MECHANICS OF BIPEDAL LOCOMOTION

R. McN. ALEXANDER

Department of Pure and Applied Zoology, University of Leeds, U.K.

INTRODUCTION

Most terrestrial animals walk or run on six or four legs. Bipedal locomotion is relatively uncommon, but its simplicity makes it relatively easy to analyse. This paper is concerned with the range of possible techniques of bipedal locomotion, and the energy cost of each. Though the approach is theoretical it is based on experimental studies of man (Cavagna, 1969), kangaroos (Dawson and Taylor, 1973; Alexander and Vernon, 1975) and running birds (Taylor et al., 1971; Fedak et al., 1973; Cracraft, 1971; Clark and Alexander, 1975). The energy cost of locomotion will be expressed as the net cost of transport (Taylor et al., 1970) which is the energy required to transport unit mass of animal a unit distance over level ground.

Consider a biped of mass \(m\) with legs of length \(l\) (when extended) (Fig. 1). It travels with velocity \(u\) over level ground, with its centre of mass at a height \(h\) above the ground. It will sometimes be convenient to write \(u = k(gh)^\frac{1}{2}\) (where \(g\) is the acceleration due to gravity) and to refer to \((gh)^\frac{1}{2}\) as the characteristic velocity. The step length is \(2b\): the

Fig. 1. The idealized biped which is discussed in the text.

centre of mass moves forward a distance \(2b\) between the instant when a foot is placed on the ground and the instant when it is raised. The centre of mass moves forward a distance \(2p\) between successive instants when a foot is placed on the ground. Note that this is the distance covered by half a cycle of leg movements in the case of man and other bipeds which move their legs alternately, but by a whole cycle in the case of kangaroos and other bipeds which move their feet in unison. It will be assumed initially that the mass of the legs and the drag exerted on the body by the air are both negligible: their effects will be considered later.

A series of idealized techniques of locomotion will be discussed and the cost of transport calculated for each. Apart from work done against drag, the net work done in each stride is zero: all positive work (work done by the muscles) is matched by negative work
(work done on the muscles) which may be done at a different stage in the stride. Costs of transport will therefore be expressed in terms of an efficiency $\eta$ such that $(1/\eta)$ units of metabolic energy are required to provide one unit of positive work plus one unit of negative work. Experiments on man indicate $\eta \approx 0.2$ (Margaria, 1968).

TECHNIQUE OF LOCOMOTION

(a) The stiff-legged walk

Suppose first that our biped walks as shown in Fig. 2a, lifting one foot as the other is set down (so that $p = b$) and keeping each leg straight while its foot is on the ground. The centre of mass moves forward in a series of circular arcs of radius $l$, each arc subtending an angle $2\phi = 2\arcsin(b/l)$. When $x = 0$ the centre of mass is at its highest point, travelling horizontally at its minimum velocity $u_0$. It accelerates as it descends and as it reaches $x = b$ its velocity has horizontal and vertical components $u_b, -v_b$, respectively. The kinetic energy gained in the descent equals the potential energy lost.

\[
\frac{1}{2}mu_b^2 + \frac{1}{2}mv_b^2 = \frac{1}{2}mu_0^2 + mgl(1 - \cos \phi)
\]

for reasonably small values of $\phi$ for which $(1 - \cos \phi) \approx \frac{1}{2} \sin^2 \phi = b^2/2l^2$. The part $\frac{1}{2}mu_0^2$ of the kinetic energy is carried over to the next step but the part $\frac{1}{2}mv_b^2$ is absorbed by the muscles as the descent is halted, and has to be replaced by work done by the muscles which give the centre of mass the vertical component of velocity $+v_b$ needed to start the next step. We need an equation giving the mechanical energy, $\frac{1}{2}mv_b^2 = E$, which is absorbed and provided afresh at every step.

Since $u_b = v_b \cot \phi$, eqn. (1) gives

\[
\frac{1}{2}mv_b^2 (1 + \cot^2 \phi) \approx \frac{1}{2}mu_0^2 + (mb^2/2l) \\
E = \frac{1}{2}mv_b^2 \approx \frac{1}{2}m \sin^2 \phi [u_0^2 + (gb^2/l)]
\]

\[
\approx \frac{mb^2}{2l^2} \left( u_0^2 + \frac{gb^2}{l} \right).
\]
\( u_0 \) cannot be less than zero, so there is a minimum possible value for \( E \). There is also a maximum value since \( E \) cannot exceed the potential energy change, approximately \( mgb^2/2l \). Thus

\[
\frac{mgb^4}{2l^3} \leq E \leq \frac{mgb^2}{2l}.
\]

Since mechanical energy \( E \) is absorbed and re-supplied every time the animal of mass \( m \) travels a distance \( 2b \) the cost of transport \( T_\ast \) is \( E/2mb\eta \) and

\[
\frac{gb^3}{4l^3\eta} \leq T_\ast \leq \frac{gb}{4l\eta}.
\]  (2)

If \( b \approx 0.5l \) (as it is for man) the minimum cost of transport is about one quarter of the maximum cost. The minimum cost occurs at zero walking speed and the maximum at the maximum speed, which will now be calculated. Since \( E \) cannot exceed the potential energy change

\[
v_b^2 \leq gb^2/l
\]

\[
u_b^2 = v_0^2 \cot^2 \phi
\]

\[
\leq gb^2 \cot^2 \phi/l
\]

and for reasonably small value of \( \phi \) for which \( \cot \phi \approx \cosec \phi = l/b \)

\[
u_b^2 \leq gl.
\]

At the maximum speed \( u_b = u_0 = u \) so

\[
u \leq (gl)^{3/4}.
\]  (3)

For a biped which, like man, has its centre of mass at about the level of the hips the maximum speed is approximately equal to the characteristic speed \((gh)^{3/4}\). Stiff-legged walking at higher speeds would involve downward accelerations greater than \( g \).

Slow human walking is reasonably similar to the idealized stiff-legged walk. Since \( l \approx 0.94 \text{ m} \) for men of height 1.80 m (Dyson, 1973) men should be able to walk in this way at speeds up to about 3 m s\(^{-1}\) (6 m.p.h.). However, normal walking techniques at speeds above about 2.2 m s\(^{-1}\) are more like the level non-pitching walk described below: the centre of mass rises and falls less than if it moved in circular arcs, and the fluctuations of kinetic energy are larger than the fluctuations of potential energy (Cavagna, 1969). First-class athletes walk 20 km in less than 1\( \frac{1}{4} \) hr i.e. at over 3.7 m s\(^{-1}\). They keep each leg straight while its foot is on the ground but use a peculiar hip action which reduces the vertical excursion of the centre of mass and so makes high speeds possible (Dyson, 1973).

(b) The level pitching walk

It is possible to walk without fluctuations of potential energy, by exerting a constant vertical force \( mg \) on the ground. Consider a biped which walks so that there is always one foot, and never more than one foot, on the ground. A vertical force \( mg \) acts through the foot on the ground (Fig. 2b). Since this force is not in line with the centre of mass (except at one instant in each step) it makes the animal pitch as it walks.
Consider the instant at time \( t \) when the centre of mass is a horizontal distance \( x \) in front of the foot. Let \( t = 0 \) when \( x = 0 \) so that \( x = ut \). Let the angle of pitch at time \( t \) (relative to the angle when \( t = 0 \)) be \( \theta \) and let the moment of inertia of the body about a transverse axis through its centre of mass be \( I \). The ground reaction \( mg \) exerts a moment \( mgx = mgut \) about the centre of mass so

\[
d^2\theta/dt^2 = mgut/I.
\]

\[
d\theta/dt = (mgut^2/2I) + \omega,
\]

where \( \omega \) is a constant of integration. Integrating again

\[
\theta = (mgut^3/6I) + \omega t.
\]

In steady running \( \theta \) must have the same value at time \( b/u \) as at time \( -b/u \). Hence, from (5)

\[
\omega = -mgb^2/6ul
\]

\[
d\theta/dt = (mg/6ul)(3u^2t^2-b^2)
\]

\[
\theta = (mg/6ul)(u^2t^2-b^2).
\]

\( \theta \) has its maximum and minimum values when \( d\theta/dt = 0 \), which occurs when \( t = \pm 3^{-1/4}b/u \). These values are given by (5a) and the difference between them is

\[
\theta_{\text{max}} - \theta_{\text{min}} = mgb^3/7.8u^2I.
\]

This is the range of angles through which pitching occurs. It will be convenient to write \( u = k(gh)^{1/4} \) and \( I = jr^2m \) when \( r \) is the radius of a sphere of the same volume as the body. Thus we obtain

\[
\theta_{\text{max}} - \theta_{\text{min}} = b^3/7.8jk^2r^2h.
\]

We will insert typical values in this equation to determine whether a real animal would be likely to pitch through large angles. For a sphere \( j = 0.4 \) and for a prolate spheroid of length eight diameters \( j = 3.3 \); we will take \( j = 1 \), corresponding to a spheroid of length three diameters. For a 70 kg man \( r = 0.26 \) m, \( h = 0.9 \) m and \( b = 0.45 \) m, so \( b/h = 0.5 \) and \( b/r = 1.7 \). These ratios are probably reasonably typical of bipeds in general though they have been obtained from data on man. Using them and \( j = 1 \), we obtain \( (\theta_{\text{max}} - \theta_{\text{min}}) = 0.2/k^2 \). A biped travelling at its characteristic speed \( (k = 1) \) could be expected to pitch through 0.2 rad or 11°. At lower speeds it would pitch more. This pitching might make it difficult for it to interpret sensory information from the eyes and ears.

Now consider the energy which would be used. The angular velocity of the body has minimum and maximum values when \( t = 0 \) and when \( t = b/u \). Equation (4a) shows that when \( t = 0, d\theta/dt = -mgb^2/6ul \) and the kinetic energy of rotation of the body is \( m^2g^2b^4/72u^2I \). Similarly when \( t = b/u \) the body is rotating in the opposite direction with kinetic energy of rotation \( m^2g^2b^4/18u^2I \). Hence in each step the body must be given kinetic energy of rotation totalling \( 5m^2g^2b^4/72u^2I \) and the cost of transport is

\[
T_b = 5mg^2b^3/144u^2I\eta
\]

\[
= 0.27g (\theta_{\text{max}} - \theta_{\text{min}})/\eta
\]

(7)
(using eqn. (6)). For a biped with the typical proportions which give \((\theta_{\text{max}} - \theta_{\text{min}}) = 0.2/k^2\), this gives

\[ T_b \approx 0.05g/k^2 \eta. \]  

This value could be much too low because we have ignored the possibility of positive and negative work having to be done simultaneously. This possibility arises because this technique of locomotion, unlike the others discussed in this paper, necessarily involves simultaneous movement of at least two joints about which the ground reaction exerts moments.

Consider the simple leg shown in Fig. 3a which consists of two segments (a thigh and a shank) of equal length \(d\). The vertical ground reaction \(mg\) exerts a moment \(mgx\) about the hip. When the hip moves forward \(\delta x\) the hip muscles must do work

\[ \delta W = -mgx(\delta \alpha + \delta \beta). \]

Note that

\[ \alpha = \arctan \left( \frac{x}{h} \right) \]

and

\[ \beta = \arccos \left( \frac{(x^2 + h^2)^{1/2}}{2d} \right), \]

so that

\[ \frac{d\alpha}{dx} = \frac{h}{(x^2 + h^2)^{1/2}} \]

and

\[ \frac{d\beta}{dx} = -\frac{x}{(x^2 + h^2)^{1/2} \left( 4d^2 - x^2 - h^2 \right)^{1/2}}. \]

Hence

\[ \delta W = -mgx \left( \frac{h}{x^2 + h^2} - \frac{x}{(x^2 + h^2)^{1/2} \left( 4d^2 - x^2 - h^2 \right)^{1/2}} \right) \delta x. \]  

We will consider first the special case when the limb segments are so long that the term involving \(d\) can be ignored. In this case

\[ \delta W \approx -mhx \frac{\delta x}{(h^2 + x^2)}, \]

and is positive for \(x < 0\). As \(x\) increases from \(-b\) to 0 the hip muscles do positive work

\[ W \approx -mh \int_{-b}^{0} \frac{xdx}{(h^2 + x^2)} \]

\[ \approx \frac{1}{8} mgh \log \left[ 1 + \left( \frac{b}{h} \right)^2 \right]. \]
If \( b/h \approx 0.5 \) (as assumed in the discussion of pitching) \( W \approx 0.22 \text{ mgb} \). While the hip muscles are doing this positive work the knee muscles do negative work, \( -0.22 \text{ mgb} \). As \( x \) increases from 0 to \( b \) the hip muscles do \( -0.22 \text{ mgb} \) and the knee muscles \( +0.22 \text{ mgb} \). In a complete step the muscles do a total quantity \( 0.44 \text{ mgb} \) positive work and a compensating quantity of negative work.

Now consider the case when \( d \) is not very large. \( \beta \) increases as \( x \) increases from \( -b \) to 0, reducing the positive work done by the hip muscles. It decreases again as \( x \) increases from 0 to \( b \), increasing the negative work done at this stage of the step. Thus as \( d \) is reduced the hip muscles come to do mainly negative work (and the knee muscles mainly positive work). Since \( (d\beta/dx)_- = -(d\beta/dx)_+ \), the total amounts of positive and negative work remain unchanged until \( d \) becomes so small that there is a stage in the step when \( (da/dx) + (d\beta/dx) = 0 \). This occurs when \( d = (b^2 + h^2)/2h \) (= 0.63h when \( b = 0.5h \)). If \( d \) is less than this, the hip muscles do negative work followed by positive work followed by negative work again (and the knee muscles do the converse) and the total quantities of positive and negative work are increased. The minimum possible value of \( d \) is \( \frac{1}{2}(b^2 + h^2) \) (= 0.56h when \( b = 0.5h \)): when \( d \) has this value the leg has to be straight when the foot is set down. Thus totals of \( +2W \) positive work and \( -2W \) negative work have to be done in each step, where \( W \) has the value given in eqn. (9), for all but the smallest values of \( d \).

We have seen that when \( b = 0.5h \), \( 2W = 0.44 \text{ mgb} \). The need to do \( 0.44 \text{ mgb} \) positive and negative work in each step adds \( 0.22g/\eta \) to the cost of transport so that (7a) can be re-written

\[
T'_b = (g/\eta) [0.22 + (0.05/k^2)].
\] (7b)

The difference between (7a) and (7b) is large, except at very low speeds \( (k \) very small). The additional cost shown in (7b) is not inevitable: it could be avoided by means of two-joint muscles appropriately arranged. Fig. 3b, c show the muscles which would be required if \( d \) was reasonably large (low values of \( d \) would make additional muscles necessary). While the foot was in front of the hip tension would be required in the muscle shown in Fig. 3b, to make the hip extend as the knee flexed. Once the foot was behind the hip tension would be required in the muscle shown in Fig. 3c, to extend the knee again as the hip continued to extend. If the muscles were arranged so that their lengths remained constant throughout the periods when they were taut, they would do no work.

I do not know of any biped which uses the level, pitching walk, as described in this section. It has been discussed because it is an obvious possibility, so that its merits and deficiencies can be compared with those of the techniques which are used.

(c) The level walk without pitch

Fig. 2c represents a technique of walking which involves neither fluctuations of potential energy nor pitching. There is always one foot, and never more than one, on the ground. The vertical component of the force on the ground is constant and equal to \( mg \). There is also a horizontal component which varies in the course of a step so as to keep the ground force in line with the centre of mass. When the centre of mass is a distance \( x \) in front of the foot this component must be \( mgx/h \). It decelerates the body while \( x \) is
negative and accelerates it again while $x$ is positive. The kinetic energy of the body falls and then rises again by an amount

$$E = \int_0^b (mgx/h) \, dx$$

$$= mgb^2/2h,$$  \hspace{1cm} (10)

and since a distance $2b$ is travelled in each step the cost of transport is

$$T_c = gb/4h\eta.$$  \hspace{1cm} (11)

It seems to be a general rule that the forces exerted on the ground by bipeds are more or less in line with the centre of mass. However, there is generally either a double support phase as in quail running (Clark and Alexander, 1975) or a floating phase with both feet off the ground as in kangaroo hopping (Alexander and Vernon, 1975) and human running. Gaits involving a floating phase will be discussed next.

(d) Simplified running

Fig. 2d represents a gait involving a contact phase during which the centre of mass travels $2b$ and a floating phase during which it travels $2a = 2(p-b)$. The vertical component of the ground force is constant throughout the contact phase and must be $mgp/b$. There is also a horizontal component which varies in such a way as to keep the ground force in line with the centre of mass.

If the fluctuations of velocity which occur in each step are reasonably small (and it will be shown that they are likely to be small) the durations of the floating phase and the contact phase must be approximately $2a/\bar{u}$ and $2b/\bar{u}$, respectively, where $\bar{u}$ is the mean velocity. During the floating phase the centre of mass must rise for a period $a/\bar{u}$ and fall for a period $a/\bar{u}$ so it must rise from its initial height $h_b$ to a maximum height $h_b + (iga^2/\bar{u}^2)$. The difference between the maximum and minimum heights is $iga(a+b)/\bar{u}^2 = \kappa a \eta/\bar{u}^2$, if $\bar{u} = k(h_b)^4$. The potential energy gained and lost in each step is

$$E_p = mgap/2k^2h_b.$$  \hspace{1cm} (12)

During the contact phase the height of the centre of mass varies between $h_b$ and $h_b - (3ab/k^2h_b)$. If $(b/h_b) = 0.5$ the variation will be between $h_b$ and $h_b - (a/4k^2)$. If long leaps were taken at low speeds, $a/4k^2$ might be quite a large fraction of $h_b$. In practice floating phases are unlikely to occur when $k < 1$, for reasons which will be explained, and generally only become long at very high speeds when $k$ is large. Hence $a/4k^2$ is likely to be only a small fraction of $h_b$ and we will not introduce much error by assuming that the horizontal component required to set the ground force in line with the centre of mass is a fraction $x/h_b$ of the vertical component, or $mgpx/bh_b$. The kinetic energy lost and regained in each contact phase will be

$$E_k = \int_0^b (mgpx/bh_b) \, dx$$

$$= mgbp/2h_b.$$  \hspace{1cm} (13)
The total (potential + kinetic) energy lost and regained in each stride is

\[ E_p + E_k = \frac{mgp}{2h_b} \left( \frac{a}{k^2} + b \right). \]  

(14)

and the cost of transport is

\[ T_d = \frac{g}{4h_b\eta} \left( \frac{a}{k^2} + b \right) \]

\[ = \frac{g}{4h_b\eta} \left[ \frac{(p - b)}{k^2} + b \right]. \]  

(15)

This reduces to equation (11) when \( p = b \).

In running, \( b \) can vary from 0 to \( p \). Eqn. (15) shows that for given \( p \) the cost of transport is least for \( b = p \) if \( k < 1 \) and for \( b = 0 \) if \( k > 1 \). For given stride length a floating phase suddenly becomes advantageous at the characteristic velocity. Above the characteristic velocity the shorter the contact phase the lower the cost of transport, but if \( b/p \) becomes very small the ground force becomes very large.

The horizontal component of the velocity fluctuates between a minimum \( u_Q \) (which occurs when \( x = 0 \)) and a maximum \( u_b \) (which is maintained throughout the floating phase). From (13)

\[ \frac{1}{2}m (u_b^2 - u_0^2) = mghp/2h_b. \]

Writing \( u_b^2 - u_0^2 \approx 2\ddot{u} (u_b - u_0) \) and \( \ddot{u} = k (gh_b)^2 \) we obtain

\[ (u_b - u_0)\ddot{u} \approx bp/2h_b^2k^2. \]  

(16)

If \( b/h_b = 0.5 \) this fractional fluctuation of velocity will be about \( p/4h_bk^2 \), which will be fairly small except in the unlikely event of long strides being taken at low speeds.

(e) A more realistic model of running

Both human running and kangaroo hopping broadly resemble the gait just described. Both involve floating phases, and in both the ground force exerted during the contact phase remains more or less in line with the centre of mass (unpublished observations and Alexander and Vernon, 1975). However, the vertical component of the ground force rises to a maximum and declines again, in the course of the contact phase. This feature was incorporated in a model designed to represent kangaroo hopping, which can also be used as a model of human running (Alexander and Vernon, 1975). The vertical component of the ground force was made proportional to \( \cos(\pi x/2b) \). Equations for \( E_p \) and \( E_k \) were obtained, from which it is easy to show that the cost of transport is

\[ T_e = \frac{g}{4h_b\eta} \left[ \frac{(p - 0.73b)}{k^2} + 0.73b \right]. \]  

(17)

Compare this with eqn. (15)
Kinetic energy of limbs

The kinetic energy of a system of particles can be expressed as the sum of the external kinetic energy (due to movement of the centre of mass of the system) and the internal kinetic energy (due to movement of parts of the system relative to the centre of mass) (Cavagna, 1969; Clark and Alexander, 1975). By ignoring the mass of the limbs we have so far ignored the internal kinetic energy associated with relative movement between them and the trunk. While its foot is on the ground the limb attains an angular velocity of about $u/h$ about the hip (since the hip is generally about level with the centre of mass) and if the moment of inertia of the limb about the hip is $J$ the associated internal kinetic energy is approximately $\frac{1}{2}J(u/h)^2 = \frac{Jgk^2}{2h}$. The internal kinetic energy associated with the forward movement of the limb in the recovery stroke may be greater or less than this, depending on the gait. However, fast gaits generally allow considerably more time for the recovery stroke than for the power stroke of each limb, so that the internal kinetic energy associated with the recovery stroke can be relatively small. It will be shown that internal kinetic energy is likely to be quite small, relative to the fluctuations of external kinetic and potential energy, except at high speeds. The recovery stroke will therefore be ignored. The internal kinetic energy $\frac{Jgk^2}{2h}$ required at each step adds $\frac{Jgk^2}{4phm}$ to the cost of transport.

In geometrically similar animals, $J$ would be proportional to $mh^2$. It will be convenient to write $J = Qmh^2$. I have calculated $J$ for the legs of men, kangaroos and quail, in the position which occurs in running or hopping as the hip passes over the point of contact of the foot with the ground (for the masses of human limb segments and the positions of their centres of mass, see Dyson, 1973). The calculations gave $Q = 0.035$ for man and the kangaroo and $Q = 0.02$ for quail. The value given for the kangaroo is for two legs, since the legs are used simultaneously in hopping. It seems reasonable to conclude that $Q \approx 0.03$ for typical bipeds, so that the part of the cost of transport attributable to internal kinetic energy is about $0.008 ghk^2/p\eta$.

Drag

The drag exerted on the body by the air is $\frac{1}{2} \rho Au^2 C_D$ where $\rho$ is the density of the air, $A$ the frontal area of the body and $C_D$ the drag coefficient. It adds $\rho Au^2 C_D/2m\chi = \rho Ah^2 ghC_D/2m\chi$ to the cost of transport. The factor $\chi$ is not the same as the efficiency $\eta$ used in previous sections of the paper, for reasons which will be explained.

The density of air at sea level is 1.3 kg m$^{-3}$. The drag coefficient will be about 1.0, as for cylinders in the appropriate range of Reynolds numbers. $Ah/m$ is 0.007 m$^3$ kg$^{-1}$ for man (see Pugh, 1971, for values of $A$) and would be the same for geometrically similar bipeds of the same density. Using these values it can be estimated that drag adds 0.005 $ghk^2/\chi$ to the cost of transport.

It remains to evaluate $\chi$. If work $W_D$ has to be done against drag in a complete step the negative work done by the muscles will probably be reduced by $\frac{1}{2} W_D$ and the positive work increased by $\frac{1}{2} W_D$. If the efficiency of negative work is $-1.2$ (Margaria, 1968) the metabolic energy used doing negative work will be reduced by 0.4 $W_D$. If the efficiency of positive work is 0.25 (Margaria, 1968) the metabolic energy used doing positive work...
will be increased by $2W_D$. Thus the need to do mechanical work $W_D$ against drag increases the metabolic energy requirement by $(2-0.4) W_D = 1.6 W_D$ and the factor $\chi$ is $1/1.6 = 0.63$. Pugh (1971) measured the oxygen consumption of men walking and running on a treadmill in a wind tunnel and obtained values of $\chi$ between 0.42 and 0.82.

**DISCUSSION**

The cost of transport for the level walk without pitch is $gb/4h\eta$ (eqn. (11)). The cost for the stiff-legged walk is $gb/4l\eta$ or about the same (if $l \approx h$) at its maximum speed ($k = 1$), but is less at lower speeds (eqn. (2), $b/l < 1$). It is at low speeds that the human walk most nearly resembles the idealized stiff-legged walk. For typical bipeds $b/h \approx 0.5$ and the cost of level walk without pitch is $0.13g/\eta$, but the cost of the level pitching walk exceeds $0.22 g/\eta$ (eqn. (7b)) unless appropriately arranged two-joint muscles are used. If the fullest use were made of two-joint muscles the cost would be $0.05 g/k^2\eta$ (eqn. (7a)) but even this would exceed the cost for the level walk without pitch when $k < 0.6$. As well as being expensive of energy, the pitching walk would involve large angles of pitch at low speeds.

The cost of transport is less for running than for the level non-pitching walk with the same value of $p$ if $k > 1$, but more if $k < 1$ (discussion following eqn. (15)). The characteristic speed, $(gh)^4$, is about $3 \text{ m s}^{-1}$ for man and $2.2 \text{ m sec}^{-1}$ for an $18 \text{ kg kangaroo}$. Men change from walking to running at about $2.5 \text{ m sec}^{-1}$ and an $18 \text{ kg kangaroo}$ changed from pentapedal locomotion to hopping at about $1.8 \text{ m sec}^{-1}$ (Dawson and Taylor, 1973). In sustained running men make $p \approx bk$ at speeds up to $k = 2$, and less than $bk$ at high speeds (Cavagna *et al.*, 1965). Kangaroos keep $p \approx bk$ up to the maximum speed for which data is available ($k \approx 3$, Dawson and Taylor, 1973). If $b \leq p \leq bk$ the cost of transport for simplified running, given by eqn. (15), lies between $0.25gb/h\eta^2$ and $0.31gb/h\eta$ for all values of $k$ greater than 1. The more realistic model of running (eqn. (17)) gives $0.18gb/h\eta$ to $0.23gb/h\eta$, for the same ranges of values of $p$ and $k$.

We can conclude that the cost of transport due to fluctuations of potential and external kinetic energy is about $gb/4h\eta$ for the level walk without pitch, for running and for bipedal hopping. If $b/h \approx 0.5$ and $\eta = 0.2$, this is $0.65g$. To this must be added the costs of providing internal kinetic energy and overcoming drag. The cost for internal kinetic energy has been estimated as $0.008gk^2/p\eta$, or $0.04gk^2/p$ if $\eta = 0.2$. When $k < 1$ we are likely to find $p = b = 0.5h$ and the cost for internal kinetic energy will be $0.08gk^2$ which is small compared to the cost of external kinetic and potential energy. When $k > 1$ we are likely to find $p = bk = 0.5hk$, so that the cost of internal kinetic energy will be $0.08gk$ or $k/8$ of the cost for external kinetic and potential energy. This will be a substantial fraction of the total cost of transport, at high values of $k$. The cost of overcoming drag has been estimated as $0.005gk^2/\chi$, or $0.008gk^2$ if $\chi = 0.63$. This will not be a very large fraction of the total cost except for very high values of $k$.

Suppose for example that $k = 3$. This is fast, but within the capabilities of both men and kangaroos. Then the cost for internal kinetic energy will be $0.24g$ (or more, if $p < bk$) and the cost of overcoming drag will be $0.07g$. If the cost for external kinetic and potential energy is $0.65g$ the total cost will be a little under $1.0g$. 


It appears from the arguments presented so far that we can expect the total cost of locomotion for the level walk without pitch, running and bipedal hopping to be about 0.65g at low speeds, rising to the region of 1.0g at very high speeds irrespective of the size of the animal. Since metabolism using 1 cm$^3$ oxygen yields about 20 J, the cost of transport in terms of oxygen consumption should lie in the range 0.3 to 0.5 cm$^3$ oxygen kg$^{-1}$m$^{-1}$. The cost of slow stiff-legged walking should be less than this.

The oxygen consumptions of various bipeds have been measured while they ran or hopped on treadmills. Costs of transport obtained in this way are shown in Table 1. The

<table>
<thead>
<tr>
<th>TABLE 1. COST OF TRANSPORT FOR BIPEDAL LOCOMOTION (cm$^3$ oxygen kg$^{-1}$ m$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>man (Cavagna, 1969) slow walk</td>
</tr>
<tr>
<td>fast walk and run</td>
</tr>
<tr>
<td>chimpanzee (Taylor and Rowntree, 1973)</td>
</tr>
<tr>
<td>monkey (Taylor and Rowntree, 1973)</td>
</tr>
<tr>
<td>kangaroo (Dawson and Taylor, 1973)</td>
</tr>
<tr>
<td>slow hop</td>
</tr>
<tr>
<td>fast hop</td>
</tr>
<tr>
<td>rhea (Taylor et al., 1971)</td>
</tr>
<tr>
<td>40g birds (Fedak et al., 1973)</td>
</tr>
</tbody>
</table>

The cost for small birds is well above the calculated range, and there seems to be no obvious explanation for its being so high (Clark and Alexander, 1975). Those for the monkey, the rhea and for the kangaroo at low speeds lie within the range. The rest are below the calculated range. The value of 0.10 cm$^3$ kg$^{-1}$m$^{-1}$ for slow human walking (1 m sec$^{-1}$, \( k = 0.3 \)) is not unexpected, as this gait approximates to stiff-legged walking. The other low values require a different explanation.

The explanation seems to be that energy is saved by elastic storage (Cavagna, 1969; Alexander and Vernon, 1975). It has been assumed so far that potential and kinetic energy lost at one stage in a step is absorbed by the muscles and degraded to heat, so that the subsequent increases of potential and kinetic energy are entirely dependent on active contraction of muscles. If some of the energy is allowed instead to stretch an elastic structure, it can be recovered in an elastic recoil without metabolic cost. The pogo-stick works on this principle. Tendons, particularly the Achilles tendon, are probably the principal elastic structures involved (Alexander, 1974). The mathematical theory presented here is extended in another paper, to take account of elastic storage of energy (Alexander and Vernon, 1975).

**SUMMARY**

A mathematical discussion is presented of various possible techniques of bipedal locomotion. The energy cost of each technique is assessed, and compared with costs determined (by other investigators) by measurements of oxygen consumption. A characteristic speed \((gh)^{\dagger}\) is defined, where \( g \) is the acceleration due to gravity and \( h \) the height of the centre of mass from the ground. At speeds below the characteristic speed, a stiff-legged walk (like the human slow walk) is most economical of energy. At speeds above the
characteristic speed it becomes advantageous to introduce a floating phase into the gait. It is generally advantageous to keep the force exerted on the ground more or less in line with the centre of mass so that the body is decelerated and then accelerated in each step. Drag, and energy required to accelerate the limbs, only become important at speeds well above the characteristic speed. Running men and hopping kangaroos save substantial amounts of energy by elastic storage in tendons.

REFERENCES


