ENERGY-SAVING MECHANISMS IN WALKING AND RUNNING

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Summary

Energy can be saved in terrestrial locomotion in many different ways. The maximum shortening speeds (v_{max}) of the muscles can be adjusted to their optimum values for the tasks required of them. The moments exerted by the muscles at different joints can be adjusted to keep the ground force in line with the leg so that muscles do not work against each other. The joints of the legs can be kept as straight as possible, minimizing muscle forces and work requirements. Walking gaits should be selected at low Froude numbers (a dimensionless speed parameter) and running gaits at high Froude numbers. Tendon and other springs can be used to store elastic strain energy and to return it by elastic recoil. This paper aims to show how these energy-saving mechanisms work and to what extent mammals exploit them. Arguments based on our rather limited knowledge of the relationship between the mechanical performance of muscle and its metabolic energy consumption are used throughout. They suggest that muscles that are optimally adapted for their tasks in running should do positive work with constant efficiency.

Energy consumption by muscles

Before we consider how energy can be saved in walking and running, we should consider how it is used. Plainly, metabolic energy must be consumed whenever muscles do work: the Principle of Conservation of Energy requires it. However, muscles may be active without performing work: they do work if they shorten while exerting tension, but if they contract isometrically (exerting tension without changing length) they do no work, and if they lengthen while exerting tension they do 'negative work', degrading mechanical energy to heat. They use metabolic energy faster when active than when resting, whether or not they are doing work; this has been demonstrated by measuring heat production, oxygen consumption and rates of ATP splitting in isolated muscles (summarized by Woledge *et al.* 1985). The reason is that the crossbridges of active muscle continually detach and re-attach, splitting ATP in each cycle.

It seems reasonable to expect the rate of metabolic energy consumption in isometric contraction, P_{iso}, to be proportional to the force F_{iso} (hence to the cross-

sectional area of active fibres) and to the resting length l of the fibres (hence to the number of sarcomeres in series). For this reason, the 'economy' of a muscle has been defined as $F_{iso}l/P_{iso}$. This has been found to be lower for fast muscles than for slow ones, presumably because their crossbridges cycle faster (Heglund and Cavagna, 1987), and it seems likely to be inversely proportional to the maximum shortening speed v_{max} (expressed in muscle lengths per unit time). We will therefore assume that the metabolic rate of muscles in isometric contraction is given by:

$$P_{iso} = KF_{iso}lv_{max}, \tag{1}$$

where the constant K has the same value for all vertebrate muscles. Heglund and Cavagna (1987) extended the concept of economy, applying it to contractions during which length changes occur as well as to isometric activity. When muscles shorten, doing work, they exert less force than when they contract isometrically but have at least as high a metabolic rate; thus, their economy is lower (Woledge et al. 1985; Heglund and Cavagna, 1987). When they are stretched and do negative work, the force rises and the rate of ATP splitting falls, so economy increases (Woledge et al. 1985). Unfortunately, the relationship between metabolic rate P and shortening speed v (muscle lengths per unit time) is not well established, because empirical data show a great deal of scatter. To illustrate the possible consequences of the relationship, I will assume that economy falls linearly with increasing v, reaching zero when $v=v_{max}$. This implies that:

$$P/F = (P_{iso}/F_{iso})v_{max}/(v_{max}-v) \tag{2}$$

(see Fig. 1A). With equation 1 this gives:

$$P/F = Klv_{max}^2/(v_{max}-v). \tag{3}$$

The rate of shortening of the muscle is lv, so its mechanical power output is Flv and its efficiency is Flv/P. Using equation 3 this gives us:

$$\text{Efficiency} = v(v_{max}-v)/Kv_{max}^2, \tag{4}$$

which has a maximum value of $0.25/K$ when $v=v_{max}/2$. Measured efficiencies show maxima at rather lower shortening speeds ($v\approx0.3v_{max}$, Woledge et al. 1985), and equation 3 could have been modified to match this, but it seems inappropriate to make the model more complex until better physiological data are available.

Optimum muscle properties

   In swimming and flight, muscles perform predominantly positive work, and the energy required for locomotion will be least if the maximum shortening speeds of the muscles are adapted so that most of the work is done when v/v_{max} is close to the value that maximizes efficiency (see for example Rome et al. 1988). This is not necessarily true for terrestrial locomotion, in which very little net work is done
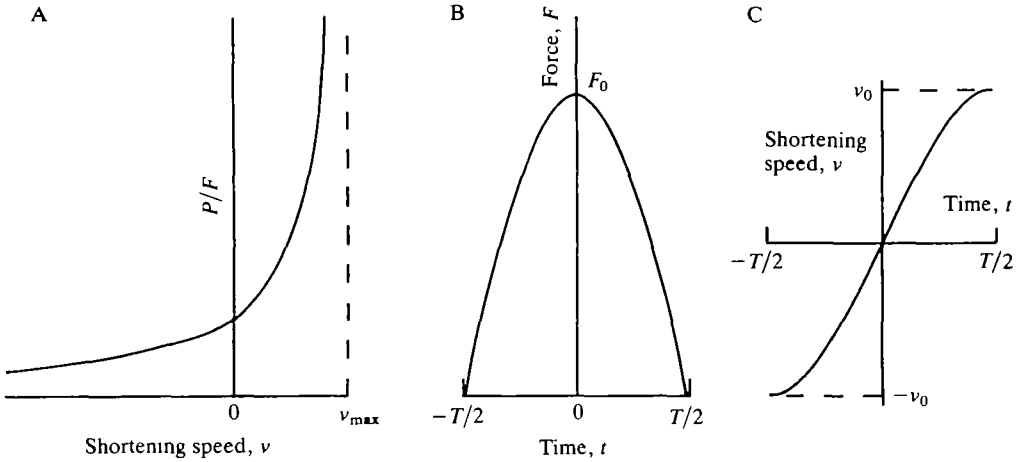
Fig. 1. (A) The metabolic rate required to generate force in a muscle shortening at different speeds. This graph shows the relationship between P/F and v suggested by equation 2. (B) The time course of changes in the force F exerted by the muscle described by equation 5. (C) The time course of the rate of shortening v of the muscle described by equation 6.

We will seek an optimum value of v_{max} for a leg muscle whose metabolic rate is given by equation 3.

Let this muscle be active throughout the period of contact of the foot with the ground, from time $-T/2$ to time $+T/2$. During that time, let the force F that it exerts rise and fall according to the equation:

$$F = F_0\cos(\pi t/T),\qquad(5)$$

where F_0 is the force at time zero and t is time (Fig. 1B). At the same time, let the muscle lengthen and then shorten as if it were a Hookean spring, so that the difference between its current length and its initial length is proportional to the current force. That implies that its rate of shortening follows the equation:

$$v = v_0\sin(\pi t/T)\qquad(6)$$

(Fig. 1C). Thus, the muscle starts lengthening at a rate v_0 when the foot hits the ground, reaches maximum length at the mid point of the period of contact when the force is F_0, and is shortening at a rate v_0 when the foot leaves the ground. These assumptions are reasonably realistic for muscles such as the gastrocnemius and plantaris of kangaroos which do approximately equal quantities of positive and negative work in each stride, but not for other muscles which do predominantly positive or negative work (Alexander and Vernon, 1975).

The metabolic rate of this muscle at time t, during the period of contact of the foot with the ground, would be:

$$P = F_0\cos(\pi t/T)Klv_{max}{}^2/[v_{max}-v_0\sin(\pi t/T)]\qquad(7)$$

(from equations 3, 5 and 6). Thus, the metabolic energy E consumed during the period of contact would be:

$$E = F_0 K l v_{max}^2 \int_{-T/2}^{T/2} \frac{\cos(\pi t/T) dt}{v_{max} - v_0 \sin(\pi t/T)}$$

$$= \frac{F_0 K l v_{max}^2 T}{\pi v_0} \ln \left(\frac{v_{max} + v_0}{v_{max} - v_0} \right). \tag{8}$$

It can be shown by calculating this energy for different values of v_{max} that it has a minimum value when $v_{max} = 1.26 v_0$. An animal with such a muscle could minimize the energy cost of locomotion by adjusting the muscle's maximum (i.e. unloaded) rate of contraction to be 1.26 times the maximum rate at which the muscle was required to shorten in the course of each step.

It is important to realize that this conclusion depends on an assumed relationship between metabolic rate, force and shortening speed (equation 3) and applies to a particular pattern of force development and length change (equations 5 and 6). The quantitative conclusion, that v_{max} should be $1.26 v_0$, may not be accurate. The purpose of this section is to show that there must be some optimal value for v_{max} and to point to the need for research that will find the optimum and compare it to measured properties of leg muscles. Moon et al. (1991) simulated the behaviour of fish muscles in swimming by stimulating isolated muscle fibre bundles repeatedly while imposing sinusoidal length changes, and they then measured ATP depletion. Similar experiments on leg muscles may help us to discover the optimal properties for them, although their task is very different from those of fish muscles that do mainly positive work.

When v_{max} has its optimum value of $1.26 v_0$, the metabolic energy consumed during a step is $1.09 K F_0 l v_0 T = 0.87 K F_0 l v_{max} T$. Integration of equation 5 shows that the mean force during the period of contact is $2 F_0/\pi$, so, if the muscle were to exert the same pattern of force while maintaining a constant length, the energy consumed during the period of contact would be $(2/\pi) K F_0 l v_{max} T$. Thus, the predicted energy consumption, for an optimally adapted muscle, is 1.4 times the energy that would be consumed in an isometric contraction involving the same pattern of force. Again, it must be stressed that the quantitative conclusion may be inaccurate. The important point is that if v_{max} is known, we may expect to be able to estimate energy costs of running by calculating the costs of isometric contractions involving the same pattern of force and multiplying by some constant factor.

Kram and Taylor (1990) discussed the energy cost of running in mammals ranging from small rodents to horses. They showed how its size-dependence could be explained by calculations that took account of the energy cost of developing force, ignoring the cost of performing work. It then seemed obvious that this implied that the additional energy cost of performing work was negligible compared to the cost of developing force. It now appears that this need not be

true, because we should expect the metabolic energy consumed by well-adapted muscles to be a constant multiple of the energy that would be used if the same pattern of force were exerted in isometric contractions.

Positive and negative work are almost equal in locomotion over level ground, so very little net work is done, although the metabolic energy consumption may be high. Thus, the efficiency of terrestrial locomotion may be judged to be very low. However, Heglund *et al.* (1982) found it useful to calculate an 'efficiency' by dividing the positive work by the metabolic energy. The muscle discussed above lengthens and then shortens by lv_0T/π, as can be shown by integrating equation 6 between times 0 and $T/2$. It was assumed to lengthen and shorten as if it were a Hookean spring, so the negative and positive work were $\pm\frac{1}{2}$(peak force)×(length change), or $\pm F_0 lv_0T/2\pi$. It was shown that when v_{max} had its optimum value, the metabolic energy consumed in a step was $1.09KF_0 lv_0T$, so the efficiency was $0.15/K$. This efficiency, for performance of positive work in a cycle of extension and shortening, may be compared to the efficiency of isotonic shortening, given by equation 4, which has a maximum value of $0.25/K$. Muscles work with efficiencies up to about 0.25 (Margaria, 1976), so we should perhaps expect to find efficiencies of performance of positive work in terrestrial locomotion of around 0.15. The data of Heglund *et al.* (1982) indicate values ranging from about 0.01 for 10 g runners to about 0.6 for 100 kg ones. The quantitative conclusion, that the efficiency should be 0.15, may well be inaccurate, because it depends on some doubtful assumptions. The conclusion that it should be constant *seems* more firmly based, and I will attempt in later sections to explain why the observed values are so much larger for large animals than for small ones.

Direction of the ground force

A running animal must exert vertical forces on the ground to support its weight. Horizontal components of force are optional and may or may not be exerted, depending on the ratios of the moments exerted by muscles at different joints. Alexander (1976) argued that an animal with simple two-segment legs would do less positive and negative work in each stride if it were to keep the ground force in line with the hip joint (by exerting no moment about the hip) than if it were to keep the force precisely vertical. An animal that keeps ground forces vertical travels with constant kinetic energy, so might be expected to use less energy than one that exerts sloping forces, and so accelerates and decelerates in each stride. However, if the ground force is kept vertical, knee muscles do positive work while hip muscles do negative work, and *vice versa*: energy is wasted by muscles doing work against each other. This could be avoided by using two-joint muscles including an extensor of the knee that was also a flexor of the hip (Alexander, 1976). The femorococcygeus muscle of kangaroos is arranged like this (Alexander and Vernon, 1975), but other mammals have no such muscle. Alternatively, the problem could be avoided by a pantograph mechanism (Waldron *et al.* 1984) but, again, mammals seem not to have adopted this solution.
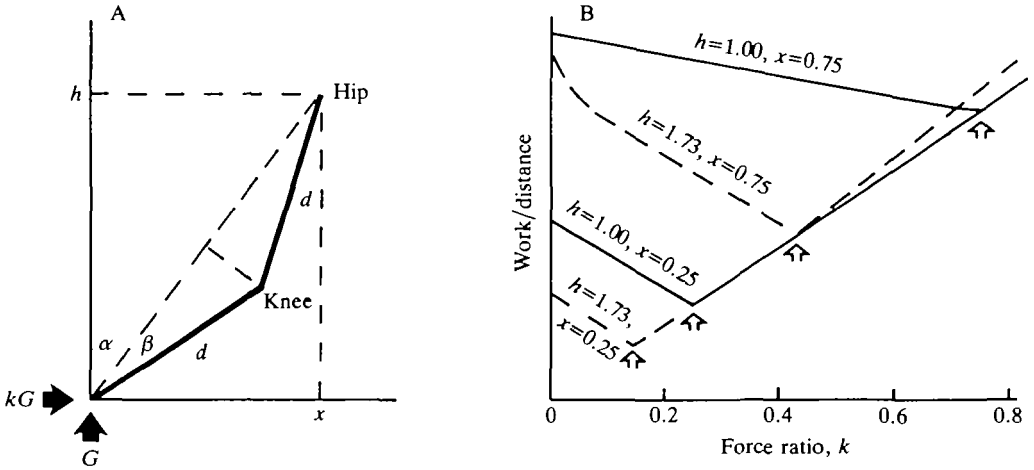
Fig. 2. A two-segment leg and the components of force on its foot. (B) The absolute value of work per unit distance for walking, as shown in A, plotted against the force ratio k, for various values of x and h. Arrows indicate the value of k that equals x/h for each curve. Each curve shows means for positive and numerically equal negative values of x.

We will consider a simple two-segment leg, whose muscles each cross only one joint, and we will seek the optimal direction for the ground force. We already know that it is better to keep the force in line with the hip than to keep it vertical, but is this the optimal direction?

The two segments of the leg each have length d (Fig. 2A). The foot is set down at the origin of Cartesian coordinates and the hip joint travels horizontally along the line $y=h$. (We will ignore the small vertical movements that would occur during a real step.) At the instant when the hip is at (x,h) the force on the foot has components G vertically and kG horizontally. We will calculate the positive and negative work done as the hip advances through an infinitesimal distance.

The angles α and β (Fig. 2) and their derivatives are given by:

$$\alpha = \arctan(x/h), \tag{9}$$

$$d\alpha/dx = h/(x^2 + h^2), \tag{10}$$

$$\beta = \arccos[(x^2 + h^2)^{\frac{1}{2}}/2d], \tag{11}$$

$$d\beta/dx = -x/[(4d^2 - x^2 - h^2)(x^2 + h^2)]^{\frac{1}{2}}. \tag{12}$$

The moments of the force on the foot about the hip and knee are given by:

$$M_{\text{hip}} = G(kh - x), \tag{13}$$

$$M_{\text{knee}} = Gd[k\cos(\alpha+\beta) - \sin(\alpha+\beta)]. \tag{14}$$

The work done by the hip and knee muscles as the hip moves forward through

ßmall distance δx are obtained by multiplying the moments by the increments of joint angle.

$$\delta W_{hip} = M_{hip}(\delta\alpha - \delta\beta), \tag{15}$$

$$\delta W_{knee} = M_{knee}2\delta\beta. \tag{16}$$

Equations 9–16 enable us to calculate dW/dx, both for the hip and for the knee. The algebraic sum of dW_{hip}/dx and dW_{knee}/dx must be kG because the hip is advancing against a force equal to the horizontal component of the force on the foot. However, the sum of the absolute values of these two derivatives will be higher if one is positive and the other negative.

Let
$$(dW/dx)_{abs} = |dW_{hip}/dx| + |dW_{knee}/dx|, \tag{17}$$

where the vertical lines indicate absolute values.

It is assumed that the forces on the feet when x is negative mirror those that act when x is positive: $k(x) = -k(-x)$ and $G(x) = G(-x)$. Thus, no net work is done during a stride. A mean was taken of the values of $(dW/dx)_{abs}$ for a positive value of x and a numerically equal negative value. This quantity represents the rates per unit distance at which the muscles do positive and negative work.

Fig. 2B shows that this quantity is minimized when k has particular values. In every case the optimum value is x/h, which means that the resultant force on the foot is in line with the hip. This has been confirmed by computation for values of x ranging from zero to $\pm d$ and for values of h ranging from d to $1.73d$. [The latter is the greatest height at which the hip can reach the point (d,h) while the foot remains on the ground.]

It may be argued that it is more important to minimize the moments at the joints, and so the forces required of the muscles, than to minimize work.

Let
$$M_{abs} = |M_{hip}| + |M_{knee}|. \tag{18}$$

The mean value of M_{abs} was calculated for a positive value of x and a numerically equal negative value. This quantity was found to be minimized in every case by making k equal x/h. Both the work required of the muscles and the total of the moments at the joints are minimized by keeping the ground force in line with the hip. This will presumably also minimize the metabolic cost of locomotion.

That conclusion applies to a two-segment leg that requires muscles at only two joints. Real legs have three or more segments: even in the human leg, muscles exert substantial moments about the ankle joint, as well as about the hip and knee. Three-segment legs will not be discussed here because their motion is indeterminate: a range of joint angles is possible for given positions of the hip and foot. Nevertheless, it seems reasonable to assume that animals that have such legs can save energy in locomotion by keeping the ground force more or less in line with the leg. The forces exerted by the feet of dogs and sheep (in all their gaits) tend, however, to be a little more vertical, at each stage of the step, than a line from paw or hoof to hip or shoulder (Jayes and Alexander, 1978).

Joint angles

In the model of Fig. 2 the ratio h/d of hip height to leg segment length may be large or small. If it is large the animal walks on relatively straight legs and if small on relatively bent ones. Which is better?

We will assume, as suggested by the previous section, that the ground force is kept in line with the hip throughout the step $(k=x/h)$. We will also continue to assume, for the present, that the path of the hip is horizontal, so that h remains constant. If the position of the centre of mass is fixed relative to the hip this implies that G, the vertical component of the ground force, is constant and equal to body weight mg.

Because the ground force is in line with the hip, only the knee muscles do work. The work done per unit distance equals the horizontal component of the ground force:

$$dW/dx = kmg = xmg/h . \tag{19}$$

If the step length is s, the negative work done in the first half of the step and the positive work done in the second half are each given by:

$$W = \pm \int_0^{s/2} (xmg/h)dx = mgs^2/8h . \tag{20}$$

Thus, for steps of given length, least work is required if hip height h is kept as large as possible.

Larger values of h also reduce the moments that the knee muscles have to exert. When $x=0$ (the hip is directly over the foot) the moment about the knee is $Gd\sin\beta$. The angle β is $\arccos(h/2d)$ (from equation 11, with $x=0$) so $\sin\beta=[1-(h/2d)^2]^{\frac{1}{2}}$, and the moment about the knee falls as hip height increases. When $h=1.73d$ (the largest value considered in the previous section) this moment is $0.50Gd$ and when $h=d$ it is $0.87Gd$. The contrast is even greater if we look not at the moment when $x=0$ but at the greatest moment that occurs during the step. With $h=1.73d$ this is again $0.50Gd$ (when $x=0$), but with $h=1.00d$ and step length $s=2d$ it occurs at the end of the step $(x=d)$ and is $1.00Gd$ (calculated from equations 9, 11 and 14, with $k=x/h$).

Small mammals such as mice run with their legs much less straight than do large mammals such as horses. Biewener (1989) showed that, largely because of this, their leg muscles have to exert forces that are much larger multiples of body weight than those exerted by the muscles of large mammals. Kram and Taylor's (1990) analysis seemed to show that, because of the relatively larger forces, small mammals must use more metabolic power than if they were to run on straighter legs. It seemed to explain the low efficiency of performance of positive work in small mammals.

In contrast, we concluded in an earlier section that well-adapted muscles should perform positive work with the same efficiency, irrespective of the forces that the muscles have to exert. If the maximum muscle force F_0 is increased by running on bent legs, the muscles need not shorten so fast in order to supply the same

mechanical power. The product lv_{max} can be reduced so that the efficiency need not change: it is necessary to increase the metabolic rate only in proportion to any increase in work per step that results from the lower hip height.

The essential difference between my analysis and that of Kram and Taylor (1990) is that they assume that v_{max} must be inversely proportional to T, while my arguments suggest it may be proportional to v_0. If muscle forces are increased by a change of posture while work requirements remain little changed, v_0 may fall although T remains constant. The question of whether metabolic power requirements depend principally on $1/T$ or on v_0 could be decided by experiments in which muscles were subjected to cyclic length changes of different amplitudes and frequencies, in the manner of the experiments of Moon *et al.* (1991) on fish muscle.

Optimum gait

So far we have assumed that the hip remains at the same height throughout the step, but now we will allow it to rise and fall. To see how this may save energy, consider the model shown in Fig. 3, which is a slightly simplified version of McGeer's (1990) 'rimless wheel'. The legs are rigid, with length r. The trunk has mass m, with its centre of mass at the hip, and the mass of the legs is negligible. Each foot is set down just before the other is lifted and while on the ground exerts a force in line with the hip. The hip joint and the trunk move along a series of arcs of radius r.

While the hip is moving along an arc, no moment acts about it so its muscles do no work. The knee is rigid so its muscles also do no work. The trunk rises and falls, decelerates and accelerates, but its gains of potential energy are matched by losses of kinetic energy, and *vice versa*, so no work is required. However, work is needed when the foot on the ground changes and the trunk starts moving along a new arc.

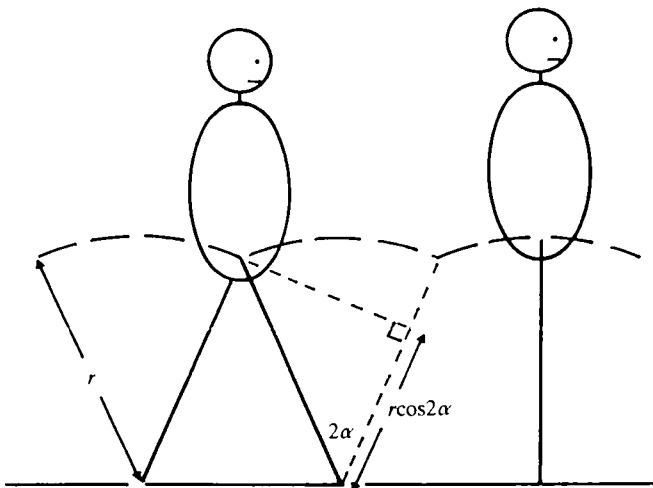The abrupt change from one arc to the next implies large, brief forces. When a

Fig. 3. The rimless wheel model of walking.

foot hits the ground, the force of the impact is much larger than the force on the other foot so we can assume that angular momentum about the impact point is conserved. Just before the impact, the centre of mass of the trunk (at the hip) is travelling with speed u. Fig. 3 shows that the perpendicular distance from its path to the impact point is $r\cos2\alpha$, where α is the angle of the legs to the vertical at that stage of the stride. Hence, the angular momentum about the impact point is $mur\cos2\alpha$. The new path of the centre of mass, after the impact, is a distance r from the impact point, so its angular momentum is now $mu_{new}r$. The speed has been reduced by the impact to u_{new}, where:

$$mu_{new}r = mur\cos2\alpha,$$
$$u_{new} = u\cos2\alpha. \tag{21}$$

The leg that is leaving the ground must now push off, doing the work W needed to replace the lost kinetic energy and re-accelerate the body to speed u.

$$W = \tfrac{1}{2}m\,(u^2 - u_{new}^2),$$
$$= \tfrac{1}{2}mu^2\,(1 - \cos^2 2\alpha). \tag{22}$$

Note that:

$$\sin\alpha = s/2r,$$

where s is step length.

$$\cos2\alpha = 1 - 2\sin^2\alpha,$$
$$= 1 - (s^2/2r^2).$$

By substituting this in equation 22:

$$W = (mu^2 s^2/2r^2)\,[1 - (s^2/4r^2)]. \tag{23}$$

Compare this with the energy cost of walking on a level path, given by equation 20; we will make the height h of the level path equal to the maximum height r of the rimless wheel. The rimless wheel gait is the more economical if:

$$(mu^2 s^2/2r^2)[1 - (s^2/4r^2)] < mgs^2/8r,$$
$$u^2/gr < r^2/(4r^2 - s^2). \tag{24}$$

Thus, it is the more economical at low speeds, but not at high ones. People and cursorial mammals walking fast generally take strides of length about $2r$ (Alexander and Jayes, 1983); since s is half a stride, this implies $s \approx r$. When $s = r$ the critical value of the Froude number u^2/gr, given by inequality 24, is 0.33. People and cursorial mammals generally make the change from walking to running at a Froude number of about 0.5 (Alexander and Jayes, 1983). The rimless wheel rises and falls in the course of each step much in the manner of walking, and the level gait is more like running (but not quite like running, in which the trunk is lowest as it passes over the supporting foot).

In the rimless wheel gait, no work is done during most of the step, but muscles may have to be active to keep the knee angle (so the effective length of the leg, r) constant. The metabolic cost of this activity will be low if the legs are kept nearly straight, minimizing the moment at the knee joint.

This comparison between idealized gaits shows that different gaits have different energy requirements and that different gaits may be the most economical at different speeds. In a more elaborate and realistic analysis, Alexander (1980) calculated the positive and negative work requirements for gaits involving different patterns of ground force. Two variables defined the pattern: the duty factor (the fraction of stride duration for which each foot is on the ground) and a parameter that described the shape of a graph against time of the force exerted by a foot on the ground. The model showed that, at low speeds, walking gaits required least work. These are gaits in which the duty factor is more than 0.5, so there are times when both feet of a pair are on the ground, and the hip is highest as it passes over the supporting foot. In the range of walking speeds, changes of speed give gradual changes in the optimal force pattern. As a critical Froude number is passed, the optimal gait changes abruptly to a run, with a duty factor less than 0.5 and the hip lowest as it passes over the foot. (The pace of the camel and the trot of most other mammals are quadrupedal equivalents of the human run.) The theory explains the change from walking to running but predicts too high a Froude number for it, probably because it ignores the energy-saving potential of elastic mechanisms (which are discussed in the next section) in running gaits.

Most quadrupedal mammals change from a trot or a pace to a gallop at a Froude number of about 2.5 (Alexander and Jayes, 1983). In the symmetrical gaits used at lower speeds, the feet of each pair move half a cycle out of phase with each other, but in galloping they are less than half a cycle out of phase. This makes it possible for the stride to be extended by bending the back while the fore feet are on the ground and straightening it while the hind feet are on the ground (Hildebrand, 1959). The model of Alexander *et al.* (1980) seemed to show that galloping required at least as much mechanical power as trotting at the same speed, but it will be shown in the next section that it may enable animals to exploit an additional elastic energy-saving mechanism. It may also reduce metabolic energy costs in another way. The bending and extension of the back increase the step duration (the time for which each foot remains on the ground). This may enable the animal to use slower muscle fibres than would otherwise be needed to reach the same speed, if Kram and Taylor's (1990) assumptions are correct.

It has been widely assumed, as in this section, that animals change gaits to minimize the energy cost of terrestrial locomotion at all speeds. However, it has been confirmed only for humans (Margaria, 1976) and horses (Hoyt and Taylor, 1981) that gait changes have this effect. In these species at least, graphs of oxygen consumption against speed for the different gaits intersect at the transition speeds so that, for example, walking is more economical for horses than trotting below the normal speed of the walk–trot transition, and trotting is more economical above the transition speed.

Elastic mechanisms

In an earlier section we discussed a muscle that lengthened and shortened 'as if it

were a Hookean spring' as the force it exerted rose and fell. (Equations 5 and 6 described this muscle's behaviour.) Such a muscle could be replaced by a spring that would have the same mechanical effect at no metabolic cost. However, only some muscles behave like this and only in some gaits.

In human running and kangaroo hopping, the animal's kinetic and potential energy are lowest as the hip passes over the supporting foot. Also, at this stage of the stride the joints of the leg are most bent and the force on the ground is greatest. The lost kinetic and potential energy could be stored at this stage as elastic strain energy in springs, and returned immediately afterwards in an elastic recoil. The gastrocnemius and (in kangaroos) plantaris muscles lengthen as they develop force in the first half of the foot's period of contact with the ground, and shorten as the force falls in the second half: they could be replaced by springs. The same is true of corresponding muscles in both the fore and the hind legs of trotting and galloping quadrupeds.

The tendons of these muscles seem to have an important role as springs. The human Achilles tendon has been estimated to store, as strain energy, 35 % of the kinetic and potential energy lost and regained in a running step at moderate speed (Ker et al. 1987). Tendons and ligaments in the feet of wallabies have been estimated to store and return 33% of the kinetic and potential energy lost and regained in slow hopping (Ker et al. 1986). Tendon is an excellent elastic material, dissipating as heat only about 7 % of the strain energy stored in it (Bennett et al. 1986). Tendons that seem to serve as springs in this way are loaded to much higher stresses than most other tendons: they therefore stretch to higher strains and store more strain energy (Ker et al. 1988).

Tendons serving as springs reduce the negative and positive work that their muscles have to do in each step. By reducing the length changes that the muscle fibres have to make, they enable the animal to run with muscle fibres of shorter resting length l or lower maximum shortening speed v_{max}: I have no information about v_{max} for the muscles in question but some of them have evolved exceedingly short muscle fibres. To quote an extreme example, the superficial digital flexor muscle of the horse fore leg has muscle fibres only 3 mm long in its humeral head, but in the course of a galloping stride the overall length of it and its tendon increases by 50–60 mm beyond the length at which it is just taut (Dimery et al. 1986). Nearly all of this length change must be elastic extension of the tendon.

It was argued in an earlier section that the efficiency with which muscles perform positive work should be constant, if they are optimally adapted to their tasks. Tendons serving as springs do not alter the quantities of work that must be done in any particular gait, but they do some of it, leaving less to be done by the muscles. Thus, the efficiency with which the muscles plus tendons do positive work in running is greater than the efficiency with which the muscles alone could do it.

The arch of the human foot flattens while the foot is on the ground in running, storing strain energy in stretched ligaments and returning it in an elastic recoil (Ker et al. 1987). In experiments that simulated the force pattern of running the arch dissipated as heat 22 % of the strain energy stored in it, considerably more than the

V % dissipated by tendon. Nevertheless, it seems to be a useful spring, storing 17 % of the kinetic and potential energy lost and regained in a running step (in addition to the 35 % stored in the Achilles tendon). It reduces the work required of the muscles. It may also reduce the forces required in the muscles by enabling the runner to keep the leg a little straighter. If the foot did not flatten, the knee would have to bend more to allow the same vertical excursion of the body's centre of mass.

Tendons and other springs can save energy effectively in running, but are probably ineffective in walking. Consider the idealized walk (the rimless wheel model) represented in Fig. 3. The leg does negative work when it hits the ground, exerting a large impact force. It does positive work, replacing the energy lost in the impact of the other foot, when it pushes off. Between these times it exerts less force, so that it cannot retain any strain energy gained in the initial impact to power the push-off. A more general argument presented by Alexander (1980) shows that elastic energy-saving mechanisms cannot be effective in fast walking.

In the gathered position in a gallop, the fore legs reach the backward extreme of their swing and the hind legs their forward extreme. Alexander *et al.* (1985) showed that much of the kinetic energy lost and regained by the legs of dogs and deer, at this stage of the stride, might be stored as elastic strain energy in the aponeurosis of the longissimus muscle (the principal extensor of the back). Bennett (1989) suggested a similar role for the fascia lata of the hind leg, which may store and return some of the kinetic energy lost by the leg at the end of its backward swing. Thus, the work required of muscles may be reduced and metabolic energy saved.

Conclusion

This paper has shown how energy is saved in walking and running by many different mechanisms, but a major puzzle remains. Arguments presented here suggest that if muscles were optimally adapted to their tasks in running, the metabolic energy they used would be a constant multiple of the positive work that they did. However, efficiencies of performance of positive work are found to be much higher in large animals than in small ones. Kram and Taylor's (1990) analysis claims to resolve the problem, but there is no firm physiological basis for their assumption that the maximum shortening speeds of muscles should be inversely proportional to ground contact time. The same contact time may require different rates of shortening of muscles, depending on their mechanical advantages and on the animals' posture.

List of symbols

d	Length of a leg segment
E	Metabolic energy
F	Force exerted by a muscle

g Gravitational acceleration
G Vertical component of the force exerted by a foot on the ground
h Height of the hip joint from the ground
k Ratio of the horizontal to the vertical component of the ground force
K A constant that appears in equation 1
l Resting length of the fibres of a muscle
m Body mass
M The moment of the ground force about a leg joint
P Rate of consumption of metabolic energy
r Radius of the circular arcs in Fig. 3
s Step length
t Time
T Step duration
u Speed of locomotion
v Rate of shortening of muscle fibres (lengths per unit time)
W Work
x, y Cartesian coordinates
α, β Angles shows in Figs 2 and 3

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