Mechanical and metabolic determinants of the preferred step width in human walking

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We studied the selection of preferred step width in human walking by measuring mechanical and metabolic costs as a function of experimentally manipulated step width (0.00–0.45L, as a fraction of leg length L). We estimated mechanical costs from individual limb external mechanical work and metabolic costs using open circuit respirometry. The mechanical and metabolic costs both increased substantially (54 and 45%, respectively) for widths greater than the preferred value (0.15–0.45L) and with step width squared ($R^2 = 0.91$ and 0.83, respectively). As predicted by a three-dimensional model of walking mechanics, the increases in these costs appear to be a result of the mechanical work required for redirecting the centre of mass velocity during the transition between single stance phases (step-to-step transition costs). The metabolic cost for steps narrower than preferred (0.10–0.00L) increased by 8%, which was probably as a result of the added cost of moving the swing leg laterally in order to avoid the stance leg (lateral limb swing cost). Trade-offs between the step-to-step transition and lateral limb swing costs resulted in a minimum metabolic cost at a step width of 0.12L, which is not significantly different from foot width (0.11L) or the preferred step width (0.13L). Humans appear to prefer a step width that minimizes metabolic cost.

Keywords: biomechanics; biped; energetics; locomotion

1. INTRODUCTION

Limbed animals have a preferred manner of locomotion. They prefer to move at certain speeds and, at a given speed, they prefer to use a particular gait and particular combination of gait variables (see e.g. Bornstein & Bornstein 1976; Margaria 1976; Hoyt & Taylor 1981; Cavanagh & Williams 1982; Cavagna & Franzetti 1986). Deviations from these preferred mechanics appear always to exact a metabolic cost. This suggests that the preferred gait variables are selected in order to minimize the metabolic cost. However, the biomechanical basis for the metabolic cost of locomotion is not well understood.

As with other gait variables, walking animals appear to prefer a particular step width. Humans, for example, prefer to walk with a step width of ca. 0.12L (expressed as a fraction of leg length L), which is measured as the lateral separation between the midlines of the feet (Bauby & Kuo 2000). It is possible that humans prefer this particular step width because it minimizes metabolic cost.

Using simple models, we predict a substantial metabolic cost to walking with wide steps using simple models (figure 1) (outlined in §2). This metabolic cost is due to a mechanical energy cost, which occurs during the transition from one stance leg to the next, that increases with the square of step width (figure 2a) (Kuo 1999). This step-to-step transition cost occurs because the centre of mass moves along an arc dictated by the stance leg and each transition to a new stance leg requires mechanical work in order to redirect the centre of mass velocity from one inverted pendulum arc to the next (figure 3) (see also Donelan et al. 2001). If muscular efficiency, i.e. the ratio of mechanical work performed by muscle to the metabolic energy consumed, is fairly constant, metabolic cost will also increase with the square of step width. ‘Walking wide’ could be very metabolically expensive.

While the costs of step-to-step transitions are minimized at the narrowest of step widths, there is a possible metabolic consequence of walking with narrow steps. At step widths narrower than foot width it becomes necessary to move the swing leg laterally in order to avoid the stance leg, thereby increasing lateral limb swing costs (figure 2b).

We tested a series of hypotheses regarding the selection of preferred step width in human walking. First, we hypothesized a mechanical cost of wide steps that increases with the square of step width. Second, assuming constant muscular efficiency, we hypothesized that the metabolic cost of steps wider than the preferred value will also increase with the square of step width. Third, we hypothesized that metabolic cost increases with narrow step widths, although we did not have a quantitative prediction for the shape of this curve. Finally, we hypothesized that the preferred step width minimizes metabolic energy consumption. Due to the trade-offs between step-to-step transition costs and lateral limb swing costs, we predicted that this preferred step width is close to the width of a single foot at its widest. In order to test these hypotheses, we measured mechanical and metabolic costs at experimentally manipulated step widths while keeping speed, step length and step frequency constant.

2. METHODS

(a) Model predictions

A previously developed model of passive dynamic walking (the anthropomorphic three-dimensional walking model) predicts...
the mechanical energy cost of increasing step width in humans (figure 1a) (see Kuo 1999). Passive dynamic walking refers to the ability of an appropriately designed two-legged mechanism to walk down a gentle slope with no additional energy input (McGeer 1990). During single support phases, the legs act as freely swinging, coupled pendula. Double support phases function as transitions between single support phases and are modelled as instantaneous, inelastic collisions between the swing foot and the ground. Each collision redirects the centre of mass velocity from one inverted pendulum-like stance limb to the next. Using approximately anthropomorphic inertial parameters, our model predicted that the mechanical energy losses incurred in transitioning from one single support phase to the next will increase with the square of step width (figure 2a).

A highly simplified and dimensionless version of this model illustrates this mechanical cost (figure 1b). This simple three-dimensional walking model condenses the leg inertia into point masses at the pelvis and feet, with the mass of the feet being much smaller than that of the pelvis (after Garcia et al. 1998). This is the simplest three-dimensional walking model because the slope and splay angle are the only free parameters. The masses are concentrated in the pelvis ($M$) and feet ($m$).
Combining equations (1)--(4) and employing power series expansions for trigonometric functions yields
\[
\Delta E = 2\beta \psi (\dot{\beta}^2) + 4\beta \dot{\psi} \ddot{\theta} + 2\beta (\dot{\psi}^2) - 2\dot{\psi} \dot{\psi} \ddot{\theta} - 2 \dot{\psi} \dot{\psi} \ddot{\theta} - 2 \dot{\theta} \dot{\theta} + \text{higher order terms.}
\]  

(5)

Keeping step length and cadence fixed (i.e. regarding \(\theta\) and \(\dot{\theta}\) as non-zero constants), we see that \(\Delta E\) is dominated by terms of degree 2 in \(\beta\), \(\dot{\psi}\) and \(\ddot{\theta}\). These variables are approximately proportional to step width and, as a result, \(\Delta E\) increases with the square of step width. Using the convention of normalizing energy by body weight and distance travelled (e.g. Kuo 2001), the dimensionless mechanical cost of transport is
\[
\text{COT}_{\text{mech}} = C_{\text{mech}} \beta^2 + D_{\text{mech}},
\]

(6)

where \(C_{\text{mech}}\) and \(D_{\text{mech}}\) are parameters that depend on step length and cadence. In the more anthropomorphic model with curved feet, \(C_{\text{mech}}\) and \(D_{\text{mech}}\) also depend on inertial properties and foot curvature (Kuo 1999). In humans, \(C_{\text{mech}}\) and \(D_{\text{mech}}\) depend on many physical attributes. In the present study, we consider these as empirical parameters to be identified from data.

Collision losses are necessary in these models in order to redirect the centre of mass velocity in transitioning from one stance limb to the next. While humans also have to redirect the centre of mass velocity as they change stance limbs, they do so not with instantaneous, inelastic collisions but, rather, with negative work by the leading leg over a finite period of time. While walking down a slope restores energy in passive dynamic walking models, muscles must perform the required positive work for animals walking on the level. The step-to-step transition cost is the negative work performed in order to redirect the centre of mass velocity from one inverted pendulum to the next and the positive work performed to replace the lost energy. Similarly, humans perform simultaneous positive and negative work with the trailing and leading legs, respectively, during the double support phase.

\[
E_k = 0.5[(\cos^2(\beta - \psi))\dot{\theta}^2 + \dot{\psi}^2].
\]

(3)

The mechanical energy lost at impact, i.e. \(\Delta E\), is
\[
\Delta E = E_k^2 - E_k.
\]

(4)

Figure 3. The mechanical costs of step-to-step transitions in the simplest three-dimensional walking model. Variables in bold denote vector quantities. (a) Each transition to a new stance limb requires redirecting the centre of mass velocity from \(v_{com}^-\) to \(v_{com}^+\). This requires negative work by the leading limb, i.e. \(v_{com}^- < v_{com}^+\). We model the heel strike ground reaction force as an impulse \(S\) acting along the leading limb. \(S\) causes an instantaneous change in the centre of mass velocity. (b) In order to maintain a steady walking speed, positive and negative work must be of equal magnitude. In this simple model, a toe-off impulse \(P\) by the trailing limb at the same time or immediately before heel strike replaces the lost energy. Similarly, humans perform simultaneous positive and negative work with the trailing and leading legs, respectively, during the double support phase.
Experimental procedures

We measured the mechanical and metabolic costs of walking at different step widths in 10 human adult subjects. These widths were each subject's preferred width and dimensionless widths equal to 0.00, 0.10, 0.15, 0.20, 0.30, 0.40 and 0.45L (expressed as a fraction of leg length L, which is measured as height to the greater trochanter). The subjects walked at the same speed (1.25 m s$^{-1}$) at all widths. All subjects (five male and five female) (mean ± s.d., body mass = 68.9 ± 12.2 kg, leg length = 0.93 ± 0.05 m and widest foot width = 0.10 ± 0.01 m) were healthy and exhibited no clinical gait abnormalities. Before the experiments began, the volunteers gave their informed consent to participate, in accordance with university policy.

We familiarized the subjects to the experimental protocol in a preliminary session. Familiarization consisted of two 10 min trials of treadmill walking at 1.25 m s$^{-1}$. The subjects walked at their preferred width during the first trial and then walked at the widest experimental width of 0.45L during the second trial. We also measured each subject’s preferred step frequency during the first trial by timing 20 steps over the last 2 min.

In order to calculate the mechanical costs as a function of step width, we measured the individual limb ground reaction forces and moments as the subjects walked across two separate force platforms at the eight different step widths. The platforms (Model LG6-4-2000, AMTI, Newton, MA, USA) were mounted in series near the midpoint of a 17 m-long walkway. We collected the three components of the ground reaction forces and moments ($F$ and $M$, respectively) from both force platforms simultaneously at 1000 Hz per channel. Infrared photocells placed on either side of the force platforms (3.0 m apart) measured the subjects’ overground walking speed. We discarded trials if the subjects’ speed was not between 1.20 and 1.30 m s$^{-1}$ or if individual feet did not fall cleanly on separate force platforms. We saved and then analysed the data for three acceptable trials from each subject for each of the eight randomized widths. We enforced the widths by having the subjects step on thin strings that were stretched tightly along the full length of the walkway (figure 4a). A metronome enforced the step frequency that each subject had freely selected during the first familiarization trial for all of the enforced widths. Although the subjects may have preferred to adjust their step frequency for different widths, we controlled this variable in order to study the effect of step width alone.

We used the individual limb ground reaction forces (figure 5a) and moments for calculating the step width, centre of mass velocities and external mechanical work of a single step from each of three trials. We defined a step as beginning with ground contact of one foot and ending with ground contact of the opposite foot. A fourth-order, zero-phase-shift Butterworth 100 Hz low-pass digital filter conditioned the ground reaction force and moment signals. We used these conditioned signals for calculating the instantaneous centre of pressure on each force platform. We calculated the preferred step width as the lateral distance between the average centres of pressure acting under each foot.

We found the centre of mass velocities $\mathbf{V}_{\text{com}}$ (figure 5b) from the vector sum of the ground reaction forces acting under both limbs. This required calculating the accelerations of the centre

\begin{align}
\text{COT}_{\text{met}} = \text{C}_{\text{met}}(w)^2 + D_{\text{met}},
\end{align}

where $C_{\text{met}}$ and $D_{\text{met}}$ are constants that depend on their counterparts in equation (6) and on the muscle. We consider these as empirical parameters to be identified from data.

We also predict that narrow step widths will be costly. One potential cost at very narrow step widths is that of moving one foot laterally in order to avoid the other (figure 2b). Given a finite amount of time for accomplishing this lateral motion within a step, there might be a significant metabolic cost associated with this foot clearance (the lateral limb swing cost). The amount of side-to-side foot motion as a function of step width may serve as a rough indicator of a change in this cost. Simple calculations based on the anthropomorphic model (Kuo 1999) predict that side-to-side foot motion will increase linearly as step width decreases below foot width (figure 2b). This foot motion is predicted to result in a substantial increase in metabolic cost.

The sum of the step-to-step transition and lateral limb swing costs will most probably have a minimum metabolic cost at a step width close to the widest foot width (figure 2). We do not have a quantitative prediction for the relative weightings of these two costs, making it impossible for us to predict the overall cost as a function of step width. However, for a large range of weightings wider steps will be dominated by the quadratic step-to-step transition cost of equation (7) because the lateral limb swing cost is zero for step widths greater than foot width. Narrower steps will be dominated by the limb swing cost but with some effect from the step-to-step transition cost. Because our experimental measurements can only resolve the energetic cost of narrow steps to a limited degree, we are satisfied with predicting a monotonic increase in energetic cost with steps narrower than preferred.

Figure 4. (a) We enforced widths ($w$) during the mechanics data collection by having the subjects walk on thin string stretched tightly along the full length of the walkway. We enforced step width during the metabolic data collection by having the subjects (b) walk on chalk lines at narrow widths and (c) walk on the outside of metal rails mounted just above the treadmill belt at wide widths.
of mass from the summed ground reaction force components and then integrating with respect to time, subject to appropriate boundary conditions (Cavagna 1975).

We estimated the mechanical cost of step-to-step transition as the negative external mechanical work performed by the leading leg during double support (figure 5c) (see also Donelan et al. 2001). The external mechanical power generated by the leading leg, i.e. \( P_{\text{lead}} \), is

\[
P_{\text{lead}} = F_{\text{lead}} \cdot V_{\text{com}},
\]

where \( F_{\text{lead}} \) is the ground reaction force acting on the double support leading limb. We found the negative external work performed by the leading leg during double support \( (W_{\text{DS, lead}}) \) by integrating equation (8) over a domain restricted to double support and for which \( P_{\text{lead}} \) is negative (denoted by DS-NEG):

\[
W_{\text{DS, lead}} = \int_{\text{DS-NEG}} P_{\text{lead}} \, dt.
\]

We determined the mechanical cost of transport \( \text{COT}_{\text{mech}} \) by dividing \( W_{\text{DS, lead}} \) (J) by the subjects’ step length (m) and body weight (N). We averaged the mechanical costs for three complete steps for each subject for each condition. In addition to the mechanical costs based on individual limbs measures of external mechanical work, we also calculated traditional combined limbs measures of external mechanical work (Cavagna 1975).

In order to determine metabolic cost as a function of step width, we measured the metabolic rates of the subjects as they walked on a treadmill at the eight different step widths. We measured their rates of oxygen consumption \( (V_{\text{O}_2}) \) and carbon dioxide production \( (V_{\text{CO}_2}) \) using an open circuit respirometry system (Physio-Dyne Instrument Co., Quogue, NY, USA) over 7 min-long trials. A resting trial in which the subjects stood quietly was conducted, after which eight step width trials were performed in random order using the speed and step widths from the mechanical data collection trials. In order to ensure that the subjects used the desired step width for trials between the narrowest and the preferred width, we instructed the subjects to walk on lines that were marked on the treadmill belt (figure 4b). We found that, for wider steps, some subjects tended to err towards their preferred width. We therefore mounted metal rails just above the treadmill belt in order to enforce a minimum step width physically for the widths between 0.15 and 0.45L (figure 4c). A metronome was again used for enforcing the subjects’ step frequency at all widths.

We calculated the metabolic cost of walking at different step widths using the measured rates of oxygen consumption and carbon dioxide production. We allowed 3 min for the subjects to reach a steady state for each 7 min trial (Poole & Richardson 1997) and then calculated their average \( \bar{V}_{\text{O}_2} \) (ml O\(_2\) s\(^{-1}\)) and \( \bar{V}_{\text{CO}_2} \) (ml CO\(_2\) s\(^{-1}\)) values for the subsequent 3 min. We discarded the last minute of the data due to a delay between breath expiration and breath analysis. We calculated metabolic force and velocities increased in magnitude while the other two components remained relatively unchanged. For clarity, we have not shown the trailing leg ground reaction forces.

\[\text{(c) Average external mechanical power as a function of step width.}\] As a result of the changes in the ground reaction forces and centre of mass velocities, the negative external mechanical work performed by the leading leg during double support \( (\text{step-to-step transition cost}) \) (shaded areas) increased at wider step widths. The values shown are means with \( n = 10 \).
power (W) for each trial using the following standard equation (Brockway 1987):

\[
P_{\text{met, gross}} = 16.58 \frac{W \cdot s}{mol \ O_2} \overline{V_{O_2}} + 4.51 \frac{W \cdot s}{mol \ CO_2} \overline{V_{CO_2}}.
\] (10)

We subtracted the metabolic power for standing from all walking values in order to derive the subjects’ net metabolic power (W). We calculated the dimensionless net metabolic cost of transport $C_{\text{net}}$ by normalizing the net metabolic power for body weight (N) and walking velocity (m s$^{-1}$).

We performed our statistical comparisons as follows. We fitted equations (6) and (7) using a nonlinear regression, with the offset $D$ subtracted from each subject’s data. We compared conditions using paired $t$-tests and repeated-measures analysis of variance (ANOVA) as appropriate, with a level of significance of $p < 0.05$.

3. RESULTS

In support of our first two hypotheses, the subjects’ mechanical and metabolic costs increased with the square of step width for steps wider than the preferred width (figure 6). Nonlinear regression yielded coefficients of $C_{\text{mech}} = 0.077L^{-2} \pm 0.013$ (95% confidence interval) and $D_{\text{mech}} = 0.024 \pm 0.003$ for the subjects’ mechanical costs. The coefficients for their metabolic costs were $C_{\text{met}} = 0.452L^{-2} \pm 0.070$ and $D_{\text{met}} = 0.179 \pm 0.017$. The ratio between $C_{\text{mech}}$ and $C_{\text{met}}$, which is a measure of efficiency, was 0.17. The metabolic cost increased in nearly direct proportion to the increase in the mechanical cost of step-to-step transitions (figure 6$c$). Both costs were substantially greater, 45 and 54% respectively, at 0.45$L$ when compared with the costs at 0.15$L$.

As predicted, the metabolic cost increased at narrow widths. It increased by 8% when compared with the 0.10$L$ width condition ($p = 0.035$) (figure 6$b$).

In support of our final hypothesis, the subjects’ preferred step width was nearly the same as the step width that minimized the metabolic cost. The preferred step width, $w^*$ = 0.13$L$ ± 0.03 (mean ± s.d.), was not statistically different from the minimum metabolic cost inferred from a quadratic fit of the enforced width data, i.e. 0.12$L$ ± 0.05, nor the foot width (measured at the widest point), i.e. 0.11$L$ ± 0.01 (repeated measures ANOVA, $p = 0.425$).

We also observed artefacts that are associated with the enforcement of step width. The metabolic cost at the non-enforced preferred width was 14% lower than that predicted from the enforced step width data ($p = 0.014$). A contrasting artefact was observed for the mechanical cost at the preferred width. There was a 15% increase over the predicted cost ($p = 0.034$).

4. DISCUSSION

These results suggest that humans prefer a step width that minimizes their metabolic costs. The minimum occurs at a step width that is approximately equal to foot width and appears to be a result of trade-offs between increasing step-to-step transition costs at wider widths and increasing lateral limb swing costs at narrower widths.

A possible explanation for the relationship between the step-to-step transition cost and metabolic cost is that it requires metabolic energy to perform positive work as well as to perform the negative work itself. Assuming efficiencies of 25 and —120% for positive and negative work, respectively (Margaria 1976), yields a ratio of 0.21. This corresponds reasonably well with our measured efficiency of $C_{\text{mech}}/C_{\text{met}} = 0.17$. More accurate data on the efficiency of performing positive and negative work will be needed in order to make better predictions of the ratio, but our results suggest that both positive and negative mechanical work contribute to the observed increases in metabolic cost.

The determinants of the metabolic cost of narrow steps are less clear. Limitations in the resolution of metabolic cost measurements and in the enforcement of step width make it difficult to resolve the shape of the narrow width cost relationship. Further studies could address lateral limb swing cost specifically, for example by artificially increasing medial shoe width in order to increase lateral foot motion.

It may be revealing that enforcement of step width itself exerts a significant metabolic cost (figure 6). We determined the metabolic cost at the preferred step width without enforcing the preferred width or the preferred step frequency. Both of these variables were constrained in the subsequent trials and adding constraints appears to increase the metabolic cost. Moreover, the use of two different enforcement techniques, for wide and narrow steps, may have affected our results. Walking humans stabilize themselves in the frontal plane by adjusting their mediolateral foot position (Bauby & Kuo 2000). Unlike the other methods, enforcing a step width with metal rails (figure 4) does not allow medial foot placement adjustments. These suppressed adjustments must instead be delayed to the following step and then performed in the lateral direction, resulting in a greater cost. Our estimates of the metabolically optimal step width may be affected slightly by the use of two different enforcement techniques. We have otherwise avoided comparing data collected using different enforcement methods.

We have made a number of assumptions in using double support negative external work by the leading leg as a measure of the step-to-step transition cost. First, we have assumed that the individual limb measure of negative external mechanical work (Donelan et al. 2001) is an accurate estimate of the total negative mechanical work performed by the muscles during double support. This assumption is justified because the angular displacements of the limbs are relatively small during double support and, unlike the forces applied to the body centre of mass, the forces applied to limbs about the body centre of mass are small. This indicates that there is little internal work performed (see Willems et al. 1995 for further discussion). Second, we have only considered the negative work performed during double support. Some negative work continues beyond double support (figure 5$c$), but, when changing only step width, its magnitude is small enough that it should not adversely affect our conclusions. Third, we have assumed that our measure of negative work also reflects the positive work required for maintaining a steady speed. This positive work appears to be performed for a short interval preceding double support and during double support. It is primarily the work during the former interval that increases with wide steps (figure 5$c$).
Figure 6. Mechanical and metabolic costs as a function of step width. (a) The mechanical costs (COT$_{\text{work}}$), in terms of leading leg double support negative work, increased with the square of step width (dashed line) ($R^2 = 0.83$). We measured the plotted step widths from the ground reaction forces and moments. (b) The metabolic cost (COT$_{\text{met}}$) also varied with step width, with a minimum value near the preferred step width (0.13$L$) and the widest foot width (0.11$L$). The metabolic cost increased with the square of step width for steps wider than the preferred value (solid line) ($R^2 = 0.91$). Note that the metabolic costs at the enforced step widths (solid squares and circles) were higher than that for the freely selected preferred width. The plotted step widths are the enforced widths. (c) The mechanical and metabolic costs compared. The mechanical costs predicted the increases in the metabolic cost for steps wider than the preferred value. In contrast, the traditional combined limbs measure of external mechanical work (Cavagna et al. 1977) is a poor predictor of the metabolic cost (grey triangles and line). The dependent variable is the cost of transport normalized by the cost of transport value at a width of $w = 0.15$. The values shown are means ± s.d.s with $n = 10$.

Fourth, we have assumed that the respective efficiencies of performing positive and negative work are fixed. We have assumed little mechanical energy transfer between limbs during double support and little muscular co-contraction. We have also neglected other costs such as those for stabilizing the trunk.

We have focused on the step-to-step transition and lateral limb swing costs as the major costs underlying the effect of step width on the metabolic cost. However, it is possible that other costs play an important role. For example, an alternative explanation for the cost of wide steps is that the subjects exerted muscle force in order to abduct their legs. However, we consider this an unlikely explanation since the amount of abduction would increase linearly with step width rather than with the square of a step’s width. Abduction would also only increase for widths above hip width, i.e. at ca. 0.3$L$, rather than the width we observed, i.e. at ca. 0.15$L$. Nor would abduction account for the measured increases in positive and negative work. An alternative explanation for the cost of narrow steps is that instability increases as step width decreases (Kuo 1999), thereby requiring additional effort for stabilizing the body (Bauby & Kuo 2000). However, even if active stabilization contributes significantly to the metabolic cost, its dependence on step width is relatively small (Kuo 1999). It does not exhibit a sharply increased cost at narrow widths as would be necessary in order to explain our results.

An implication of our results is that traditional combined limbs measures of external mechanical work (Cavagna 1975) and measures based on them are poor predictors of metabolic cost at wide step widths. While the metabolic cost increased by 45% with step width (figure 6c) ($p = 3.8e-8$), the combined limbs measure of external work did not change significantly (figure 6c) ($p = 0.347$). It did not change with step width because the increases in positive and negative work occurred largely during double support (figure 5c) and combined limbs measures do not account for such situations (Donelan et al. 2001). Another measure based on combined limbs external work is ‘percent recovery’, which is intended to indicate how ideally the inverted pendulum mechanism operates (Cavagna et al. 1977). The percent recovery for our subjects actually increased slightly with wide steps (76–78%) ($p = 0.045$), even though their metabolic costs increased substantially.

Measures of mechanical work and recovery based on combined limbs forces may therefore be misleading when applied to animals that walk with naturally wide steps. For example, Griffin & Kram (2000) recently measured the mechanical work and per cent recovery for walking penguins. They sought to understand why penguins consume twice the metabolic energy of other animals of the same mass in walking. They found that penguins appeared to perform no greater external mechanical work than other animals of similar mass using combined limbs measures and calculated unusually high per cent recovery values. They therefore concluded that the waddling gait of penguins was not responsible for their expensive gait. A similar conclusion might be drawn for humans, even though a wide gait clearly results in a higher metabolic cost. A re-evaluation of wide walking animals seems warranted.
Another implication of our study is that wide gaits may contribute to the high metabolic cost of walking in some clinically interesting subject groups. Young children (Whittle 1996), healthy elderly (Murray et al. 1969) and patients with Parkinson’s disease (Murray et al. 1978) walk with relatively wide steps, perhaps to increase their lateral base of support, thereby providing a larger margin of safety for side-to-side motion of the centre of mass. However, many such groups have a higher metabolic cost when compared with healthy adults walking at the same speed (Calloway & Zanni 1980; Waters et al. 1983a,b; Voorrips et al. 1993). The increased metabolic cost in these subject groups may be partially explained by the increased step-to-step transition costs associated with wide gaits.

Our findings provide further evidence that legged animals prefer locomotor mechanics that minimize their metabolic cost. They prefer to move at speeds that minimize their metabolic cost (see e.g. Bornstein & Bornstein 1976; Margaria 1976; Hoyt & Taylor 1981) and, at a given speed, their preferred gait and the parameters of that gait minimize their cost (see e.g. Margaria 1976; Hoyt & Taylor 1981; Cavanagh & Williams 1982; Cavagna & Franzetti 1986; current study). While this suggests that locomotion mechanics determine the metabolic cost of walking, the underlying biomechanical principles are not well understood. The dominant biomechanical principles underlying the relationship between metabolic cost and step width appear to be step-to-step transition and limb swing costs. It is likely that similar costs also translate to human walking sagittal plane mechanics (Kuo 2001). Furthermore, step-to-step transition and limb swing costs potentially apply not only to bipeds, but also to all animals that walk on relatively stiff limbs.

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