (Eqn 1). The hip torque amplitude (Fig. 3B) increased approximately with $f^{0.5}$ (Eqn 5, $R^2=0.97$), with regression coefficients, with f in units of s^{-1} and yielding units of N m, of $C_T=49.42\pm 4.89$ (95% confidence interval, CI) and $D_T=-31.34\pm 2.63$ (mean \pm s.d.). The rate of positive work $\dot{W}^{(+)}$ (Fig. 3C) performed on the leg remained nearly constant with swing frequency, with an average value of 0.073 ± 0.014 $W\ kg^{-1}$. A linear regression yielded a slope of -0.015 ± 0.017 (CI) $W\ s\ kg^{-1}$, not significantly different from zero ($P>0.05$ from 95% CI).

There was a substantial decrease in EMG burst duration (Fig. 4A) with swing frequency. Burst duration decreased

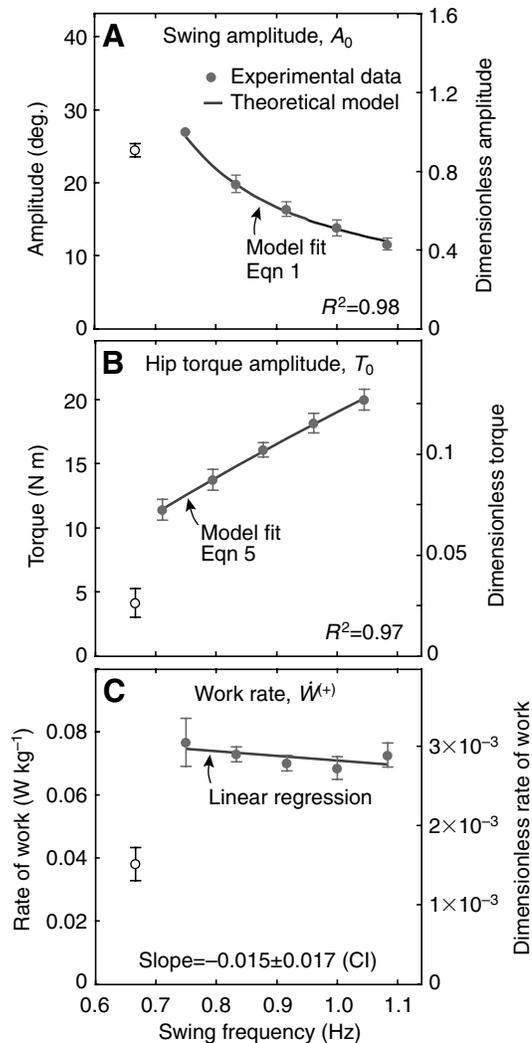


Fig. 3. Mechanics of leg swinging as a function of frequency f , were modeled well by a forced pendulum. (A) Subjects performed leg swinging at decreasing amplitudes (filled symbols) with increasing frequency. Target swing amplitudes were selected (Eqn 1) to maintain a constant average rate of positive mechanical work. An additional trial (open symbols) was performed at smaller amplitude of 0.67 Hz, to provide an independent test of metabolic energy predictions. (B) Hip torque amplitude T_0 increased with $f^{0.5}$ ($R^2=0.97$), as predicted by the pendulum model (Eqn 5). (C) The average rate of positive mechanical work, $\dot{W}^{(+)}$, remained nearly constant for frequencies between 0.75 Hz and 1.08 Hz. A linear fit to these data yielded a slope not significantly different from zero ($P>0.05$). These data demonstrate that the experimental conditions successfully produced leg swinging at a variety of frequencies but keeping rate of mechanical work constant, facilitating the isolation of the cyclic force cost. Data fits were performed using dimensionless variables (right-hand axis) with body mass, gravitational constant, and leg length serving as base units; conventional units are shown (left-hand axis) for convenience. Data values shown are means \pm s.d. ($N=6$).

approximately in inverse proportion to frequency, with $R^2=0.72$ for MH and $R^2=0.72$ for RF ($P<0.05$ for both MH and RF). This decrease was accompanied by an increase in average RMS of

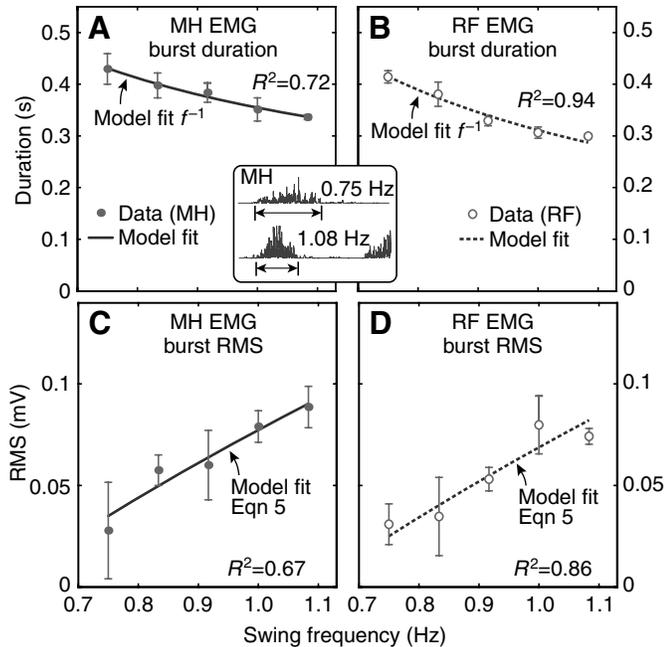


Fig. 4. Electromyography (EMG) data showed decreasing burst durations and increasing amplitudes as a function of swing frequency. (A) Medial hamstring (MH) and (B) rectus femoris (RF) average burst durations, τ , decreased in inverse proportion to swing frequency f ($P < 0.05$; $R^2 = 0.72$ and 0.94 , respectively), as expected. Burst durations were determined from rectified EMG (as shown by inset diagram). Root-mean-square (RMS) amplitudes of (C) MH and (D) RF increased with leg swing frequency ($R^2 = 0.67$ and 0.86 , respectively), roughly similar to hip torque amplitude (Eqn 5). RMS amplitudes were determined from low-pass filtered, rectified EMG. Data shown (filled and unfilled circles) are means \pm s.d. ($N = 6$ for A–C; $N = 3$ for D). Model fits were performed in accordance with predicted trends (f^{-1} and Eqn 5, respectively), with coefficients determined by least-squares fits.

EMG bursts (Fig. 4B). The contraction duration for MH decreased from 0.430 ± 0.030 s to 0.338 ± 0.005 s (mean \pm s.d.) as swing frequency increased, and duration for RF decreased from 0.414 ± 0.011 s to 0.300 ± 0.004 s. Average RMS increased from 0.028 ± 0.023 mV to 0.089 ± 0.010 mV for MH, and 0.031 ± 0.010 to 0.074 ± 0.004 mV for RF. Although RMS of EMG bursts was not explicitly expected to be proportional to hip torque, it followed a similar trend to torque (Eqn 5, $R^2 = 0.67$).

Even though the rate of positive mechanical work was nearly constant with frequency, the rate of metabolic energy expenditure increased substantially ($P < 0.05$). Subjects consumed an average of 4.46 ± 0.72 ml O_2 s^{-1} when standing quietly. When swinging the leg at 0.75 Hz, subjects consumed a net average of 2.23 ± 0.44 ml O_2 s^{-1} (mean \pm s.d.), equivalent to 0.66 ± 0.13 W kg^{-1} . Net metabolic rate \dot{E} increased by 52.9%, to 3.44 ± 0.22 , equivalent to 1.01 ± 0.07 W kg^{-1} at 1.08 Hz (Fig. 5A). Metabolic rate increased approximately with $f^{2.5}$ as in Eqn 7 ($R^2 = 0.95$). The regression coefficients were $C_E = 0.433 \pm 0.138$ (CI) and $D_E = 0.459 \pm 0.370$ (mean \pm s.d.), with f in units of s^{-1} and metabolic rate in units of W kg^{-1} . These

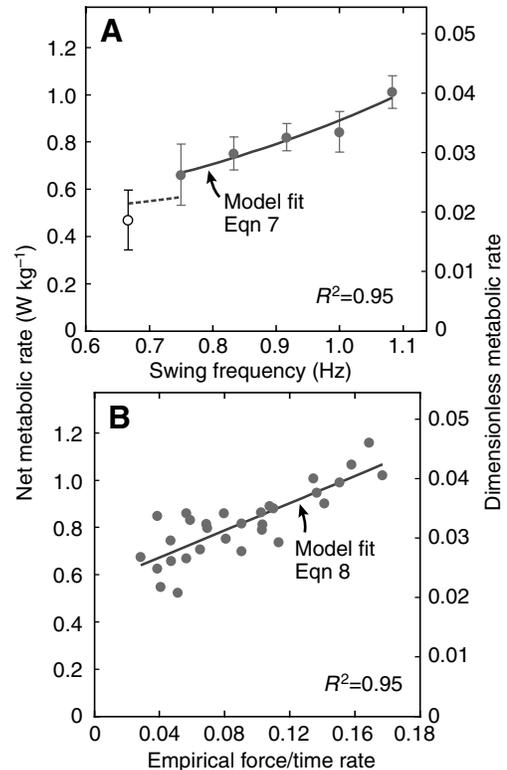


Fig. 5. Metabolic rate was predicted well by the cyclic force hypothesis. (A) Metabolic rate, \dot{E} , increased ($P < 0.05$), approximately with frequency f raised to the 2.5 power, as in Eqn 7 ($R^2 = 0.95$). The same prediction, extrapolated to the low-amplitude trial performed at 0.67 Hz (broken line), also agrees reasonably well with the independently measured data (open symbol). (B) Metabolic rate also increased approximately linearly with the empirically measured rate of force/time \dot{F}_T , as in Eqn 8 ($R^2 = 0.95$).

same regression coefficients were able to extrapolate to the low-amplitude trial at 0.67 Hz. Adjusting for the smaller amplitude used at 0.67 Hz, the coefficients yielded a predicted rate of 0.54 W kg^{-1} , agreeing well with the corresponding metabolic rate, 0.47 ± 0.13 W kg^{-1} .

In a separate comparison, \dot{E} also increased approximately linearly with the empirical force/time \dot{F}_T (Eqn 8; $P < 0.05$), with $R^2 = 0.95$ (Fig. 5B). The regression coefficients were $C_F = 2.88 \pm 0.90$ (CI) and $D_F = 0.56 \pm 0.36$ (mean \pm s.d.), expressed in dimensionless units.

Discussion

The purpose of this study was to distinguish between two potential explanations for the metabolic cost of swinging the leg. Pendular mechanics make it possible to swing the leg at the natural frequency with very little muscular work or force, but increasing effort is needed to swing the leg quickly. One possible explanation for this increasing cost is for the work performed by muscle fascicles during each leg swing (work hypothesis). Another explanation is that energy is expended to produce muscle force for short durations (cyclic force

hypothesis). Previous results showed a sharp increase in energy expenditure rate with swing frequency when swing amplitude was kept fixed (Doke et al., 2005), but these conditions did not allow the two potential costs to be distinguished. In the present study, we kept strict control over the mechanical work rate. When the rate of positive mechanical work is kept fixed, the two potential costs yield highly disparate energy expenditure predictions. This facilitates the determination of whether the cost of generating force is significant.

The work hypothesis does not explain the increases in energy expenditure we observed. By varying the amplitude of swinging according to the prescribed function of frequency (Eqn 1), subjects kept the rate of mechanical work nearly constant. Assuming constant efficiency of work, metabolic rate would also be expected to be constant, in contrast to the 52.9% increase observed here. Actomyosin ATPase efficiency decreases with movement speed (e.g. Howard, 2001), but this cannot explain the increased energy expenditure. The angular velocity of leg motion (amplitude of $\dot{\theta}$) actually decreased with swing frequency, implying an increase in efficiency and therefore a decreasing metabolic rate from the work hypothesis. Nor does series elasticity explain the increase, because the amount of elastic energy stored and returned per cycle would be expected to increase with swing frequency (Kuo, 2002), reducing the proportion of active work performed. The observed increase in metabolic rate must therefore be attributed to mechanisms other than the amount or efficiency of work performed.

Our results support the cyclic force hypothesis. It predicts that, under conditions of fixed rate of positive mechanical work, metabolic rate will increase approximately with the 2.5 power of swing frequency. Empirical results agreed well with this prediction ($R^2=0.95$). A related prediction is that metabolic rate \dot{E} will increase approximately linearly with \dot{F}_τ , the empirically measured rate of force/time (Eqn 8). Our results also agreed well with this linear prediction ($R^2=0.95$). We previously observed a similar linear relationship under a different set of conditions, with swing amplitude fixed (Doke et al., 2005). The same cyclic force model is consistent with both the present and previous sets of conditions.

This is not to suggest that muscle fascicles perform no work during leg swinging, or at no energetic cost. Active contractile work is almost certainly performed on the leg, but in amounts and with energetic costs that cannot explain the increases in metabolic rate observed here. Under the conditions of constant rate of work performed on the leg (Eqn 1), muscle fascicle work would be expected to contribute to the constant offset D_E in metabolic rate, or even a decreasing term due to movement speed or elasticity. Unfortunately, it is difficult to determine the amount of this contribution without making more direct measurements. Depending on the duty factor of force production and the compliance of passive series elastic elements, the fascicles themselves can theoretically account for practically any proportion of the work performed on the leg. The work performed on the leg serves as an upper bound on, rather than an estimate of, the work produced by muscle fascicles. However, regardless of the amount of such work, the

associated energetic costs would not be expected to contribute to the observed increases in metabolic rate.

Our results may be viewed as a decrease in apparent efficiency of muscle work. Apparent efficiency, defined as rate of mechanical work performed on the leg divided by rate of metabolic energy expended, decreased with frequency of contraction. Here, the rate of work was nearly constant, so that the average delta apparent efficiency (change in work rate divided by change in metabolic rate) was -1.08% . This is far lower than the peak efficiency of human muscle of about 25% (e.g. Woledge et al., 1985), indicating that energetic costs other than actomyosin ATPase may be substantial. This decrease may be due to energetic costs not related to cross-bridge activity.

The high energetic costs here may be associated with calcium transport. Others have long implicated SR ATPase activity in overall energy cost (Bergstrom and Hultman, 1988; Hogan et al., 1998). SR ATPase can be as much as 50% greater than actomyosin ATPase (Szentesi et al., 2001), depending on the contraction conditions and muscle fiber type (Homsher and Kean, 1978). In leg swinging, where little contractile work need be performed, Ca^{2+} pumping may even dominate the increases in energy cost observed here. We have proposed a crude quantitative model for cyclic force production, in terms of behavior of the leg. Although the trends in energy expenditure agreed with our model, our experiment did not directly test the mechanism for the trends.

Two types of experimentation may further elucidate the energetic cost of moving the legs. Preparations that isolate single muscle fibers or single muscles provide the best means of imposing controlled contraction conditions and measuring local energy expenditure (e.g. Hogan et al., 1998). In whole animals, embedded sensors make it possible to measure tendon lengths *in vivo* (e.g. Hoyt et al., 2005), while energy expenditure may be assessed through conventional respirometry or by more sophisticated methods for estimating local expenditure (Marsh et al., 2004). Both types of experiments can provide more direct measurements than were possible in the present study. Isolated leg swinging is useful as a functional behavior, but the associated metabolic cost may ultimately be understood through studies of a more reduced nature.

The metabolic cost of producing cyclic force may be relevant to the motion of the legs during walking. Walking is certainly more complex than the isolated leg swinging performed here, where the legs were kept straight, did not support body weight, and performed no net work over a full cycle. These same simplifications were intended to separate the cost of moving the legs relative to the body from other costs, for performing work on the body center of mass and for supporting body weight. If net work is performed at the hips during walking, it must ultimately contribute to motion of the body center of mass, rather than to that of the legs themselves (otherwise the frequency of swinging would continually increase). The forced back-and-forth motion of the legs, even with no net work, necessitates the production of force for short durations. Our previous study (Doke et al., 2005) demonstrated a substantial energetic cost for isolated

swinging of the leg, under conditions that approximated the range of hip torque and swing amplitude used in walking. The complexity of walking, with work and force produced about other joints such as the knee, would only be expected to add to the cost predicted for cyclic force.

We propose that two energetic costs trade off against each other to determine the optimum step frequency of walking (Kuo, 2001). The first cost is for work performed on the body center of mass. The leading leg performs negative work on the body center of mass with each step, necessitating an equal amount of positive work to maintain a steady walking speed. This positive work may be performed throughout the gait cycle, but appears to be performed largely by the trailing leg simultaneous with the negative work of the leading leg. This work appears to exact a proportional metabolic cost, termed the step-to-step transition cost (Kuo et al., 2005). The second energetic cost is for forced motion of the legs. If this cost is dominated by the production of cyclic force, it will increase with stride frequency (typically 0.9 Hz when walking at 1.3 m s⁻¹) (Doke et al., 2005), whereas step-to-step transition costs increase with stride length. Walking speed is the product of stride length and frequency, and the optimum combination at a given speed is predicted by the trade-off between the theoretical costs of step-to-step transitions and cyclic force.

We have shown that mechanical work alone cannot explain the metabolic cost of swinging the leg quickly. The amount of work performed by muscle fascicles can potentially be much lower than that performed on the leg. Series elasticity makes it possible to swing the leg back and forth without performing any active contractile work. But regardless of the amount of work, muscle force is needed to move the leg at higher than the natural frequency. The metabolic cost of producing this force appears to be predicted well by cyclic force hypothesis.

List of symbols and abbreviations

<i>A</i>	amplitude
<i>C, D</i>	constants
\dot{E}	rate of energy expenditure
EMG	electromyographic
<i>f</i>	frequency
<i>F</i>	force
<i>g</i>	gravity
<i>l</i>	leg length
<i>M</i>	body mass
MH	medial hamstring
RER	respiratory exchange ratio
RF	rectus femoris
RMS	root-mean-square
SR	sarcoplasmic reticulum
<i>t</i>	time
<i>T</i>	torque
\dot{W}	work rate
θ	angle
τ	duration

Appendix

We applied a simple pendulum model of leg swinging. Assuming negligible damping, the equation of motion for a single-link pendulum, with position θ measured with respect to vertical, is:

$$I_h \ddot{\theta}(t) + mg l \sin \theta(t) = T(t), \quad (\text{A1})$$

where m is the mass of the leg, l is the distance from the hip to the leg's center of mass, g is gravitational acceleration, and $T(t)$ is the hip torque applied by muscle. We lump the parameters into a single parameter ω_n , the pendular natural frequency (in rad s⁻¹; $\omega_n = 2\pi f_n$, where f_n is in Hz), to yield the linearized equation:

$$\ddot{\theta}(t) + \omega_n^2 \theta(t) = T(t) / I_h. \quad (\text{A2})$$

The natural frequency may be affected slightly by the soft tissues that surround the hip, but is dominated by leg inertia (Doke et al., 2005). The linearization and subsequent analysis depend on a small-angle approximation, $\sin \theta \approx \theta$. At the largest leg amplitude observed here, 25° (similar to the amplitude in normal human walking), the error introduced by the approximation is about 3.2%. We assume that the leg is driven sinusoidally:

$$\theta(t) = A(\omega) \cos \omega t, \quad (\text{A3})$$

where $A(\omega)$ is the amplitude as a function of frequency of motion ω . Substituting Eqn A3 into Eqn A2 yields:

$$T(t) = I_h A(\omega) \times [\omega_n^2 - \omega^2] \cos \omega t. \quad (\text{A4})$$

We assume that the muscle force acting on the leg is proportional to $T(t)$. The (zero-to-peak) amplitude of Eqn. A4, termed T_0 , behaves according to:

$$T_0 \propto A(\omega) \times |\omega_n^2 - \omega^2|. \quad (\text{A5})$$

Although no net work is performed on the leg over a cycle, both positive and negative work must be performed during each swing to drive the leg at fast frequencies. The average rate of positive mechanical work is found by integrating the product of torque and angular velocity over the duration of positive mechanical power, and then dividing by the period, to yield:

$$\dot{W}^{(+)} \propto A^2(\omega) \times |\omega_n^2 - \omega^2| \omega. \quad (\text{A6})$$

For movements faster than the natural frequency, the work rate is dominated by the leading term, $A^2 \omega^3$.

The separate effects of work and force can be distinguished by varying amplitude such that rate of work remains fixed with frequency, but not torque amplitude. This is accomplished with an amplitude:

$$\text{constant work rate: } A(f) \propto |f_n^2 f - f^3|^{0.5}, \quad (\text{A7})$$

expressed in terms of frequency f in Hz.

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