A new model predicting locomotor cost from limb length *via* force production

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Summary

Notably absent from the existing literature is an explicit biomechanical model linking limb design to the energy cost of locomotion, COL. Here, I present a simple model that predicts the rate of force production necessary to support the body and swing the limb during walking and running as a function of speed, limb length, limb proportion, excursion angle and stride frequency. The estimated rate of force production is then used to predict COL *via* this model following previous studies that have linked COL to force production. To test this model, oxygen consumption and kinematics were measured in nine human subjects while walking and running on a treadmill at range of speeds. Following the model, limb length, speed, excursion angle and stride frequency were used to predict the rate of force production both to support the body's center of mass and to swing the limb. Model-predicted COL was significantly correlated with observed COL, performing as well or better than contact time and Froude number as a predictor of COL for running and walking, respectively. Furthermore, the model presented here predicts relationships between COL, kinematic variables and body size that are supported by published reduced-gravity experiments and scaling studies. Results suggest the model is useful for predicting COL from anatomical and kinematic variables, and may be useful in intra- and inter-specific studies of locomotor anatomy and performance.

Key words: biomechanics, locomotion, cost of locomotion, energetics, force production, humans, running, walking.

Introduction

As our understanding of locomotor biomechanics has improved over the past half-century, a number of theoretical models have been proposed for predicting kinematic parameters, ground reaction forces and, less often, locomotor cost from anatomical variables. However, while limb length and proportion have been linked to energy cost of locomotion (e.g., Alexander and Jayes, 1983; Hildebrand, 1985), no current model incorporates these variables explicitly as determinants of locomotor cost. This study presents a mathematical model, based on the force production hypothesis (Kram and Taylor, 1990; Taylor 1994), that predicts the energy cost of locomotion for walking and running gaits as a function of limb length and proportion, and tests this model in a sample of humans.

Physiological studies have demonstrated empirically that the metabolic cost of locomotion primarily derives from the muscular force required to accelerate the body's center of mass as it oscillates through the stride cycle. Notably, the rate of force production, as proposed by Kram and Taylor (1990), predicts the rate of oxygen consumption during locomotion more accurately than other parameters, including the work done in moving the center of mass and limbs through a stride cycle (Heglund et al., 1982; Cavagna and Kaneko, 1977). Added-mass studies of quadrupeds and bipeds (Taylor et al., 1980; Kram, 1991; Wickler et al., 2001; Griffin et al., 2003)

and gravity-manipulation studies of running humans (Farley and McMahon, 1992) have shown that the muscular force needed to generate the vertical component of ground reaction force, acting in opposition to gravitational acceleration, accounts for the majority of locomotor cost (see Taylor, 1994). In addition, the muscular force generated during braking and propulsion, associated with the horizontal component of ground force generation, also contributes as much as one-third of locomotor cost (Chang and Kram, 1999; Gottschall and Kram, 2003). Comparisons of bipeds and quadrupeds (Roberts et al., 1998a,b) suggest these determinants of locomotor cost work similarly for both, although differences in muscle fiber length and effective mechanical advantage of the limb joints may lead to higher costs for bipeds.

The relationship between limb length and locomotor energy cost is less clear. Alexander and Jayes (1983) initially proposed that various gait parameters, including locomotor cost, are dynamically similar and would scale by Froude number, a dimensionless constant that corrects for size between pendular systems. Thus, the cost of locomotion for a given animal at a given speed could be predicted by calculating the Froude number, $U^2(Lg)^{-1}$, where U is travel speed and L is limb length. While there is some support for this proposal from studies of human walking (Alexander, 1984; Minetti et al., 1994), Froude numbers do not predict the scaling of cost or kinematic

parameters during running (Minetti et al., 1994; Donelan and Kram, 2000). Furthermore, recent studies that manipulate gravity during walking have shown that stride length (Donelan and Kram, 1997) and energy cost (Farley and McMahon, 1992) are not constant at a given Froude number, suggesting dynamic similarity as proposed by Alexander and Jayes (1983) may not adequately describe walking mechanics.

An inverse relationship between locomotor cost and limb length has also been proposed for running gaits, which are typically considered to act as mass-spring systems rather than pendular systems. Kram and Taylor (1990) suggested that 'larger animals with longer limbs and step lengths will have lower transport costs,' as the magnitude of the vertical impulse decreases with longer stance periods. However, while stance phase duration, or contact time, t_c, has been shown to correlate with limb length (Hoyt et al., 2000), numerous within- and between-species studies have found no relationship between limb length and the cost of locomotion (walking humans, Censi et al., 1998; running humans, Ferretti et al., 1991; Cavanaugh and Kram, 1989; Brisswalter et al., 1996; interspecific studies, Steudel and Beattie, 1995). In the best study to date comparing short- and long-legged humans (mean limb length 79 cm and 95 cm, short- and long-legged groups, respectively), Minetti et al. (1994) found locomotor cost was lower for long-legged individuals during walking but higher during running. This difference between walking and running gaits, and the lack of a clear relationship between limb length and locomotor cost, suggests a simple relationship between limb length and locomotor cost is unlikely.

One complication in predicting the effect of limb length on locomotor efficiency is the cost of accelerating the limb during swing phase. While initial studies suggested swing cost is negligible (Taylor et al., 1974, 1980; Mochon and McMahon, 1980), more-recent studies have demonstrated that the muscular force required to swing the limb can constitute a significant portion of total locomotor cost. Several studies have measured the increase in energy cost when mass is added to the limb and have shown that energy costs increase directly with increased moment of inertia (Martin, 1985; Myers and Steudel, 1985; Steudel, 1990). More recently, Marsh et al. (2004) in a study of guinea fowl, measured energy consumption using blood flow in the limb muscles of guinea fowl and found limb swing contributed over 20% of total locomotor cost over a range of speeds. Thus, it appears a tradeoff may exist between the force required to support the body and the force required to swing the limbs. As limb length increases contact time increases and a lower rate of force production is necessary to support the body, but more force is required to swing the longer limb.

The model presented here predicts both the force required to support bodyweight and the force required to swing the limb as functions of limb length and proportion. Following Kram and Taylor (1990), the predicted rate of force production (i.e. the mean muscular tension required per step multiplied by step frequency) is then used to predict the rate of oxygen consumption. Predicted oxygen consumption is then tested against observed oxygen consumption in a sample of human recreational runners over a range of running and walking speeds. These results show that the model provides a useful framework for understanding the link between limb length and the cost of locomotion for both walking and running, incorporating both the cost of supporting the bodyweight and swinging the limb.

Materials and methods
The LiMb model
Justification and assumptions

The model presented here predicts the mass-specific rate of energy expenditure (V_{O_2} kg^{-1} s^{-1}), hereafter cost of locomotion, COL, from the muscular force generated to support the body's center of mass (COM) and swing the limbs. To facilitate discussion and comparison with other models, the present model is termed the LiMb model, as it incorporates the force generated to swing the limb and support body mass (M_b) in predicting COL.

The primary assumption of the LiMb model follows directly from the force production hypothesis (Kram and Taylor, 1990; Taylor, 1994): the mass-specific rate of energy consumption is a linear function of the rate of muscular force production. This assumption requires that the relative shortening velocities of muscles and the force exerted on the ground per unit of active muscle are independent of body size and speed. Empirical studies suggest these criteria are met. *In vivo* studies have shown that most muscles supporting bodyweight during locomotion contract isometrically during steady walking and running, and therefore at a constant relative shortening velocity. This has been demonstrated in turkeys (Roberts et al., 1997), walking humans (Fukunaga et al., 2001), and wallabies (Biewener et al., 1998), although other studies suggest shortening contractions may be employed as well (Gillis and Biewener, 2001; Daley and Biewener, 2003). Nevertheless, as long as the relative amount of muscle shortening work does not change with speed or size, this assumption still holds. Additionally, interspecific comparisons over a range of animal size have demonstrated that the effective mechanical advantage, EMA, of extensor muscles scales inversely with muscle fiber length (EMA $\alpha M_b^{-0.26}$, Biewener, 1989; fiber length $\alpha M_b^{0.26}$, Alexander et al., 1981) suggesting that a given volume of muscle should exert the same force on the ground independent of body size. Indeed, one important result of Kram and Taylor (1990) was that the ratio of metabolic energy expenditure to the rate of muscular force production was constant across running speed, body mass, and species. Thus the available evidence suggests that energy expenditure during locomotion may be predicted by the rate of muscular force production without including major complexities of muscle physiology.

Total predicted force production for the LiMb model is considered to depend on three components: vertical force, horizontal force and limb swing. Estimated force production for each component is derived separately.

Vertical forces

Vertical force production for both walking and running is estimated from the change in vertical momentum of the body's COM. While 'passive' mechanisms, such as energy storage and release *via* tendons or the exchange of potential and kinetic energy, may reduce the mechanical work done by the muscles thereby improving energy economy (Roberts et al., 1997), such mechanisms still require muscular force to prevent the limb from collapsing (i.e. to support bodyweight) and, to the extent the muscles perform true mechanical work, to lift the COM. Therefore, in the LiMb model, positive (upward) accelerations are viewed as a product of muscular force production while negative (downward) accelerations of the COM are a product of gravity. 'Passive' mechanisms to reduce mechanical work, not considered explicitly in the LiMb model, can be viewed as the efficiency with which oxygen consumption is translated into force production. Accelerations of the COM require an equivalent muscular force; passive mechanisms mediate the cost of producing this force. Because the COM experiences free-fall during running but not during walking, vertical accelerations are linked to kinematic and anatomical variables differently for each gait and are, therefore, derived separately for walking and running.

1. Running

Vertical force production during running is derived as follows (see Fig. 1): during steady running on level surface, the positive (upward) vertical acceleration, a_y, produced by muscular force must be equal in magnitude to that of gravity, g. Furthermore, average positive vertical acceleration during contact time, t_c, must equal that of gravity during step period, T_{step}, or $t_c a_y = T_{step} g$. For a simple two-dimensional model in which the limbs are treated as simple cylinders with no feet, the knees are modeled as telescoping (prismatic) joints, and protraction of the hind limb is equal to retraction, contact time during one step is a function of hind-limb length L, excursion angle ϕ, and running speed U, such that:

$$t_c = U^{-1}[2L\sin(\phi/2)] . \tag{1}$$

Average acceleration during stance phase, a_y, must then equal:

$$a_y = T_{step} g U[2L\sin(\phi/2)]^{-1} . \tag{2}$$

Because $F=Ma$, mean positive vertical acceleration, $\bar{a}_y$, is equivalent to the mean mass-specific force produced during contact time ($\bar{a}_y = \bar{F}M_b^{-1}$), or the average force of the vertical GRF impulse produced during stance phase. Treating the vertical impulse produced during stance phase as a single (virtual) muscle contraction with mean tension $\bar{F}$, the rate of muscular force production is equivalent to Eq. 2 multiplied by step frequency, f_{step}. Because $f_{step} = T_{step}^{-1}$, the rate of muscular force production given by Eq. 2 is:

$$\bar{F}M_b^{-1}s^{-1} = g U[2L\sin(\phi/2)]^{-1} . \tag{3}$$

As outlined above, this model assumes the rate of oxygen consumption to be proportional to the rate of force production. As force is related to oxygen by some constant k, the LiMb
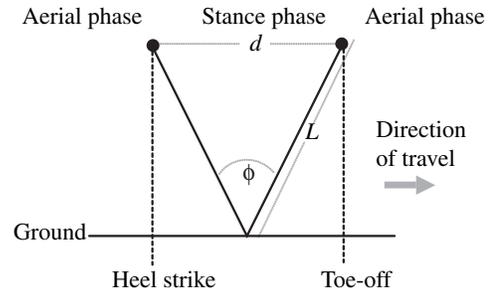

Fig. 1. Movement of the limb through stance. Thick line indicates position of lower limb and COM at heel strike and toe-off. L, limb length; ϕ, excursion angle; U, running speed. For this model: step length is $d = 2L\sin\phi/2$; contact time per step is $t_c = U^{-1}d$ and $t_c = U^{-1}[2L\sin(\phi/2)]$.

model predicts the mass-specific cost of locomotion (V_{O_2} kg^{-1} s^{-1}) for running, COL_{run}, based on vertical ground force production:

$$COL_{run} = kg U[2L\sin(\phi/2)]^{-1} . \tag{4}$$

Eq. 4 is similar to the prediction for locomotor cost proposed by Kram and Taylor (1990; their equation 1: $COL_{run}=kg t_c^{-1}$), with the exception that t_c^{-1} has been replaced with the equivalent expression ($U[2L\sin(\phi/2)]^{-1}$). However, by incorporating hind-limb length, running speed and excursion angle as independent variables, this model has greater utility for comparative studies investigating the different effects of these variables on locomotor costs.

2. Walking

Vertical force production during walking is predicted as follows (see Fig. 2). In a walking gait the COM follows a sinusoidal trajectory, alternately accelerating upward *via* muscular force production and downward *via* gravity. The rate of muscular force production necessary to achieve this change in momentum (i.e. to prevent the limb from collapsing) is a function of the vertical change in position of the COM through stance phase (i.e. the amplitude of oscillation) and the duration of each step. In a simple 'stick-figure' model, the amplitude equals $L[1-\cos(\phi/2)]$, and step duration equals $U^{-1}[2L\sin(\phi/2)]$. Given equal periods of upward and downward acceleration of duration $U^{-1}[L\sin(\phi/2)]$, the average vertical velocity of the COM during the first half of stance phase equals $+L[1-\cos(\phi/2)](U[L\sin(\phi/2)])^{-1}$, while the average vertical velocity during the second half equals $-L[1-\cos(\phi/2)](U[L\sin(\phi/2)])^{-1}$. Note that in this case the vertical velocity of the COM is a function of walking speed, which determines both the horizontal and vertical velocity of the COM as is traverses its sinusoidal trajectory with gravity acting as a restoring force. The movement of the COM in this case is analogous to that of a ball rolling along a sinusoidal track; the forward speed of the ball also determines its vertical velocity.

Assuming maximum vertical velocity is equal to twice the average vertical velocity (the mathematically simplest case),
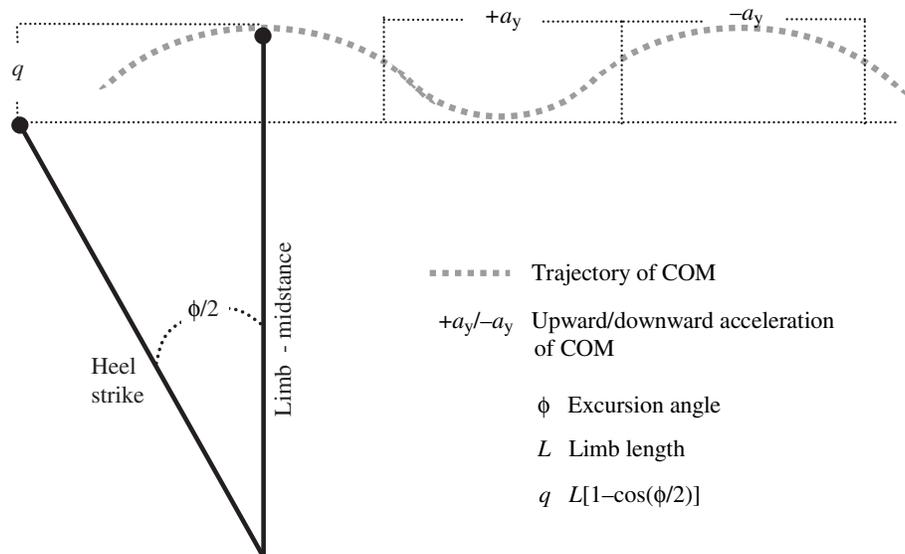
Fig. 2. Vertical acceleration of the COM during walking as derived *via* the LiMb model. During walking the COM follows a sinusoidal trajectory in the sagittal plane resulting in alternating periods of upward and downward acceleration ($+a_y$ and $-a_y$) during which the COM is accelerated. Maximum velocity, $\pm V_{max}$, is a function of the precise shape of the COM trajectory. Assuming that $V_{max}=2V_{avg}$ during normal walking, the change in velocity (i.e., the mass-specific change in momentum) during one period of acceleration, $\Delta V_y=4L[1-\cos(\phi/2)](U^{-1}[L\sin(\phi/2)])^{-1}$ and thus $\Delta V_y=4U[1-\cos(\phi/2)\sin(\phi/2)]^{-1}$. Given the duration of acceleration, $U^{-1}[L\sin(\phi/2)]$, this requires an average acceleration $\bar{a}_y=4U[1-\cos(\phi/2)]\sin(\phi/2)^{-1}(U^{-1}[L\sin(\phi/2)])^{-1}$ and thus $\bar{a}_y=4U^2L^{-1}[1-\cos(\phi/2)]\sin(\phi/2)^{-2}$. Because $\sin(\phi/2)^{-2}=([1-\cos(\phi/2)][1+\cos(\phi/2)])^{-1}$, this simplifies to $\bar{a}_y=4U^2L^{-1}[1+\cos(\phi/2)]^{-1}$.

the change in velocity between steps (i.e. during the trough of the COM trajectory) must equal $4L[1-\cos(\phi/2)]$. This change in velocity occurs over a period of time equivalent to $U^{-1}[L\sin(\phi/2)]$, and therefore average vertical acceleration for one step is given by:

$$\bar{a}_y = 4L[1-\cos(\phi/2)](U^{-1}[L\sin(\phi/2)])^{-2} . \tag{5}$$

Two such periods of upward acceleration occur per each stride. Treating one period of acceleration as the product of one virtual muscular contraction with average force $\bar{F}M_b^{-1}$ (as for running), the mass-specific rate of force production for walking is found by multiplying Eq. 5 by $2f$, where f is stride frequency. Doing this gives the predicted COL for walking based on vertical ground force production:

$$COL_{walk} = 8kfU^2L^{-1}[1+\cos(\phi/2)]^{-1} . \tag{6}$$

As in running, k is a constant relating force generation to oxygen consumption.

In addition to the force needed to perform this change in momentum (Eq. 6), there is the constant acceleration of gravity, g. Here, I make the simplifying assumption that the force required to resist gravity and maintain an upright posture is equivalent to the metabolic cost of standing quietly, although these costs probably differ. As the cost of standing is subtracted from the 'net' cost of locomotion, it is not included in the model prediction of walking cost.

Note that the form of Eq. 6 is similar to a Froude number in that the rate of energy expenditure scales with U^2 and L^{-1}. However, Eq. 6 differs in that gravitational acceleration is not

included: vertical force production is a function of inertia, not weight. Furthermore, stride frequency and excursion angle are included. The implications of these differences are discussed below.

Horizontal forces

To estimate horizontal forces, I make the simplifying assumption that the combined vertical and horizontal ground reaction forces, GRF, produce a resultant vector that passes through the COM throughout stance phase. Empirical studies of ground reaction forces suggest this assumption is valid (Chang et al., 2000; Lee et al., 2004), and that horizontal GRF covaries with vertical GRF (Breit and Wahlen, 1997; Chang et al., 2000). Furthermore, it is assumed that horizontal deceleration during the first portion of stance phase and horizontal acceleration during the second portion are generated *via* muscular contraction.

Instantaneous horizontal force (see Fig. 3) during stance phase must, therefore, equal $F_i\tan\theta_i$, where F_i is the instantaneous vertical GRF and θ_i is the instantaneous protraction or retraction angle of the limb. The summed horizontal force for one stance phase, F_x, is therefore:

$$F_x = \sum F_i\tan\theta_i . \tag{7}$$

The time course of both vertical ground force production and excursion angle are, therefore, necessary to compute F_x. To approximate this value, I assume the average force for both braking and propulsive impulses, $\bar{F}_x$, is equivalent to the product of the mean value for θ_i and the mean vertical mass-specific GRF
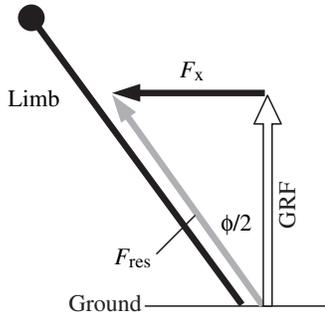
Fig. 3. Deriving the horizontal force component of the LiMb model. Diagram shows the position of the limb (Limb) at heel strike and the instantaneous vertical GRF vector (open arrow, GRF). The horizontal force (F_x) required to produce a resultant (F_{res}) that is directed toward te COM (filled circle) is given by $F_x = GRF \times \tan(\phi/2)$.

during stance phase, $\bar{F}_v$. The mean value for θ_i is equivalent to $0.5(\phi/2)$, $\bar{F}_x$ for the braking or propulsive GRF is estimated as $\bar{F}_x = 0.5\bar{F}_v\tan(\phi/2)$, and the combined horizontal force production (braking + propulsion) for one step is estimated as:

$$\bar{F}_x = \bar{F}_y\tan(\phi/2) \ . \tag{8}$$

It follows that mass-specific horizontal force production can be calculated using the mass-specific mean vertical GRF, $\bar{F}_y M_b^{-1}$:

$$\bar{F}_x M_b^{-1} = \bar{F}_y M_b^{-1}\tan(\phi/2) \ , \tag{9}$$

and the rate of horizontal force production is therefore estimated as:

$$\bar{F}_x M_b^{-1} s^{-1} = \bar{F}_y M_b^{-1} s^{-1}\tan(\phi/2) \ . \tag{10}$$

Note that $\bar{F}_y M_b^{-1} s^{-1}$ is the value estimated for running (Eq. 3) as the mass-specific rate of vertical force production. Combining Eq. 3 and 10, therefore, gives combined (vertical plus horizontal) force production for running:

$$\bar{F}M_b^{-1} s^{-1} = gU[2L\sin(\phi/2)]^{-1}[1+\tan(\phi/2)] \ . \tag{11}$$

Similarly, combined (vertical plus horizontal) force production for walking is estimated as:

$$\bar{F}M_b^{-1} s^{-1} = 8fU^2L^{-1}[1+\cos(\phi/2)]^{-1}[1+\tan(\phi/2)] \ . \tag{12}$$

The LiMb model therefore predicts COL for walking and running, based on vertical and horizontal ground force production, as:

$$COL_{run} = kgU[2L\sin(\phi/2)]^{-1}[1+\tan(\phi/2)] \ , \tag{13}$$

$$COL_{walk} = 8kfU^2L^{-1}[1+\cos(\phi/2)]^{-1}[1+\tan(\phi/2)] \ . \tag{14}$$

Limb swing

The work done to swing the limb can be calculated using the equation for work done on a pendulum (Hildebrand, 1985):

$$work = 2gM_LD\phi^2 \left| 1-T^2 T_0^{-2} \right| \ , \tag{15}$$

where D is the radius of gyration, M_L is the mass, T is the driven period, and T_0 is the natural, or resonant, period of the limb. Work is in Nm×rad, or $\tau\phi$, and $\tau=Fr$, where r is the

effective lever arm of the muscle. The rate of force production, $\bar{F}s^{-1}$, is found by multiplying both sides of the equation by the stride frequency f and dividing by excursion angle ϕ, and r, which produces:

$$\bar{F}s^{-1} = 2fr^{-1}gM_LD\phi \left| 1-T^2 T_0^{-2} \right| \ . \tag{16}$$

Dividing both sides of this equation by body mass M_b produces the mass-specific rate of force production necessary to swing the limb. This rate of force production is the predicted cost of limb swing, C_{limb}:

$$C_{limb} = 2bfgM_LM_b^{-1}D\phi \left| 1-T^2 T_0^{-2} \right| \ , \tag{17}$$

where b relates force to oxygen. Note that b subsumes r, as the oxygen/force ratio will be a function of the mechanical advantage of the muscles (Roberts et al., 1998a,b). Also, because limb swing involves different muscle groups than those used to support the body, and requires non-isometric contractions, it is not expected that $b=k$, the term relating force production to oxygen consumption for vertical and horizontal ground forces (Eq. 4, 6, 13, 14). When Eq. 17 is used to predict limb swing cost without b (i.e. when $b=1$) the estimated value is less than 1% that of stance phase cost (Eq. 13, 14), more than an order of magnitude less than found for guinea fowl (Marsh et al., 2004), and less than is suggested by weighted-limb studies (Martin, 1985; Myers and Steudel, 1985). Since the relationship between muscular architecture, contraction rate, force production and oxygen consumption are not currently known well enough to predict b a priori, a reasonable estimate must be made. Here, I use $b=30$, as this produces values of C_{limb} in line with Marsh et al. (2004). The sensitivity of the model predictions to different estimates of b will be discussed below.

Total mass-specific force production (vertical + horizontal + limb swing) for walking and running is, therefore, predicted *via* the LiMb model as:

$$COL_{run} = kgU[2L\sin(\phi/2)]^{-1} [1+\tan(\phi/2)] + C_{limb} \ , \tag{18}$$

$$COL_{walk} = 8kfU^2L^{-1}[1+\cos(\phi/2)]^{-1} [1+\tan(\phi/2)] + C_{limb} \ . \tag{19}$$

Testing the LiMb model

To test the LiMb model, nine human subjects (five male, four female; body mass range: 53.3–94.3 kg) volunteered to perform a set of walking and running trials at a range of speeds on a custom-built treadmill (tread dimensions: 2×0.6 m) at the Concord Field Station in Bedford, MA, USA. Subjects were recruited to maximize variation in limb length (range: 79–112 cm); all were healthy, fit, recreational runners (self reported miles/week running: 6–25, median N=15) ages 20–35 with no history of running-related injury or illness. Subjects wore their personal running shoes for all trials. IRB (Human Subjects Committee) approval was obtained from Harvard University prior to the study, and written informed consent was obtained from each subject prior to participation. Subjects were paid for their participation in accordance with Harvard University IRB guidelines.

Table 1. *Correlation coefficients for model predictions, contact time and Froude number* vs *observed cost of locomotion*

	Running				Walking			
	Eq.	r	N	P	Eq.	r	N	P
Vertical force	4	0.40	27	0.04	6	0.96	34	<0.01
Vertical + Horizontal	13	0.50	27	0.01	14	0.96	34	<0.01
Vert. + Horiz. + Limb	18	0.66	27	<0.01	19	0.97	34	<0.01
Contact time	–	0.54	27	<0.01	–	–	–	–
Froude number	–	–	–	–	–	0.95	34	<0.01

Limb length was measured as the vertical distance from the greater trochanter, determined by palpation, to the floor while shod. Subjects walked at four speeds, ranging from 1.0–2.5 m s^{-1}, or their fastest sustainable walking speed, and ran at three speeds ranging from 1.75–3.5 m s^{-1}. The range of running speeds was tailored to each subject such that the slowest running speed was slower than the subject's volitional walk–run transition speed. Subjects performed 6–10 min trials at each speed while wearing a loose-fitting mask. Air was pulled through the mask at 200–300 l min^{-1}; this air was sampled and oxygen concentration monitored at 5 Hz using a paramagnetic analyzer (Sable Systems PA-1B; Las Vegas, NV, USA). The system was checked for leaks for each trial by bleeding N_2 into the mask at a known rate and plotting (N_2 rate/mass-flow rate) against the observed decrease in O_2 content of the sub-sampled air; this relationship was consistent across trials ($N=9$, $r^2=0.98$, $P<0.001$, second-order polynomial regression, no outliers).

Oxygen consumption was monitored during the trial in real time to ensure that steady-state aerobic metabolism was achieved, and the rate of oxygen consumption V_{O_2} (s^{-1}) was measured following Fedak et al. (1981) using data from the last minute of each trial. The resting rate of oxygen consumption, measured while standing for 6 min prior to the start of locomotor trials, was subtracted from the rate of oxygen consumption for each trial, and the difference divided by body mass to calculate the COL (V_{O_2} kg^{-1} s^{-1}) for each trial, where V_{O_2} is in ml.

Kinematic data was also collected during each trial using a high-speed infrared camera system (Qualysis®; Qualysis Motion Capture Systems, Gothenburg, Sweden) operating at 240 Hz. Reflective markers were adhered to the skin overlying the greater trochanter and to the subject's shoe over the calcaneal tuberosity and distal fifth phalange. Qualysis® data analysis software was then used to measure: protraction angle at heelstrike (heel–trochanter–floor), retraction angle at toe-off (toe–trochanter–floor), contact time duration (heel strike frame–toe-off frame) and stride frequency. Swing period was estimated as (stride frequency)$^{-1}$. These variables, with speed, were used to calculate the rate of force production for each trial using equations from the model.

Estimating limb swing cost

To determine limb swing costs it was necessary to estimate the radius of gyration, mass and resonant frequency of the limb for each subject. Limb mass was estimated as 16% of body mass, following Dempster (1955). The radius of gyration $D=hL$, where h is a measure of mass distribution; a value of 0.56 was used for h following Plagenhoef (1966).

The resonant period T is also a function of limb length L and shape h, as $T_0=2\pi[I(MgL)^{-1}]^{0.5}$, and $I=h^2L^2M_L$. Thus:

$$T_0 = 2\pi(h^2Lg^{-1})^{0.5} . \tag{20}$$

Predictions

To test the utility of the LiMb model, predicted COL was plotted against observed COL. This was done using the equations for vertical force production (Eq. 4, 6), vertical plus horizontal force production (Eq. 13, 14), and total force production (Eq. 18, 19) to determine the contribution of each component in predicting COL. It was predicted that each additional component would improve the correlation between predicted and observed COL.

Next, the LiMb model (Eq. 18, 19) was compared with t_c^{-1} and Froude number as alternative predictors of COL$_{run}$ and COL$_{walk}$, respectively. The LiMb model was predicted to outperform contact time and Froude number in predicting locomotor cost, as the model incorporates horizontal force production and limb swing costs.

Finally, I tested the prediction that k, the constant relating oxygen consumption to force production, was the same for walking and running gaits. This was predicted because walking and running employ isometric contractions in the same muscle groups over similar ranges of limb excursion. Therefore, muscle length, effective mechanical advantage and relative shortening velocity and, therefore, k, should be independent of gait. In fact, Kram and Taylor (1990) found k was nearly constant across a large range of body sizes and limb design (e.g. rabbit to horse); it seems likely, therefore, that k should be similar between gaits within a species.

Least squares regression was employed in each of the above tests to determine the percentage of observed variation explained by a given predictor with each trial treated as an independent data point. To test for differences in k between gaits, k was determined as the slope of the LSR for predicted *versus* observed COL for walking and running, and these slopes were compared following Zar (1984, pp. 292).

Results

The predicted rate of force production correlated significantly with observed COL for both running and walking
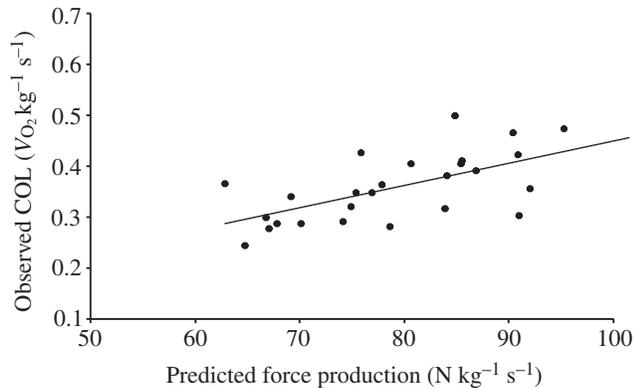
Fig. 4. Predicted *versus* observed COL for running trials. Line indicates LSR (N=27, r^2=0.43, P<0.01).
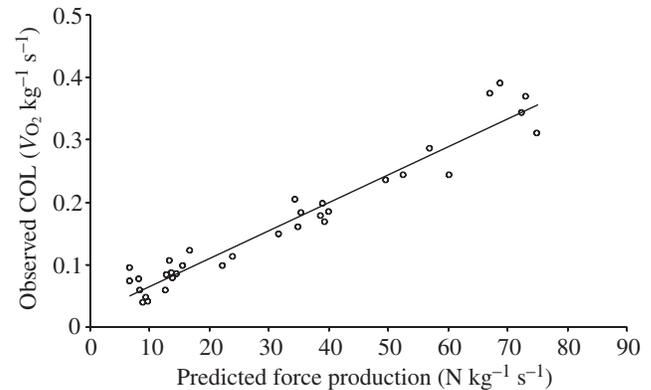

Fig. 5. Predicted *versus* observed COL for walking trials. Line indicates LSR (N=34, r^2=0.94, P<0.001).

(Table 1). For running, the correlation between predicted and observed COL improved as each component of force production was added (Table 1). Vertical force production (Eq. 4) predicted only 16% of the variance in observed COL_{run} (N=27, r^2=0.16, P<0.05), while including horizontal force production (Eq. 13) increased explained variance to 25% (N=27, r^2=0.25, P=0.01). Adding the cost of limb swing (Eq. 18) had the largest effect, increasing explained variance in observed COL_{run} to 43% (N=27, r^2=0.43, P<0.001) (Fig. 4). The low correlation coefficient is likely a result of between-subjects differences in the force/oxygen constant, k, as will be discussed in the following section.

For walking, vertical force production (Eq. 6) and vertical + horizontal force production (Eq. 14) each explained 92% of the variance in observed COL_{walk} (N=34, r^2=0.92, P<0.001 for both conditions), while total force production (Eq. 19) explained 94% (N=34, r^2=0.94, P<0.001) (Fig. 5). Thus, while predicted force production explained a much higher percentage of the variance in observed COL_{walk}, the horizontal-force and limb-swing components did not improve the correlation between predicted and observed COL_{walk} significantly.

The model performed as well or better than other predictors of cost. While predicted COL_{run} (Eq. 18) explained over 40% of the variance in observed COL_{run}, the inverse of contact time predicted less than 30% (N=27, r^2=0.29, P<0.01). For walking, predicted COL_{walk} (Eq. 19) predicted over 90% of the variance in observed COL_{walk}, as did Froude number (N=34, r^2=0.91, P<0.001). While the model outperformed (i.e. produced greater correlation coefficients) contact time and Froude number as predictors of observed COL, comparisons of correlation coefficients (Zar, 1984, pp. 313) revealed these differences were not significant (P>0.05).

The percentage of estimated total force production contributed from vertical, horizontal, and limb-swing components was similar for walking and running. For running, vertical force production accounted for 63.7% (s.d. ±7%) of estimated force production, while horizontal forces accounted for 19.8% (±1%) and limb-swing 16.5% (±6%). For walking, vertical forces accounted for 49.7% (±11%), horizontal forces

for 21.3% (±5%), and limb-swing for 29% (±15%) of total estimated forces. However, limb-swing estimates are considerably lower when only normal walking speed (1.5 m s^{-1}) is considered; vertical forces at this speed, rated as the most 'comfortable' speed by subjects, account for 59.8% (±5%), horizontal for 25.0% (±3%), and limb-swing for 15.2% (±8%) of total estimated force production. The contribution of each force component changes markedly with speed, particularly for walking, as shown for a representative subject in Fig. 6. Clearly, the proportion of total estimated force production was not correlated with the proportion of variance in COL explained by a given component.

The force/oxygen constant, k, was not significantly different between gaits. The slope of the LSR for predicted *versus* observed COL_{run} was 0.0044, which was not significantly different than the slope for walking (slope=0.0045; P>0.05). Similarly, the y-intercept of the LSR equations for walking (0.021) and running (0.012) were not significantly different (P>0.05).

Values for k from this dataset are lower than that reported by Kram and Taylor (1990) (mean k=0.0092, s.d.=0.0022). This is probably a result of estimated forces being greater when incorporating vertical, horizontal and limb swing costs as in the LiMb model, rather than only considering vertical forces as in Kram and Taylor (1990). When only vertical force production is used to predict COL (Eq. 4, 6), the value for k given by LSR is 0.0061, which is near the 95% confidence interval calculated from Kram and Taylor (1990) (95% CI=0.0063–0.0119).

Discussion
Force production and COL
The rate of force production predicted by the LiMb model for both walking and running explained a significant amount of the variance in observed COL_{walk} and COL_{run}. The agreement between predicted force production and observed locomotor cost further supports the proposal that the metabolic cost of locomotion is a function of muscular force production
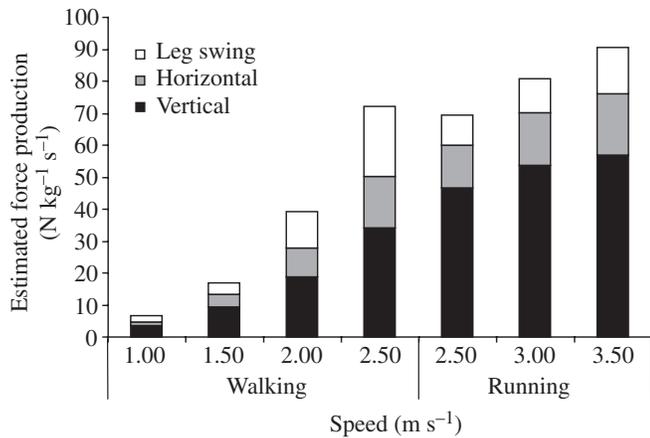
Fig. 6. The contribution of vertical, horizontal and leg-swing forces to total estimated force production during walking and running. Data for one representative subject (Female, 66 kg, hind-limb length: 95 cm.
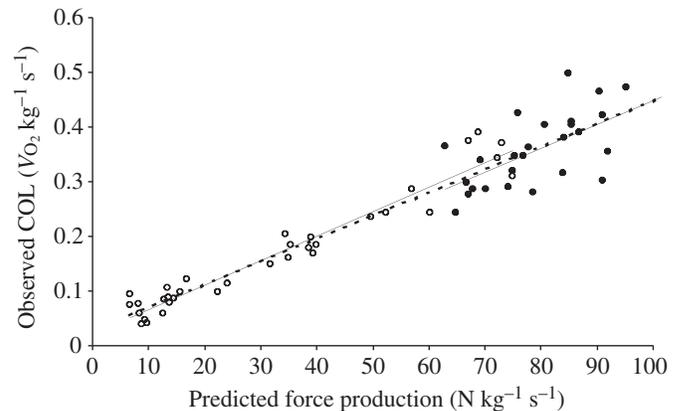

Fig. 7. Predicted *versus* observed COL for walking and running trials. Solid lines: LSR for walking (open circles) and running (filled circles). Broken line: LSR for all trials combined ($N=61$, $r^2=0.91$, $P<0.001$).

(Kram and Taylor, 1990; Taylor, 1994; Griffin et al., 2003). The success of the model suggests force production, and therefore COL, can be predicted reliably from anatomical variables (limb length and proportion) and basic kinematic parameters (speed, stride frequency and excursion angle). As results here show, such an approach can be more successful than other indices of locomotor cost, at least during running.

Vertical force production accounted for 50% or more of total estimated force production across speeds for both walking and running gaits, more than horizontal force and limb-swing combined. However, while vertical force production alone is a good predictor of COL for walking, it is a poor predictor in running in this dataset, with horizontal force and limb-swing contributing markedly to the predictive power of the LiMb model. Thus, the proportion of total force accounted for by a given component does not necessarily reflect the power of that component in predicting COL. This might be expected, as the regularity with which a given force component increases with total cost, and therefore the predictive power of that component, need not necessarily correspond with the magnitude of the force. Furthermore, force components that are highly correlated will not improve the fit of the model when combined. For example, estimated vertical and horizontal forces are highly correlated for walking ($N=34$, $r^2=0.99$, $P<0.01$) but less so for running ($N=27$, $r^2=0.48$, $P<0.01$); consequently, combining horizontal and vertical force production improves the fit of the LiMb model for running, but has no effect for walking (Table 1). This distinction between the magnitude of a given force component and its reliability as an index of COL may be relevant to studies seeking to identify discrete components of locomotor cost.

If muscular force production is the primary determinant of energy expenditure during locomotion, predicted rate of force production should relate to observed COL similarly across gaits in which similar muscle groups and shortening velocities are employed. Indeed, this appears to be the case; the

relationship between predicted force production and observed energy expenditure, as determined by LSR, is similar for walking and running (Fig. 7). Thus, while no single model may successfully describe the mechanics of mass-spring running gaits and pendular walking gaits (Donelan and Kram, 2000), results of this study suggest models using a common paradigm of force production to predict energy cost may be successful across different gaits and activities. If so, it may be possible to compare directly force production and cost across widely different activities (e.g. walking *versus* climbing), providing a new means of comparing anatomical specialization and locomotor performance.

Walking

The LiMb model was particularly effective in predicting COL_{walk}. Predictions of the model fit observed COL_{walk} ($r^2=0.94$) as well or better than other proposed models for walking cost, including Froude number ($r^2=0.91$) and the collision model proposed by Donelan et al. (2002, fig. 6; $r^2=0.89$). The success of the model for walking suggests the cost of walking is primarily a function of the change in momentum inherent in the sinusoidal trajectory of the COM through a stride: the upward acceleration of the COM through the troughs of this trajectory requires muscular force. In addition, limb swing contributes to cost, particularly at higher walking speeds in which swing periods are far shorter than the natural period of the lower limb. The 'determinants of gait' described by Saunders et al. (1953) and others serve to minimize walking cost by lowering the amplitude of the COM trajectory and by increasing the duration (thereby decreasing the magnitude) of upward acceleration.

Because walking cost is predicted as a function of inertia rather than weight, the LiMb model for walking may explain deviations from dynamic similarity reported previously (Farley and McMahon, 1992; Donelan and Kram, 1997). The LiMb model predicts relative stride length, S_{rel} (stride length/limb
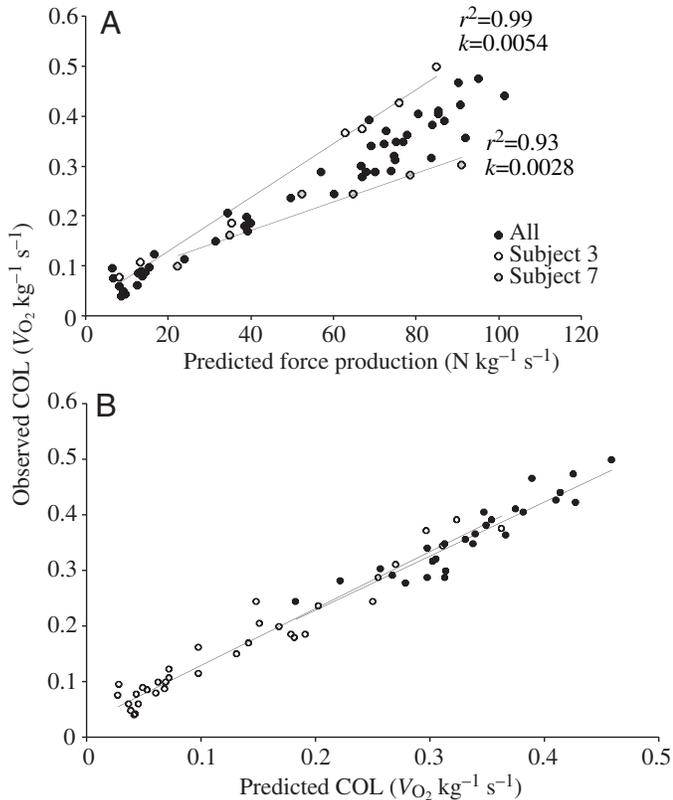
Fig. 8. Between-subjects variation in *k*. (A) While the LiMb model predicted over 90% of the variance in COL for each subject, differences in *k*, measured as the slope of the LSR for each subject, were marked. Data for two subjects are highlighted here against data from all subjects. (B) Predicted *versus* observed COL, using estimates of *k* derived for each subject. Line indicates LSR. open circles, walking trials (*N*=34, r^2=0.95, *P*<0.01); filled circles, running trials (*N*=27, r^2=0.87, *P*<0.01).
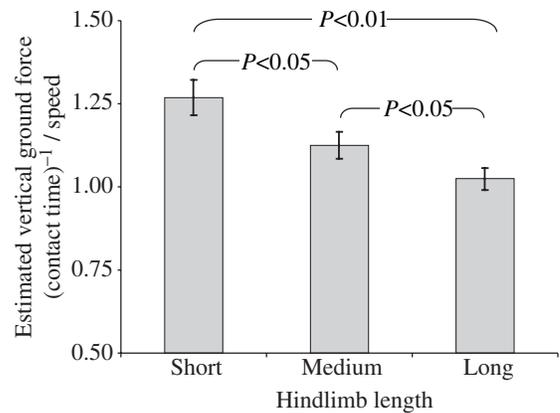

Fig. 9. The effect of limb length on vertical force production during walking and running. The magnitude of vertical ground force at a given speed, estimated as (contact time)$^{-1}$ / speed, decreases with hind-limb length. Group means are calculated from individual trials (walking and running trials combined). *P*-values are given for each comparison, calculated *via* Student's one-tailed *t*-test assuming unequal variance. Error bars indicate the standard error of the mean. Ranges for each hind limb-length category are: short 79–80 cm (*N*=2 subjects); medium 89–95 cm (*N*=4); long 103–112 cm (*N*=3).

length), will be a function of excursion angle ($S_{rel} \approx 4\sin\phi/2$) independent of gravity. Similarly, COL$_{walk}$ is predicted to be dependent on speed but independent of gravity, as the positive (upward) change in momentum of the COM during walking is a function of speed, not gravity (see Eq. 5, 6). Both of these predictions run counter to dynamic similarity, which predicts relative stride length to be inversely proportional to *g*, and COL$_{walk}$ to be a function of Froude number ($U L^{-1} g^{-1}$). Results from reduced gravity experiments, in which gravitational acceleration, *g*, is manipulated *via* a harness, fit LiMb model predictions better than those of dynamic similarity: stride length (Donelan and Kram, 1997) and COL$_{walk}$ (Farley and McMahon, 1992) were found to be largely independent of *g* but not walking speed. Thus, while the LiMb model did not explain significantly more of the variance in observed COL$_{walk}$ than Froude number, it does appear to outperform predictions of dynamic similarity in reduced-gravity conditions.

Preferred step length, step frequency and speed relationships noted previously (see Bertram and Ruina, 2001) for walking humans may also be explicable *via* the LiMb model. Speed is equivalent to the product of step frequency, 0.5*f*, and step length, 2*L*sinϕ/2 and, therefore, at any given speed a range of step frequencies and step lengths are possible. However, COL$_{walk}$ for a given speed is predicted (Eqn 14) to increase more steeply with frequency than with excursion angle. Thus the LiMb model predicts long step lengths and low frequencies to be preferred, which may explain why humans do not minimize step length during walking as predicted by collision models of walking mechanics (Donelan et al., 2002). Indeed, an interesting tradeoff may exist: high frequency and short steps impose high costs as predicted by the present model while greater step length increases collision costs, resulting in a U-shaped cost/step-length curve for a given speed. If so, at any given speed, there will be one frequency/step length combination that minimizes combined cost. Support for this hypothesis is offered by Bertram and Ruina (2001), who investigated walking speeds, step frequencies and step lengths chosen when one of these variables was constrained. The frequency/speed relationships chosen under the three constraint conditions were consistent with an energy-minimizing strategy.

Running

The relationship between predicted and observed COL$_{run}$ shows considerably more variation (r^2=0.43) than in walking (Fig. 4). While the LiMb model outperforms contact time (r^2=0.29) as a predictor of cost, the variation between predicted and observed cost begs explanation. One likely source of increased variance in COL$_{run}$ *versus* COL$_{walk}$ is between-subjects differences in the force/oxygen constant, *k*. The LiMb model (Eqns 18, 19) predicts COL assuming that *k* is constant across subjects, but this is unlikely. Differences in the *k* (measured as COL/t_c) have been noted previously

(Weyand et al., 2001) and might be expected, as differences in variables, such as muscle-fiber type, running mechanics and limb-proportion, will likely lead to differences in the efficiency with which oxygen consumption is translated into force production. Because k determines the slope of the predicted–observed COL regression, differences in k will lead to greater variance in running trials, in which predicted force production is greater. To examine whether differences in k explain the variance in COL_{run}, k was determined for each subject empirically as the slope of the LSR between predicted and observed COL for all trials (walking and running). While the fit of the LSR for each individual was excellent ($N=7$ trials per subject, mean $r^2=0.98$, range: 0.93–0.99, $P<0.001$ for all subjects), differences were observed in estimates of k (mean=0.0043, range 0.0028–0.0054, $N=9$ individuals, see Fig. 8A). Using these estimates of k to predict oxygen consumption *via* Eq. 18 and 19 reduced the amount of unexplained variance considerably, and the fit of the LiMb model was similar for walking ($N=34$, $r^2=0.95$, $P<0.001$) and running ($N=27$, $r^2=0.87$, $P<0.001$) (Fig. 8B). This suggests between-subjects differences in k explain most of the variance from predicted COL, but further work is necessary to test this hypothesis.

As in walking, the LiMb model for running agrees with previous results from reduced gravity experiments. COL_{run} is expected to increase proportionally with gravity (Eq. 19), but be independent of body mass, because COL_{run} predicted by the LiMb model is mass-specific. Farley and McMahon (1992) reported COL_{run} increases in direct proportion to gravity. Furthermore, Chang et al. (2000), in an investigation of the separate effects of gravity and inertia on running mechanics, found vertical and horizontal force impulses (a measure of predicted cost *via* the present model) changed in direct proportion to gravity but were independent of body mass. Another study, examining the effect of gravity on walk–run transition speeds (Kram et al., 1997), found preferred transition speeds decrease in proportion to gravity. Because COL_{run} changes in proportion to gravity while COL_{walk} is independent, the model predicts walk–run transition speeds, approximated as the speed that $COL_{run}=COL_{walk}$, to decrease with decreased gravity, in agreement with Kram et al. (1997).

Limb swing

Limb swing costs as predicted by the LiMb model are consistent with previous studies in that these costs are low at normal walking speeds but considerably greater at fast walking and running (Fig. 6). However, predicting limb swing cost is complicated by the necessity of estimating an oxygen/force constant, b, and by the necessary constraint that hind-limb inertial properties are estimated. This dependence on b is especially critical for running, in which estimates of COL_{run} have a greater impact on the fit of the model. At low values of b (e.g. $b<10$), estimated swing costs relative to the cost of accelerating the COM are so low as to be negligible, and the fit of the model for running does not exceed that for Eq. 13.

Similarly, at high values for b (e.g. $b>100$), predicted limb swing cost dominates predicted COL_{run}, and the fit of the model is diminished. Using an estimate of b that produces swing costs similar to those reported by Marsh et al. (2004) produces a good fit, but further work is necessary to determine if this value ($b=30$) is reasonable. For example, it is clear that limb proportion and therefore inertial properties differ between guinea fowl and humans. Similarly, while the method used here to estimate hind-limb inertial properties produces a reasonable fit to the data, future work needs to improve these estimates by incorporating anatomical data from individual subjects.

The effect of limb length on COL

The LiMb model predicts a somewhat complicated relationship between limb length and COL in which longer limbs decrease the cost of accelerating the COM (Eq. 13, 14) but increase the cost of limb swing (Eq. 18, 19). Data from this study as well as others strongly suggests longer limbs do in fact decrease the magnitude of vertical ground forces (i.e. the change in vertical momentum of the COM) at a given speed. In the present human sample, vertical ground force at a given speed, estimated as $t_c^{-1} U^{-1}$, was significantly greater for subjects with shorter legs (Fig. 9), a result predicted by the LiMb model (Eq. 4, 6). Similarly, Hoyt et al. (2000) found contact time was strongly correlated with limb length in comparisons between species. However, while longer limbs decrease the force necessary to support bodyweight, the increased cost of swinging longer, heavier limbs apparently eliminates a simple univariate relationship between limb length and locomotor cost. As a result, COL in this study was negatively correlated with limb length only at moderately fast walking speeds ($2.0~\text{m s}^{-1}$: $r=-0.87$, $P<0.01$, $N=9$) where the cost of accelerating the COM is high but swing cost is low. The trade-off between the force needed to accelerate the COM and that needed to swing the limb obviates a simple relationship between limb length and COL, at least for within-species comparisons in which swing costs explain much of the variance in COL.

This trade-off may be less salient for comparisons of COL between species, resulting in a simple inverse relationship between limb length and COL. Kram and Taylor (1990) and other studies (Taylor et al., 1974, 1980; Taylor, 1994) have suggested the force produced to support bodyweight determines the scaling of COL with body size between species. Swing cost, in contrast, may be less important in between-species comparisons as decreases in stride frequency offset increases in limb length with body size (Hildebrand, 1985; Heglund and Taylor, 1988). If the force produced to accelerate the COM does in fact determine the scaling of COL, the LiMb model predicts COL to scale inversely with limb length: vertical and horizontal ground forces are a product of L^{-1} (Eq. 13, 14). This prediction is supported by interspecific comparisons of COL. Because limb length scales as $M_b^{0.33}$ (Alexander et al., 1979), the LiMb model predicts COL to scale as $M_b^{-0.33}$. This

exponent (–0.33) is similar to the scaling relationship reported by Taylor et al. (1982; exponent: –0.32, 95% CI –0.29 to –0.34). This agreement between predicted and observed scaling suggests the LiMb model may be useful for between- as well as within-species investigations of locomotor cost. Moreover, it suggests limb length may drive the interspecific scaling of COL, as suggested by Kram and Taylor (1990) and others.

Abbreviations

ϕ	excursion angle; the angle included by the limb through stance phase
a	acceleration (where a_y is vertical acceleration, a_x is horizontal acceleration)
b	ratio of oxygen consumption / force production while swinging the limb, in ml/N
COL	cost of locomotion; the mass-specific rate of energy consumption during locomotion
COM	center of mass of the body
d	horizontal distance moved by the COM during stance phase
D	radius of gyration of the limb
EMA	effective mechanical advantage
F	force (where F_y is vertical force, F_x is horizontal force)
f	frequency (f_{step} is step frequency)
g	gravitational acceleration
GRF	ground reaction force
h	index of mass distribution of the limb; $h=D/L$
I	moment of inertia
k	ratio of oxygen consumption / force production, in ml/N
L	limb length
M	mass (M_b body mass, M_L limb mass)
q	vertical displacement of the COM during walking
r	effective lever arm of the muscles that swing the leg
S	stride length
S_{rel}	relative stride length
T	period (T_0 is natural period)
T_{step}	Step period, defined as the period between two consecutive (contra-lateral) heelstrikes
t_c	Contact time; the duration of stance phase
U	travel speed
V_{O_2}	volume of O_2 consumed
v	shortening velocity of a muscle (v_{max} is maximum velocity)

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