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Mechanics and energetics of swinging the human leg

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Summary

We measured how much metabolic energy is expended to swing a human leg. A previous dynamical model of walking predicted that increasing metabolic costs for walking with step length and step frequency trade-off against each other to determine the optimum step combination at a given speed. Simple pendulum dynamics indicate that the cost of walking at high step frequencies could be associated with driving the legs back and forth relative to the body, at a rate increasing approximately with the fourth power of frequency, possibly due to the low economy of producing muscle force for short durations. A similar cost would be expected for isolated swinging of a leg at faster than its natural frequency. We constructed an apparatus to measure work performed on the leg, and measured metabolic cost as human subjects (N=12) swung one leg at frequencies 0.5–1.1 Hz and fixed amplitude. Rate of mechanical work ranged from 0.02–0.27 W kg^{-1} over these frequencies. Net metabolic rate for leg swinging (subtracting that for quiet standing) increased from 0.41–2.10 W kg^{-1}, approximately with the fourth power of frequency (R^2=0.92) and in proportion to a hypothesized cost of force production for short durations. The costs of producing force and work could account for the increase. In a crude comparison, moving the legs back and forth at a typical stride frequency of 0.9 Hz, might consume about one-third of the net energy (2.8±0.8 W kg^{-1}) needed for walking at 1.3 m s^{-1}.

Key words: metabolic energy, locomotion, biomechanics, muscle, force production.

Introduction

Swinging of the leg is an important part of human locomotion. The back-and-forth motion of the legs has been likened to that of a pendulum, and evidence suggests that pendular dynamics may be responsible for much of the swing phase of gait (Mochon and McMahon, 1980). A pendulum can move at its natural frequency with minimal energy input, but mechanical force and work requirements increase sharply with frequency of motion. Swinging the leg at high frequencies might therefore cost metabolic energy. The metabolic cost of walking also increases with step frequency, and this increase might partially be explained by the cost of moving the legs. Here we test whether fast leg swinging is metabolically costly.

The metabolic cost of active leg motion has previously been considered mostly in running animals. Taylor et al. (1980) argued that the cost of running is dominated by the generation of force to support body weight for short durations of ground contact (Kram and Taylor, 1990), rather than to move the legs (Taylor, 1994). But loading the limbs of running humans (Myers and Steudel, 1985) or dogs (Steudel, 1990) causes metabolic cost to increase more than for the same loads applied to the center of mass, suggesting that moving the limbs does require energy. Marsh et al. (2004) used more direct measurements of blood flow to estimate energy expenditure in the swing-phase muscles of guinea fowl. They estimated that 26% of the energy used by the limbs was for the swing phase.

The cost of driving the legs back and forth relative to the body may be significant during human walking. Griffin et al. (2003) proposed that little energy is needed to move the legs during walking because human energy expenditure increases in proportion to carried load. But again, expenditure increases several times more when the limbs are loaded (e.g. Soule and Goldman, 1969) as opposed to the trunk, therefore implying the opposite. Another argument for a cost for moving the legs is derived from a mathematical model of walking (Kuo, 2001). We hypothesized that mechanical work must be performed to redirect the center of mass from the pendular arc dictated by the stance leg, especially in the transition from one step to the next (Kuo, 2002). Metabolic energy is needed to perform this work (Donelan et al., 2002a,b), which itself could be minimized by taking short steps. But the actual metabolic minimum for a given speed occurs at a longer step length, indicating a separate cost for short but fast steps (Kuo, 2001). To account for this trade-off, our model required a metabolic cost for walking at high step frequencies increasing roughly with the fourth power of step frequency. The force and work needed to move the legs relative to the body might explain this proposed cost of high step frequencies. In particular, a cost for producing force over short durations – applied to fast leg motions and called the 'force/time hypothesis' here – could potentially account for the trade-off against high step frequencies. Regardless of the specific dependency on magnitude or duration of work or force, our model predicted a substantial cost for moving the legs relative to the body, associated with neither center of mass redirection nor body weight support.

A simple approach for estimating this cost is to study leg swinging itself without walking. The loading conditions must necessarily differ between isolated leg swinging and actual walking, but the range of hip torques and leg angles can roughly be matched. The metabolic cost of leg swinging could potentially depend on the work produced by muscles, and possibly even the force/time cost predicted for walking. But regardless of the particular cause, both of these possibilities predict a sharply increasing metabolic cost for swinging at higher than the leg's natural frequency.

The purpose of the present study was to measure the mechanics and metabolic energetics of swinging the human leg by itself. We tested how much metabolic rate increases with frequency of swinging and considered possible contributions to the cost of moving the legs.

Materials and methods

We constructed a simple apparatus for measuring torque and displacement of a single swinging leg. We collected data from human subjects at a variety of frequencies above the natural pendular frequency, and at constant amplitude. Potential contributors to metabolic cost include rate of work and the force/time hypothesis. Before describing the experiments themselves, we use a simple pendulum model to quantify the predictions arising from these possible contributors.

Model

A simple pendulum model (Fig. 1) illustrates the mechanics of moving the leg. Employing a small angle approximation, and measuring the angular displacement θ from vertical, the equations of motion are

$$\dot{\theta} + \omega_{\mathrm{n}}{}^2 \theta = T \tag{1}$$

where ω_{n} is the pendular natural frequency and T is the moment of applied muscle force normalized by leg inertia. Natural frequency ω_{n} (in rad s^{-1}; in Hz, $f_{\mathrm{n}} \overset{\Delta}{=} \omega_{\mathrm{n}}/2\pi$) depends mainly on inertial properties, such as the location of the leg center of mass, but may also be affected by parallel elastic elements, such as from passive tissue compliance about the hip. The pendulum is assumed to be driven approximately sinusoidally with fixed amplitude A and frequency $\omega \overset{\Delta}{=} 2\pi f$,

$$\theta(t) = A \cos \omega t \,. \tag{2}$$

Active movement of the leg requires muscle force or torque, increasing with the square of swing frequency. Combining (1) and (2), the torque is

$$T(t) = A\,(-\omega^2 + \omega_{\mathrm{n}}^2) \cos \omega t \,. \tag{3}$$

The amplitude, T_0, therefore behaves according to

$$T_0 \propto |\,\omega^2 - \omega_{\mathrm{n}}^2\,| \,. \tag{4}$$

The most obvious potential metabolic cost is for performing work on the limb, increasing with the cube of swing frequency. The mean rate of work performed on the pendulum is

$$\dot{W} = \frac{2\omega}{\pi} \int_0^{\pi/2\omega} T \cdot \dot{\theta} \mathrm{d}t \;\; . \tag{5}$$

Each cycle of pendulum swing involves both positive and negative work, both exacting a positive metabolic cost (Hill, 1938). Substituting Equations (2) and (3) into (5), the mean rate of positive work, $\dot{W}^{(+)}$, for the pendulum model is

$$\dot{W}^{(+)} = \frac{A^2}{\pi} \omega \left| \omega^2 - \omega_{\mathrm{n}}^2 \right| , \tag{6}$$

with an equal magnitude of negative work.

Another possible contributor to metabolic cost is the force/time cost derived from our model of walking, increasing with the fourth power of swing frequency. This exponent was required to explain the preferred step length *vs* speed relationship. In our formulation of the force/time hypothesis, when muscle force is produced in bursts, metabolic cost increases with force but with an economy inversely proportional to burst duration time (Kuo, 2001). The force in question is proportional to hip torque amplitude, and the burst duration is proportional to swing period $\tau = 1/f$. The proposed metabolic cost, labeled 'rate of force/time' or $\dot{F}_\tau$, is

$$\dot{F}_\tau \propto \frac{T_0}{\tau} \cdot f \,. \tag{7}$$

Substituting Equations (2)–(4) into (7) yields the model prediction

$$\dot{F}_\tau \propto |\,\omega^4 - \omega^2 \cdot \omega_{\mathrm{n}}^2\,| \,. \tag{8}$$

This fourth power prediction only applies to fast motions above the leg's natural frequency, because of the high force requirements and short durations. For slower motions, work will likely dominate metabolic cost.

The mechanics and metabolic energetics of isolated leg swinging can be measured experimentally. It is straightforward to compare leg-swinging mechanics against the pendulum model, but it is more difficult to differentiate between contributions to metabolic cost, because metabolic rate may depend not only on work and force but also other factors not considered. Rather than attempting to test for one potential cost against another, we tested for an increase in metabolic rate proportional to the larger (fourth power) component in a combined cost including both rate of work and rate of force/time.

Experimental procedure

We measured mechanical and metabolic costs of swinging the leg at different frequencies in twelve young adults. All subjects (six males, six females; body mass M=64.8±8.3 kg,

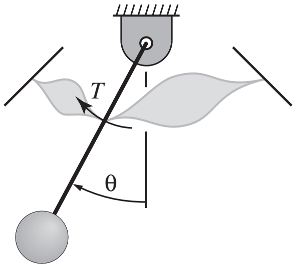

Fig. 1. Isolated leg swinging was modeled as a simple pendulum. Leg angle θ was defined relative to vertical, and torque T due to muscle force was defined as positive in the same direction as θ. We assumed a relatively constant moment arm for muscle force. Torque and rate of work requirements increase with the square and cube, respectively, of swing frequency f (Hz) or ω (rad s^{-1}) above the natural frequency, f_n or ω_n respectively.

leg length l=0.88±0.07 m, mean ± S.D.) were healthy and exhibited no clinical gait abnormalities. They gave their informed consent to participate in this study prior to the experiment. Seven different swing frequencies, f, ranging from approximately 0.5–1.1 Hz, were tested on each subject's left leg, all with a peak-to-peak amplitude $2A$ of approximately 45°. The trial order was randomized to reduce fatigue effects.

We constructed an apparatus for estimating work performed on the limb through measured leg displacement and reaction forces (see Fig. 2), effectively acting as an ergometer. This apparatus consisted of a metal frame, to support the upper body, mounted atop a force platform. Subjects stood inside the frame with one leg on a raised block so that the other leg could swing freely. Their upper bodies were strapped securely to the frame, with their weight distributed between one leg and two armrests. A lightweight knee splint was used to keep the swinging leg straight. An optical encoder, rotating about an axis through the hip and attached to the swinging leg, was used to measure the leg angle with respect to vertical. This angle was also displayed to the subject on a computer screen, along with visual targets showing 45° peak-to-peak amplitude. Subjects were asked to swing the leg between the targets, in time with a metronome set to twice the swing frequency, so that there was an audible cue for swinging of the leg in each direction. Subjects typically learned to follow the metronome after a few minutes' practice.

Reaction forces were measured using a force platform (AMTI Biomechanics Platform Model OR6-5; Watertown, MA, USA) underneath the ergometer frame. The platform collected forces and moments simultaneously at a sampling rate of 120 Hz. Assuming that the swing leg alone was in motion, the ground reaction forces were equal to the hip reaction forces. We used anthropometric measurements and regression equations (Yeadon and Morlock, 1989) to determine the distance from the hip to the leg center of mass, r, as well as the leg moment of inertia. These were used, with measured leg kinematics, in inverse dynamics equations (Kuo, 1998) for a single rigid leg to calculate the hip reaction torque, T.

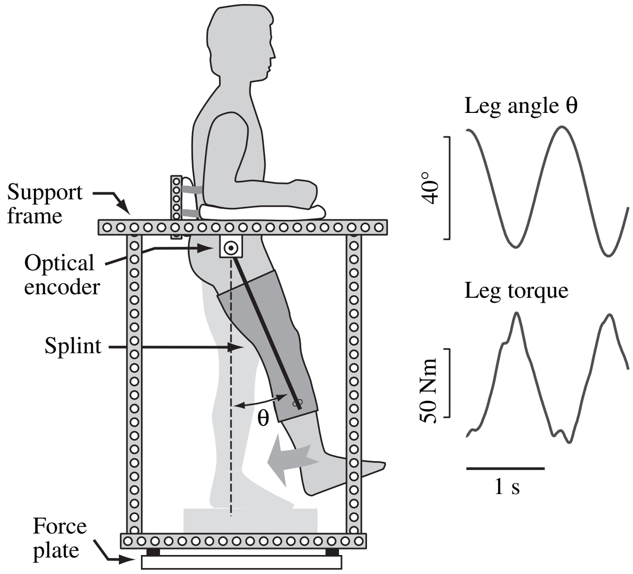

Fig. 2. Experimental apparatus. Subjects performed leg swinging while attached to a rigid frame, with weight supported by both arms and one leg. Subjects were strapped to the metal frame, with leg angle θ measured by optical encoder. Force plate underneath the frame measured ground reaction forces, used to compute leg torque produced at hip (representative data shown).

We used the kinematic and reaction force data to calculate the torque and work performed on the leg. The average rate of positive mechanical work performed on the swing leg, $\dot{W}^{(+)}$, was found by integrating the half-wave rectified mechanical power (product of T and $\dot{\theta}$), and dividing by the entire data collection time for the trial. An equal magnitude of negative mechanical work was also performed, because there was zero net work performed on the leg. We also computed the amplitude of the first fundamental component of the hip torque, T_0, after first applying a low-pass filter with a cut-off frequency of twice the swing frequency. The force/time was calculated from Equation (7).

We measured the metabolic cost of swinging the leg using an open circuit respirometry system (VMax29, SensorMedics Corp., Yorba Linda, CA, USA). Each trial was 6 min long, with the first three minutes used to allow oxygen consumption to reach steady state, followed by 3 min of data collection. The first trial for each subject was used to measure the resting metabolic rate with no leg motion, with the subject standing quietly on one leg while attached to the ergometer frame. This resting rate was used as a baseline that was subtracted from each subsequent data set to yield net metabolic rate. Trials 2–8 were leg swinging trials conducted in random order, with a short resting period given between each. Finally, we conducted a walking trial, in which the subject walked at 1.3 m s^{-1} on a motorized treadmill.

Net metabolic rate, $\dot{E}$, was computed from the average rate of oxygen consumption, subtracting the rate for quiet standing. We assumed a rate of 20.9 W for 1 ml s^{-1} O_2. Although we did not measure lactate concentration, we did monitor the respiratory exchange ratio (RER). In all trials, RER was <0.9, indicating that the exercise was primarily aerobic.

To account for differences in subjects' body size, we performed our analysis using dimensionless variables, with M, $\boldsymbol{g}$, and l as base units. For example, energy rates $\dot{W}^{(+)}$ and $\dot{E}$ were made dimensionless by the factor $A^2M\boldsymbol{g}^{1.5}l^{0.5}$, and force/time $\dot{F}_\tau$ by $AM\boldsymbol{g}^{1.5}l^{0.5}$. For convenience of data presentation, frequencies are presented in units of Hz, and energy rates additionally in the more commonly used units of W kg^{-1}, converted back by an appropriate mean non-dimensionalizing factor.

We first tested the degree to which isolated leg swinging resembled forced motion of a pendulum. We used regression tests to compare measured T_0, $\dot{W}^{(+)}$ and $\dot{F}_\tau$ with the amounts given by Equations (4), (6) and (8), respectively. In terms of frequencies in Hz, the regressions were

$$T_0 = C_\mathrm{T} \cdot |f^2 - f_\mathrm{n}^2| + D_\mathrm{T} \tag{9}$$

$$\dot{W}^{(+)} = C_\mathrm{W} \cdot |f^3 - f \cdot f_\mathrm{n}^2| + D_\mathrm{W} \tag{10}$$

$$\dot{F}_\tau = C_\mathrm{F} \cdot |f^4 - f^2 \cdot f_\mathrm{n}^2| + D_\mathrm{F}\,, \tag{11}$$

each with a constant of proportionality C, and a constant offset D. The offset is ideally zero; for example in Equation (6), theoretically, no work is needed to swing a rigid leg at its natural frequency. However, in practice, we found that subjects performed some work at all frequencies, perhaps because of energetic losses in the leg and experimental apparatus, and because some control is needed to follow the beat of the metronome, probably resulting in force and/or work related to small corrective actions. We therefore included the possibility of a non-zero offset in Equations (9)–(11).

We next compared the measured net metabolic rate $\dot{E}$ against the force/time hypothesis using two regressions. The first was of the form

$$\dot{E} = C_\mathrm{E} \cdot |f^4 - f^2 \cdot f_\mathrm{n}{}^2| + D_\mathrm{E} \tag{12}$$

to determine how metabolic cost increased as a function of swing frequency. In this test, we found that subjects exhibited varying offsets in their metabolic rate. We therefore allowed for different individual offsets in the overall regression for Equation (12). The second regression was a linear fit between $\dot{E}$ and $\dot{F}_\tau$:

$$\dot{E} = C_\mathrm{EF} \cdot \dot{F}_\tau + D_\mathrm{EF}\,. \tag{13}$$

Because the force/time hypothesis only applies to fast swinging of the leg, these tests were performed only for frequencies above 0.7 Hz.

We also compared leg swinging with walking. In terms of mechanics, we compared a typical subject's hip work loops at all swing frequencies against published data for normal walking at 1.3 m s^{-1} (Whittle, 1996). Metabolic rates were compared between leg swinging and walking at 1.3 m s^{-1}.

Results

The mechanics of leg swinging agree well with the pendulum model, in terms of both peak-to-peak torque and rate of positive mechanical work (see Fig. 3). Hip torque amplitude, T_0, increased approximately with the square of swing frequency (Fig. 3a), fitting well with Equation (9), R^2=0.96. The fitted model had a minimum equivalent to 1.47 N–m, occurring at a frequency of f_n=0.64 Hz, which was not significantly different from the natural frequency derived from leg inertia properties, 0.64±0.02 Hz (S.D.) (P=0.51, t-test). Rate of positive mechanical work performed at the hip, $\dot{W}^{(+)}$, also increased sharply but with the cube of swing frequency (Fig. 3b) as in Equation (10), R^2=0.93. The minimum $\dot{W}^{(+)}$ equivalent to 0.02 W kg^{-1} also occurred at the natural frequency, rising to a maximum of 0.27 W kg^{-1} at the highest frequency. The regression coefficients for T_0, converted to dimensional units, were C_T=53.63±2.36 Nm s^{-2} (95% confidence interval, CI), D_T=0.47±0.94 Nm (CI). The coefficients for $\dot{W}^{(+)}$ were C_W=0.31±0.02 W s^{-3} kg^{-1} (95% confidence interval, CI), D_W=0.02±0.01 W kg^{-1} (CI).

The rate of force/time $\dot{F}_\tau$, increased with fourth power of swing frequency (Fig. 3c), fitting well with Equation (11), R^2=0.95. The dimensionless regression coefficients were C_F=1.52±0.07 (CI), D_F=0.001±0.002 (CI).

Examining the metabolic rate, we found it increased substantially with swing frequency (Fig. 4a), fitting well with the force/time hypothesis (Equation 12), R^2=0.92. The data ranged from 0.41±0.26 W kg^{-1} (S.D.) to 2.10±0.31 W kg^{-1}. The regression coefficients were C_E=2.04±0.23 W s^{-4} kg^{-1} (CI), with offset D_E=0.30±0.22 W kg^{-1} (S.D.). The second regression demonstrated that $\dot{E}$ increased approximately linearly with $\dot{F}_\tau$ (Fig. 4b), R^2=0.85. The coefficients were C_EF=6.62±0.74 (CI), with offset D_EF=0.015±0.005 (S.D.).

When walking at 1.3 m s^{-1}, subjects chose a stride frequency of about 0.9 Hz and consumed metabolic energy at net rate 2.8±0.8 W kg^{-1}. Work loops for a typical subject showed a range of hip torques and angles for comparison with walking (Fig. 5).

Discussion

We sought to determine the degree to which isolated swinging of a leg is metabolically costly. The mechanics of a pendulum predict that sharply increasing force and work are required to move the leg quickly. Production of muscle work and force for short durations (force/time hypothesis) might both require metabolic energy.

The observed increases in mechanical (Fig. 3) and metabolic (Fig. 4) measurements confirm that pendulum mechanics are relevant to the leg motion. Even though no net work is performed over an entire cycle, force and work are necessary within each cycle to move the leg faster than its natural frequency. The sharp increase in mechanical demands must be met by muscle, probably causing the fourfold increase in metabolic cost.

Mechanical work is probably responsible for much of the metabolic cost. Some active work is almost certainly performed by muscle fibers, but not necessarily as much as the measured work performed on the limb. Series elasticity, in tendon and other structures, can also perform work on the limb passively (Kuo, 2001), thus lowering the proportion performed actively. In addition, the highest forces occur at the extremes of leg motion when speed is lowest, so that muscle fibers can be nearly isometric. The actual muscle fiber work during leg swinging and its true contribution to metabolic cost are unknown here.

Metabolic cost may also increase with short durations of force production, as indicated by the observed correlation to $\dot{F}_\tau$, consistent with the force/time hypothesis. Others have previously observed increases in metabolic rate with short force durations in situations as disparate as supporting body weight in running (Roberts et al., 1998) and propelling the body in cross-country skiing (Bellizzi et al., 1998), although with varying formulations. The cost might be attributed to increasing recruitment of less economic fast-twitch muscle fibers for short durations of force production (Kram and Taylor, 1990), but this explanation alone is probably

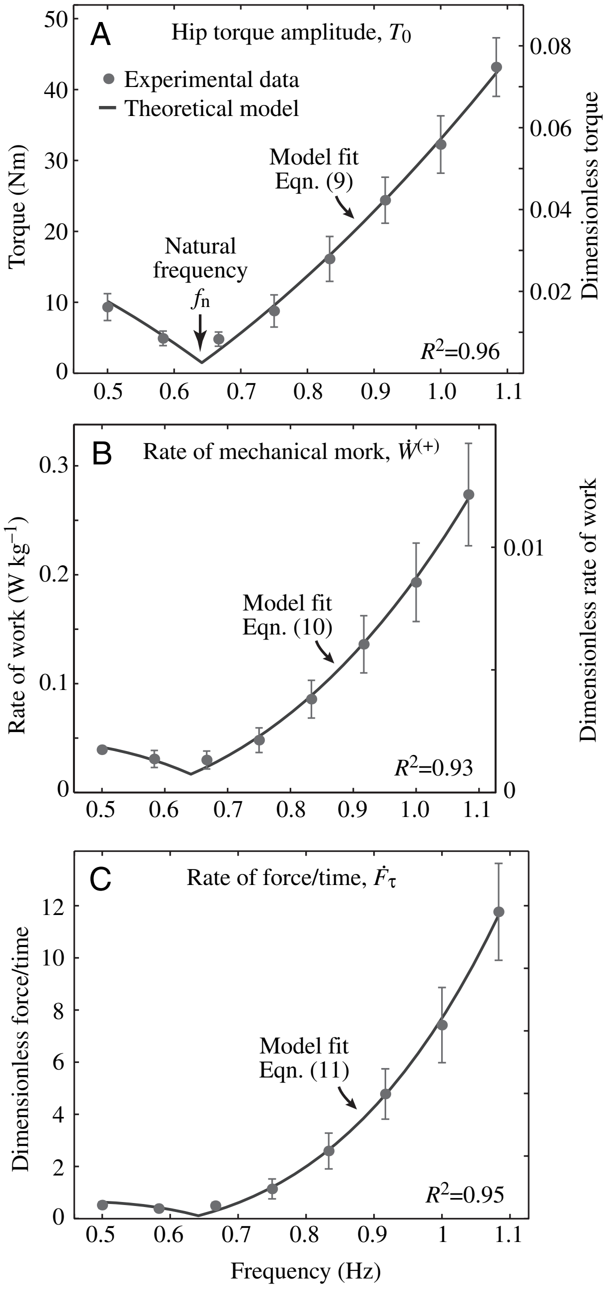

Fig. 3. Mechanics of leg swinging as a function of frequency f, in terms of torque, work, and force/time, were modeled reasonably well by a forced pendulum (Equations 9–11). (a.) Hip torque amplitude, T_0, increased approximately with f^2 above natural frequency f_n (R^2=0.96). (b.) Rate of mechanical work, $\dot{W}^{(+)}$, increased approximately with f^3 (R^2=0.93). (c.) Rate of force/time, $\dot{F}_\tau$, increased approximately with f^4 (R^2=0.95). Metabolic cost is hypothesized to increase with both rate of work and force/time, for frequencies above the natural frequency f_n=0.64 Hz. 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 shown are mean ± S.D.

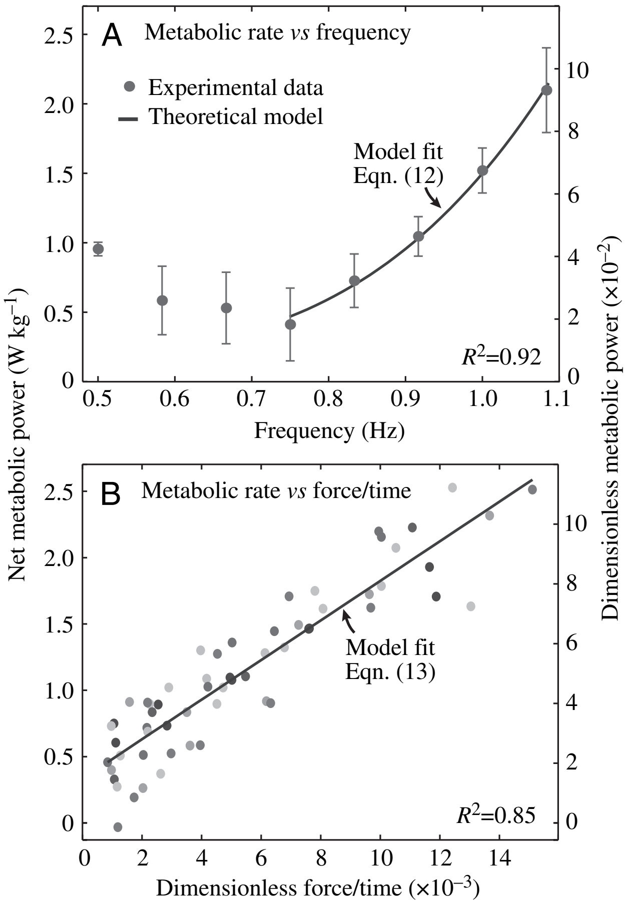

Fig. 4. Metabolic rate increased over fourfold with frequency of isolated leg swinging, for motion faster than the leg's natural frequency. (A) $\dot{E}$ *vs* frequency of leg swinging f, showing metabolic rate increasing approximately with f^4 as predicted by force/time hypothesis (Equation 12). Data shown are for all frequencies applied, but the curve fit was only performed on data for fast leg swinging. (B) $\dot{E}$ *vs* $\dot{F}_\tau$, showing metabolic rate increasing approximately linearly with the hypothesized force/time cost (Equation 13). Rate of mechanical work is also likely to contribute, but cannot accurately be distinguished from force/time in overall metabolic cost.

insufficient to explain the fourfold increase in cost seen here. Isolated muscle measurements also demonstrate a substantial increase in energetic cost of producing force for shorter durations, even when fiber type recruitment is relatively fixed (Hogan et al., 1998). A possible explanation is the energetic cost of activation–deactivation dynamics, in particular calcium pumping associated with the sarcoplasmic reticulum (Bergstrom and Hultman, 1988; Hogan et al., 1998; Verburg et al., 2001).

Our results suggest that metabolic rate depends on work and force/time, but cannot distinguish between their relative contributions. The fit to the larger fourth-power cost (Fig. 4a) means that the force/time hypothesis cannot be excluded. But neither can the contribution of rate of work be excluded. In the absence of a hypothesis for how these two costs might sum – most likely in a nonlinear fashion – it would not be fruitful to add another term for work. Such a term would only add a third degree of freedom to the fit of Equation (12) without explaining the many other factors that might affect metabolic cost. Further differentiation of costs might require experiments that manipulate force and duration as separate independent variables.

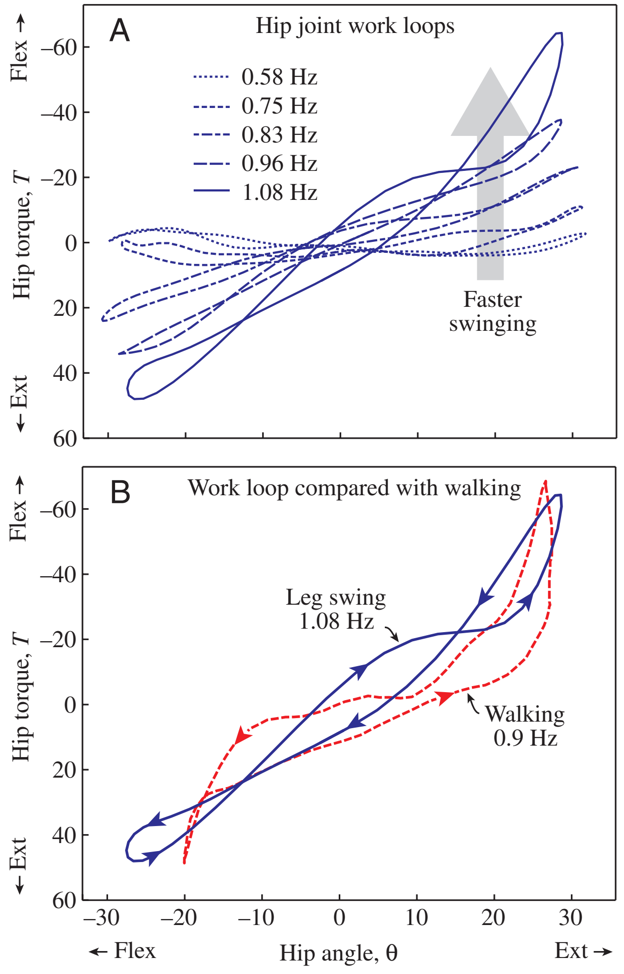

Fig. 5. Work loops of hip torque *vs* angle for a typical subject: (A) as a function of frequency; and (B) compared with normal walking. (A) Work loops varied mostly in terms of torque rather than amplitude or contained area. (B) Compared with normal walking at 1.3 m s^{-1} (data from Whittle, 1996), isolated leg swinging occurred at a comparable range of torques and angles, although walking occurs at a lower stride frequency of 0.9 Hz and with more work at the hip.

The conditions of isolated leg swinging were only roughly comparable to human walking in terms of hip torque and amplitude, but with a lower frequency. Our experiment sought to separate the problem of moving the legs relative to the body from that of loading and propelling the center of mass. But lacking the actual loads of walking, isolated leg swinging cannot simultaneously match both the forces and kinematics of walking. At f=1.08 Hz, the ranges of hip torques and angles are roughly similar to that of normal walking at 1.3 m s^{-1} (Fig. 5), but not to the stride frequency of about 0.9 Hz. Swing and stride frequency could alternatively be matched, f=0.9 Hz, but the torques would then be considerably lower than for walking. By using similar torque and amplitude but lower frequency, our conditions conservatively involved less work than that performed on the leg during walking.

We also used a splint to restrict greatly the knee motion that would normally occur in walking. If the knee were instead allowed to bend, the leg could theoretically be moved at higher frequency for the same hip torque. But as noted above, the same hip torque at a higher speed would not be expected to require less metabolic power, and if active torque were produced at the knee it might also exact a metabolic cost. Allowing knee motion could alternatively enable the same swing frequency at lower hip torque and, therefore, lower rate of work and lower metabolic cost. But our intent was to approximate the hip torques used in walking, and doing so with a knee splint is likely to produce an underestimate of the cost of moving the leg during walking because of the lower speed.

A more significant limitation of this experiment was that subjects exerted considerable effort to hold their bodies immobile during leg swinging, despite our efforts to strap their bodies to the rigid measurement apparatus. In walking, reciprocal leg motion allows reaction forces to be produced between the legs and against each other rather than an external frame. In terms of reaction forces, isolated swinging of a single leg might be roughly comparable to moving both legs during walking.

The most conservative walking comparison is, therefore, with the condition of isolated leg swinging at f=0.9 Hz, which would cost approximately 0.95 W kg^{-1}, or about one-third of the rate for walking at the same stride frequency. It is conservative because it likely underestimates the hip torque and work needed to move both legs in walking, it does not include possible costs of moving the knee, and it assumes that the reaction forces for swinging a single leg are similar to those for moving both legs during walking.

In actual walking, it is difficult to experimentally isolate moving the legs from supporting body weight or redirecting the center of mass. When a leg is in contact with the ground, it is somewhat arbitrary to assign muscle activity to one function or another. But there might be a significant metabolic cost even if moving the legs were narrowed to the swing phase alone, as evidenced by the findings of Marsh et al. (2004). Swing-phase activity of guinea fowl hip muscles accounted for about one-fourth of metabolic cost even at slow speed of $0.5\,\mathrm{m\,s^{-1}}$. Assuming a hip height of 0.2 m and a stride frequency of 1.5 Hz (Gatesy and Biewener, 1991), the one-fourth estimate applies to a slightly slower dimensionless speed and stride frequency than humans (speed 0.36 *vs* 0.44, stride frequency 0.21 *vs* 0.27, guinea fowl *vs* human, respectively). Legs of guinea fowl are also a slightly lower proportion of body mass than in humans, approximately 10% *vs* 16% per leg (Fedak et al., 1982). A comparable cost for the human swing phase alone appears reasonable, both in relation to these data, and to our one-third estimate for moving the legs relative to the body including both swing and stance phases.

We do not interpret the one-third cost estimate to conflict with Mochon and McMahon's (1980) notion that much of the swing phase is ballistic. These authors noted that muscle activity occurs mostly at the start and end of swing, with the motion being largely passive in between. For fast leg motions, the highest torques are needed only at the extremes of motion, and there could be substantial intervals of time that need minimal muscle activity (Kuo, 2002). Even with a high metabolic cost, the swing phase appears to be governed by pendulum dynamics.

We originally hypothesized a cost for moving the legs to explain why humans do not walk with short steps to minimize the costs of transitioning between inverted pendulum arcs (Kuo, 2001). Large increases in metabolic cost for leg swinging may be sufficient to explain the increasing cost of walking with step frequency. The approximate fourth power exponent of frequency is also consistent with the optimum combination of step length and frequency preferred by humans. Low economy of force production for short durations is a potential explanation for this cause, but more detailed physiological studies would be necessary to test this further.

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