

# Walking and Running

R. McNeill Alexander

*Legs and leg movements are subtly adapted to minimize the energy costs of locomotion*

You are walking along, going to an appointment, when you realize that you are rather late. You walk faster, and then faster still. You may double your speed, but your pattern of movement remains the pattern we call walking. Then, suddenly, you break into a run, an obviously different pattern of movement. Why did you do that? Why use one technique of movement at low speeds, and a dramatically different technique at high speeds? The change is made at a very predictable speed—about 2.5 meters per second (6 miles per hour) for normal-sized adults. This paper will examine why this is so by analyzing the two patterns of movement.

As Figure 1 shows, walking involves each foot being on the ground for slightly more than half the time, so that there are stages, for example stage *d*, when both are on the ground simultaneously. While a foot is on the ground, its leg remains fairly straight; therefore, the trunk is highest when the leg is vertical. This occurs at stage *b*, when the trunk is passing over the supporting foot. The trunk is lowest at stage *d*, when both feet are on the ground.

Figure 2 shows running, during which each foot is on the ground for less than half the time, so that there are stages, such as stage *d*, when both are off the ground. The person is traveling in a series of leaps and must therefore be highest in mid leap, at stage *d*. His supporting leg is bent at stage *b*, as the trunk passes over the supporting foot. The trunk is lowest at this stage.

## A simple model

We will make a first attempt at explaining why people walk only at fairly low speeds, by formulating the simple mathematical model illustrated in Figure 3. This mathematical man sets one foot down at the instant he lifts the other. While each foot is on the ground, he keeps its leg rigidly straight, so that his hip joint moves along an arc of a circle centered on the foot. His legs are sufficiently light, compared to his trunk, for their mass to be ignored. Thus his center of mass occupies a fixed position in his trunk and moves along arcs of the same radius as the path of the hip joint. This radius is the length *l* of

the leg. The man's walking speed is *v*.

Here we need a standard formula from mechanics. A point moving with speed *v* along an arc of a circle of radius *l* has an acceleration  $v^2/l$  toward the center of the circle. Thus the center of mass of the mathematical man has an acceleration  $v^2/l$  toward the supporting foot. At stage *b* in Figure 3 this acceleration is vertically downward. Since the man cannot pull himself down but can only fall under gravity, his downward acceleration  $v^2/l$  cannot exceed the acceleration of free fall, *g*; that is,  $v^2/l \leq g$ , which by algebraic transformation gives  $v \leq \sqrt{gl}$ .

Thus the mathematical man cannot walk faster than  $\sqrt{gl}$ . On earth, *g* is about 10 m/sec<sup>2</sup>, and leg length (from the hip joint to the ground) is typically 0.9 m for an adult; therefore, the maximum walking speed is about  $\sqrt{10 \times 0.9} = 3$  m/sec. This is only a little faster than the approximately 2.5 m/sec at which real adults break into a run. Children have shorter legs than adults, and the theory correctly predicts that they will have to begin running at lower speeds; small children often have to run to keep up with walking parents. The theory also seems to explain why accident victims sometimes find that they can move faster than they expected on crutches: a man on crutches moves in arcs about 1.4 m instead of the usual 0.9 m for walking.

The simple theory thus is reasonably successful in predicting the speeds at which people break into a run. However, there is one observation that seems very damaging to the theory. Athletes in walking races travel at 4 m/sec, well above the theoretical maximum of 3 m/sec. The racing walk is unquestionably a style of walking, by our definition: there is a stage when both feet are on the ground, and each leg is kept fairly straight while its foot is on the ground.

The trick that makes high walking speeds possible is done with the back, as is illustrated by the racewalker in Figure 4. At stage *a* (the equivalent of stage *a* in Figure 3) she keeps the back straight, as it would be in an ordinary walking gait. But at stage *b* she bends the lower part of the back, sticking the pelvis out (see Dyson 1973); it lowers the body's center of mass relative to the hip joint of the supporting leg. Thus the center of mass no longer moves in arcs of radius *l* (as in Fig. 3) but in arcs of larger radius, rising and falling less, and higher speeds are possible.

The racing walk shows that the speed limit suggested by the equation is not an absolute limit for real people. It would be an absolute limit only if people behaved as the simple model assumed.

R. McNeill Alexander is Professor of Zoology at the University of Leeds, England. His research has been concerned with applying the principles of engineering mechanics to the study of animals and humans; for the past decade he has focused mainly on the mechanics of movement on legs. He is the author of a number of books, including *Animal Mechanics* (1963, 2nd ed., Blackwell Mosby). Address: Department of Pure and Applied Zoology, University of Leeds, Leeds LS2 9JT, UK.

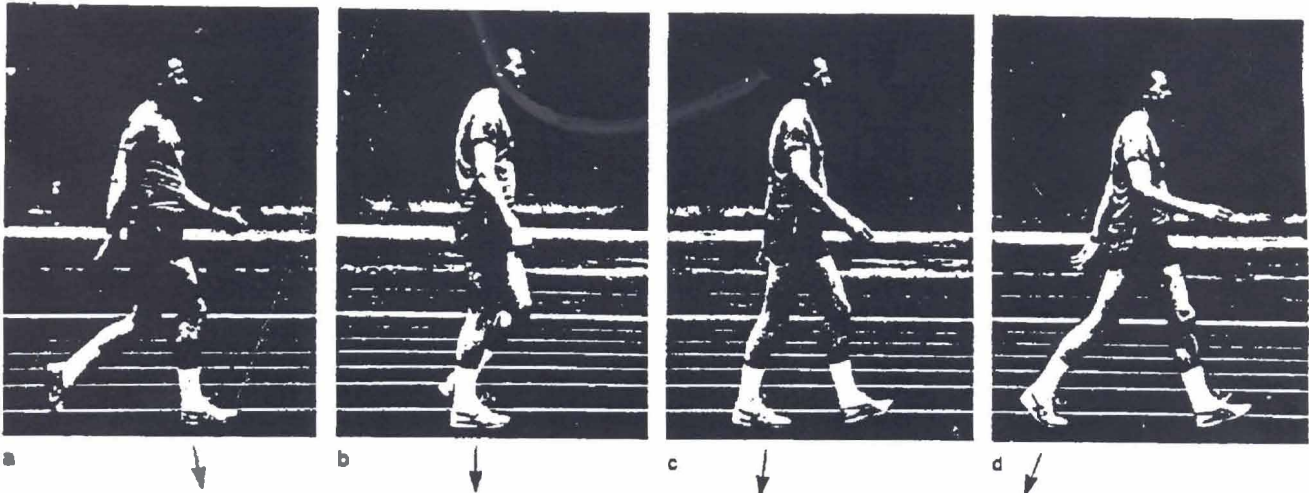


Figure 1. Four successive stages of a walking stride illustrate the dynamics of the forces involved in walking, which entails both feet being on the ground simultaneously for part of the stride (stage d). The arrows show the directions of the forces exerted by

the foot on the ground and demonstrate that walking involves alternate braking (stage a) and acceleration (c and d) in every stride, an inherent inefficiency that increases as walking speeds increase.

## Energy costs

We move now from the relatively simple question "What is possible?" to the more sophisticated question "What is best?" We will test the plausible hypothesis that people adjust their gaits so as to keep energy costs as low as possible.

It would be difficult to measure energy costs of various gaits directly, but it is relatively easy to measure oxygen uptake and carbon-dioxide production. From these the energy costs of walking and slow running can be calculated, since it can be safely assumed that at these speeds all energy is being released by oxidizing food-stuffs. The energy cost of sprinting is much more difficult to estimate because a sprinter builds up an oxygen debt (Margaria 1976).

Figure 5 compares the power required for walking, running, and cycling, as calculated from analyses of the gases breathed out during these activities. Notice that

the graphs for walking and running intersect. A runner traveling slower than 2.3 m/sec uses more power than a walker at the same speed. A walker traveling faster than 2.3 m/sec would use more power than a runner at the same speed. People normally make the change from walking to running at about the right speed to ensure that they use the cheaper gait for each particular speed.

Hoyt and Taylor (1981) made similar studies of horses, which walk at low speeds, trot at intermediate speeds, and gallop at high speeds. They trained small ponies to run on a conveyor belt in a laboratory and to use different gaits on command, so that they could be made to trot, for example, at speeds at which they would normally walk. They found that at speeds up to 1.5 m/sec walking required less power than trotting or galloping, that trotting was cheapest between 1.5 and 4.5 m/sec, and that galloping was cheapest at higher speeds. When allowed to choose their gaits, the horses used the

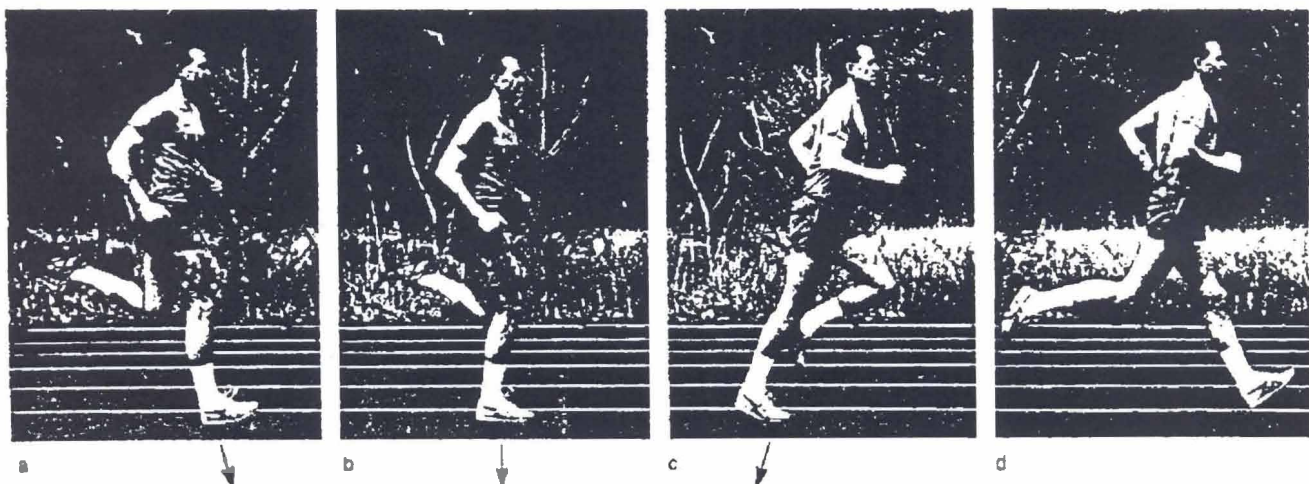


Figure 2. Running differs from walking primarily in that it entails both feet being off the ground simultaneously for part of the stride (stage d). The force arrows indicate that braking and acceleration occur as in walking. However, much of the otherwise

lost energy in running is stored between stages a and b in the form of elastic strain in the tendons, and is then released between stages b and d.



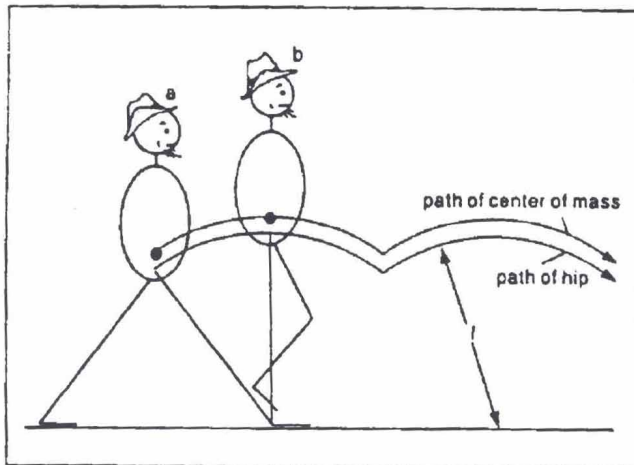


Figure 3. Walking involves an alternate raising and lowering of the body's mass by an amount depending on the length of the legs,  $l$ . The speed at which a person can walk has an upper limit largely because the downward acceleration of the body's mass from its highest point in the stride (stage *b*) cannot exceed the acceleration of gravity.

cheapest gait at each particular speed.

Suppose now that someone wants to travel at 2.3 m/sec. According to the graph in Figure 5, if he moves steadily at that speed in either a fast walk or a slow run, he will use 690 watts. However, he could travel the same distance in the same total time by walking more slowly for part of the distance and running faster for the rest. He might, for example, walk for a while at 1 m/sec and run for a while at 4 m/sec; in this case, if his mean speed was 2.3 m/sec, his mean power consumption would be only 630 watts. People often walk and run alternately, rather than use a steady fast walk or a steady slow run. This does not seem to have been investigated systematically; however, Hoyt and Taylor (1981) showed that horses avoid the awkward, inefficient speeds at the borderlines between the preferred speeds for walking, trotting, and galloping.

Only a small fraction of the total power required for walking and running is needed to overcome friction in the joints and air resistance, because the joints are well lubricated, and because air resistance is negligible at low walking speeds (in still air) and rises to only about 13% of the total power requirement for fast sprinting (Pugh 1971). And yet, as Figure 5 shows, movement on legs expends much more energy than movement on wheels: a cyclist, despite having to move his bicycle as well as his own body, uses less than half as much power as a runner at the same speed. Why is motion on legs so expensive?



Compared to cycling, walking and running expend so much energy primarily because the mechanical energy of the body fluctuates in every stride. As an analogy, suppose that instead of driving your car steadily you pressed alternately on the accelerator and the brake. You would give your car kinetic energy whenever you accelerated, and discard it again as heat when you braked. You would waste energy and use more fuel than necessary. Similarly, energy (both kinetic and potential) is alternately given to the body and discarded in walking and running.

To understand how these energy fluctuations happen, we must examine the forces exerted by the feet. These forces can be recorded by means of force-sensitive panels set into the floor; electrical outputs from these force plates can signal the three components, one vertical and two horizontal, of any force that acts on the plate, and can also indicate the coordinates of the point of application of the force.

The arrows representing forces in Figures 1 and 2 are based on force records made when people walked over force plates. Notice that the forces are generally not vertical. When a foot is first set down, it exerts a forward component of force, tending to decelerate the body. Later it exerts a backward component, tending to accelerate the body. Thus walking involves alternate braking and accelerating.

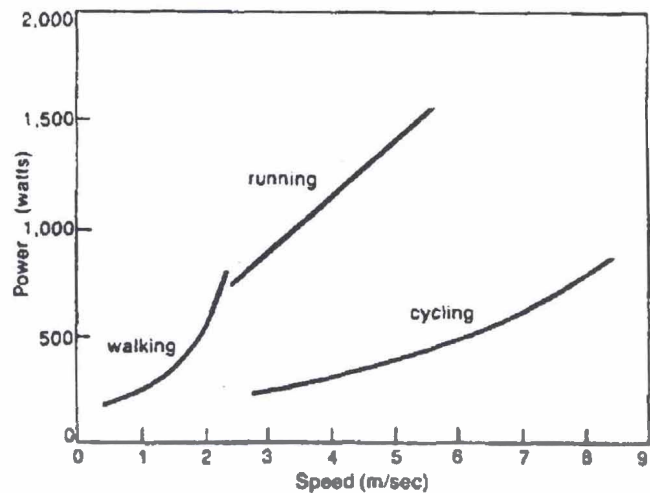
At the same time, as we have seen, walking also involves alternate rising and falling. The body is highest when moving most slowly (stage *b* in Fig. 1) and lowest when moving fastest (stage *d*); therefore, potential energy is highest when kinetic energy is lowest, and vice versa, as in a swinging pendulum. The fluctuations of total mechanical energy are thus kept fairly small, and the energy cost of walking is less than it might otherwise be (Margaria 1976).

## Force patterns

To see how the energy fluctuations are regulated, we have to examine the patterns of force exerted on the ground (Alexander and Jayes 1980). Only the vertical components of force will be examined in detail; these are shown plotted against time in Figure 6. The horizontal components are adjusted by muscle action to keep the resultant force always approximately in line with the hip, so any particular pattern of vertical components implies a corresponding pattern of horizontal ones.

Figure 4. The racing walk differs fundamentally from an ordinary walking gait not at stage *a*, when the body's center of mass is at its lowest point, but at stage *b*, when the center of mass is at its highest point but is kept lower than in ordinary walking by the bending of the lower back and the tilting of the hips. Thus, because the fluctuation in the height of the center of mass is minimized, higher speeds than are possible in ordinary walking can be achieved; as Figure 3 shows, it is largely this fluctuation that limits walking speed. (Photograph by H. Hosley.)

Figure 5. The power requirements for walking, running, and cycling by an adult man are plotted here against speed. The graphs for walking and running, which are far less economical means of locomotion than cycling, intersect at about 2.3 m/sec; walking is more efficient than running below this speed, running is more efficient above it. The data were calculated from measurements of oxygen consumption and carbon-dioxide production. (Data from Margaria 1976 and Pugh 1974.)



The force record for slow walking shows the vertical component of force rising rapidly after the foot is set down, and falling rapidly before the foot is lifted; but for most of the period of contact with the ground this force maintains a fairly constant plateau level. At moderate walking speeds the force record shows two humps instead of a plateau, and the two humps become more accentuated as speed increases further.

At the onset of running (bottom graph) two abrupt changes can be seen in the force record. First, both feet are off the ground simultaneously for part of the stride. Second, there is an abrupt change from a two-humped to an essentially single-humped force pattern (with a small subsidiary hump when the foot strikes the ground and is decelerated suddenly).

These patterns of force used in walking and running can be described quite accurately by means of two parameters,  $\beta$  and  $q$ , for which values are given in Figure 6. The duty factor  $\beta$  is the fraction of the duration of the stride for which each foot is on the ground; it is more than 0.5 for walking and less than 0.5 for running. The shape factor  $q$  describes the shape of the force record (it is one of the coefficients of a Fourier series that describes the record);  $q$ , which would be zero for a force record shaped like a half-cycle of a sine curve, is negative for bell-shaped records, which are produced by running, and is positive for two-humped records, which are produced by walking. As walking speed increases,  $q$  increases gradually; it switches abruptly to a negative value at the transition to running.

The different values of  $\beta$  and  $q$  can be explained with the help of a mathematical model that calculates the work done per cycle of walking or running at a given speed for all possible combinations of  $\beta$  and  $q$  (Alexander 1980). A leg pressing on the ground, exerting a force parallel to its length, does work whenever it extends, increasing the distance from the sole of the foot to the hip joint. The leg degrades mechanical energy to heat whenever it shortens, bringing the hip joint nearer to the sole. In a cycle of steady walking on level ground, if friction can be ignored, the work done and the heat dissipated are equal.

Figure 7 shows values calculated from the mathematical model for two different speeds. The work requirement for a moderate walking speed is least for  $\beta \approx$

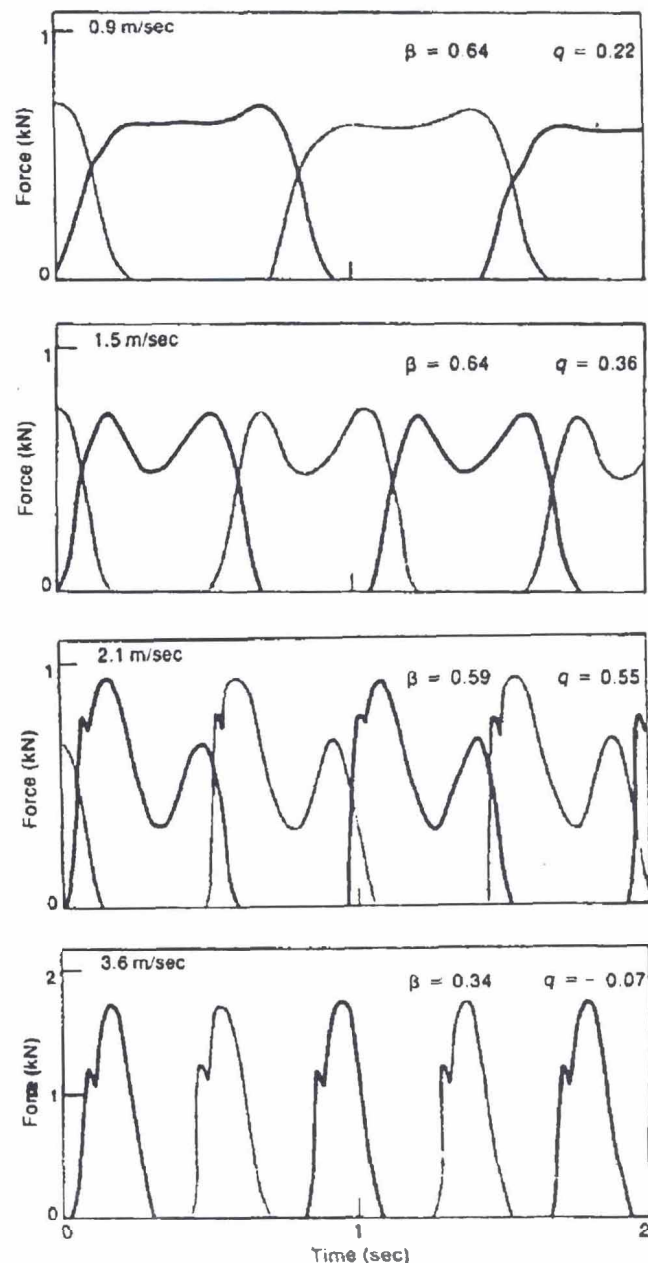


Figure 6. The vertical components of forces exerted by the feet of a man are plotted against time for slow, moderate, and fast walking speeds (top 3 graphs) and for running (bottom graph); dark-colored lines designate the forces exerted by one foot, light-colored lines the other. The force pattern in each graph is characterized by a duty factor  $\beta$ , which is that fraction of the duration of a stride during which each foot is on the ground, and by a shape factor  $q$ , which describes how much the shape of the curve deviates from a half-cycle of a sine curve, whose  $q$  would be zero. (From Alexander 1982.)



0.65 and  $q \approx 0.3$ , values close to the ones that people are observed to use. The graph for the higher speed shows the work requirement to be least for the lowest possible values of  $\beta$  and  $q$ —that is, for running. Similar graphs for other speeds show that to minimize work requirements at low speeds  $\beta$  should be fairly large and  $q$  should have a small positive value. As speed increases,  $q$  should increase gradually for optimum efficiency until a critical speed is reached, at which point a catastrophe—in the mathematical sense—occurs, and the optimum shifts suddenly to the lowest possible values of  $\beta$  and  $q$ .

The model says that to minimize energy costs, people should adjust their force patterns to suit their speeds very much as Figure 6 shows they do. There is, however, an important discrepancy between the predicted and the observed behavior: the model predicts too high a speed for the transition from walking to running. This seems to be because it ignores the effects of elasticity in tendon and muscle, which are capable of saving energy in running (as will be shown) though not in fast walking.

The relation between walking speed and the optimum value of the shape factor  $q$  can be explained as follows. At the stage of a walking stride when both feet

are on the ground, the trunk is lowest and must have an upward acceleration; the total vertical force exerted on the ground by the two feet must therefore exceed body weight. However, at the stage when the trunk passes over the supporting foot, the trunk is highest and must have a downward acceleration, so the force on the foot must be less than body weight. Thus the vertical force on the ground must fluctuate in the course of a stride. In fast walking the stride frequency is increased, and large accelerations are therefore needed to maintain the same amplitude of vertical movement. Larger fluctuations of the force on the ground are needed, and they are obtained by increasing  $q$ .

This mathematical model ignores the masses of the legs and consequently any work required to accelerate them in the course of the stride. However, a complementary model by Mochon and McMahon (1980) takes into account the masses of the legs, although it ignores the pattern of force exerted on the ground. Their model shows that the legs behave like jointed pendulums and can be swung forward effortlessly, provided that the time available for the swing lies between certain limits; it shows that the gaits people use have forward-swing times within these limits. This model is consistent with electromyographic observations, which show very little activity in the leg muscles during the forward swing.

## Elastic mechanisms

Human running uses much less energy than might be expected. Between stages *a* and *b* of a running stride (Fig. 2), the body's center of mass is slowing down and falling; the body is losing kinetic energy and gravitational potential energy. The total of these forms of mechanical energy is decreasing, because the leg, which is shortening while pressing on the ground, is acting as a brake. Between stages *b* and *c*, however, the center of mass is speeding up and rising; the total of kinetic and gravitational potential energy is increasing, because the leg, which is extending while pressing on the ground, is doing work. Suppose that the mechanical energy removed in the braking phase were degraded to heat, as in the brakes of a vehicle. Then the work required to replace it in the second phase would have to be supplied entirely by metabolic activity in the muscles. The metabolic energy required has been calculated, taking into account the known efficiency of muscle (Cavagna and Kaneko 1977); it is 1.8 times the actual energy consumption shown in Figure 5 for slow running, and 3.0 times the actual consumption for fast running.

The reason that running is so much more efficient than might be expected seems to be that much of the energy is not in fact degraded to heat. Some of it is converted to elastic-strain energy, which is stored up between stages *a* and *b* and released again in an elastic recoil between stages *b* and *c*. The mechanism is like that of a bouncing ball, which converts kinetic energy to elastic-strain energy as it deforms on hitting the ground, and which then makes the reverse conversion as it recoils and leaves the ground again (Margaria 1976).

Two different tissues have been suggested as the springs that store the strain energy: the leg muscles themselves and the tendons that connect them to the bones. When a muscle is stretched, its tendon is also

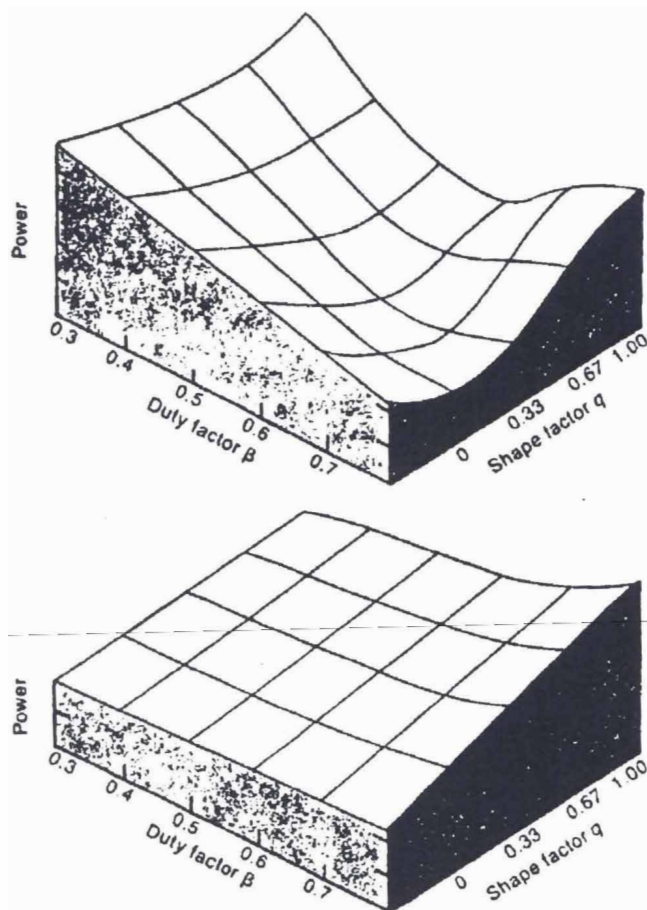


Figure 7. The calculated power requirements at two given speeds are plotted for a range of combinations of the duty factor  $\beta$  and the shape factor  $q$ . At 1.8 m/sec (top) the greatest economy is achieved with  $\beta$  having a value of 0.65 and with  $q$  having a value of 0.3, indicating that walking is most efficient at this speed, since running would produce a negative  $q$ . At 5.1 m/sec, the greatest economy is achieved with the lowest values of  $\beta$  and  $q$ , indicating a running gait. (After Alexander 1980.)

stretched by the same force; but which is the more important energy store?

Whichever stretches more will store more elastic-strain energy. Active muscle fibers can be stretched by no more than about 3% of their length before they "give," degrading any further work done on them to heat (Flitney and Hirst 1978). Tendons can be stretched 6% before breaking but are probably not stretched quite so much in normal use. In cases in which muscle fibers are much longer than their tendon (see Fig. 8), most of the elastic-strain energy will be stored in the muscle fibers. If the muscle fibers are much shorter than the tendon, most of the elastic-strain energy will be stored in the tendon (Alexander and Bennet-Clark 1977).

Whether it is tendon or muscle that is more important in storing elastic-strain energy can be determined by examining the muscles principally involved at the appropriate stage of the running stride. To save energy in the manner suggested, a muscle and its tendon must be stretched between stages *a* and *b* of running and must then shorten by elastic recoil between stages *b* and *c*. The most important of the leg muscles that are active during these stages, while the foot is on the ground, are the extensor muscles of the hip, knee, and ankle.

The principal extensor muscles of the hip, which run along the backs of the thighs, shorten progressively in stages *a* through *c* and therefore cannot serve usefully as springs (Brandell 1973); these muscles have relatively short tendons. The extensor muscles of the knee, which are in the front of the thigh, and of the ankle, which are in the calf, lengthen and then shorten as required, and they probably do serve as springs. Both have long tendons and short muscle fibers, the extensor muscles of the ankle having a particularly large tendon, the Achilles tendon, which connects them to the heel. Therefore, it is probable that in running most of the elastic-strain energy is stored in the tendons.

The suggestion that tendons serve as springs may seem surprising. However, tendon can do so because, although it cannot be stretched much, it is very strong and can store a great deal of elastic-strain energy. Very large forces act on tendons; in running, for example, there would be about a 400-kg force acting on the Achilles tendon of an average-sized man (Alexander and Vernon 1975). Tendon has excellent elastic properties; tests on sheep showed that tendon can return in an elastic recoil 93% of the energy that had previously been used to stretch it (Ker 1981).

The properties of tendon are more or less the same in all mammals, but the legs of hooved mammals such as sheep or horses are much more specialized than those of humans to take advantage of tendon elasticity. Some of the principal muscles in the lower parts of their legs have very long tendons and exceedingly short muscle fibers; consequently, they make good springs but have very little capacity for active shortening. In the extreme case of the camel, the muscle fibers have almost disappeared from several important muscles, leaving long tendons running virtually uninterrupted between their attachments to the bones.

This peculiarity of the camel made it particularly suitable for experiments designed to discover the relative importance of different tendons as elastic energy stores (Alexander et al. 1982). It was found that the most important tendons are in the parts of the legs marked by

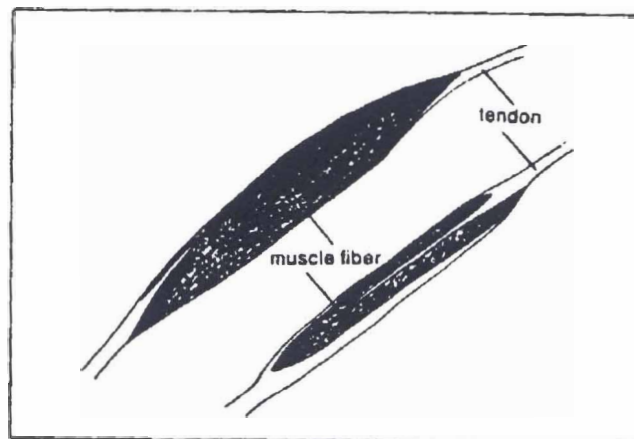


Figure 8. In contrast to muscles having relatively short tendons (*top*), muscles that have long tendons (*bottom*) are specially adapted to store elastic-strain energy in running.

arrows in Figure 9. These parts correspond to the soles of the feet and the palms of the hands in humans. People have strong tendons and ligaments in the soles of the feet, and these, along with the Achilles tendon, may serve as important stores of elastic-strain energy.

## Other mammals and mathematical models

This article has been concerned primarily with humans, but, as has been implied, the same biomechanical principles apply also to four-legged mammals, such as horses or camels; indeed, they apply to other mammals of at least the range of sizes from cats to elephants. Most mammals in this range move on fairly straight legs, as people also do. Smaller mammals such as mice run in a much more crouched position, on strongly bent legs (Jenkins 1971). Also, the very small mammals seem generally to have relatively thick tendons, which stretch so little in running that they save very little energy by elastic storage.

Most mammals the size of cats and larger walk and run using the same mechanical principles as in the corresponding human gaits. A cat or a horse walking is essentially similar to two people walking one behind the other. A quadrupedal mammal trotting is like two people

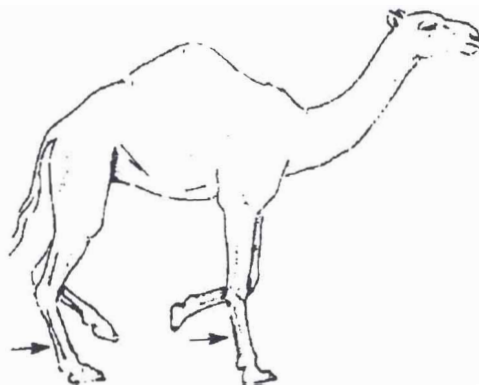


Figure 9. The muscles in the lower portions of a camel's legs are composed almost entirely of tendon, an adaptation for energy-efficient running. The arrows show the positions of the tendons that are most important as stores of elastic energy.



running one behind the other. It is only in the gallop, the gait used at the highest speeds, that quadrupeds do anything fundamentally different from people. Galloping involves bending movements of the back, so that the back muscles as well as the leg muscles contribute to the power required.

Mice do not seem to walk and elephants do not gallop, but most quadrupedal mammals, in the size range from cats to rhinoceroses, use three principal gaits: they walk at low speeds, trot at intermediate speeds, and gallop at high speeds. The speeds at which they change gaits depend on their sizes; a dog may have to gallop to keep up with a trotting horse.

The simple mathematical model of walking presented at the beginning of this article suggests that animals should change gaits at speeds proportional to the square roots of their leg lengths. A more general argument based on the theory of physical similarity suggests the same (Alexander and Jayes 1983). Mammals from the size of cats upward behave very much as the theoretical arguments suggest. For example, camels' legs are about nine times as long as cats' legs, and camels change gaits at about three times the speeds of the corresponding changes for cats. It must be emphasized that these are speeds of gait changes, not top speeds. Camels seem to be faster than cats, but they are not three times as fast.

Many recent investigators have used mathematical models to study human movement in subjects ranging from champion athletes to patients in need of replacement joints. In many cases, these mathematical models represent the human body in quite elaborate detail, taking account of the dimensions and masses of the various segments of the body, the lever arms of muscles, and so on. Such models are simplified representations of the human body but are nevertheless complicated.

In contrast, the models described in this paper have been simplified to the bare essentials: the mass of the body and the length of the legs were the only anatomical data required, except in the discussion of tendon elasticity. The danger of such an approach is that the models may not behave like their complicated counterparts in the real world, but this danger can be reduced if care is taken to check the effects of each simplifying assumption. The advantage of such an approach is its power to reveal basic principles that do not depend on the fine details of body structure. Indeed, the principles that have emerged apply not only to humans, but to large mammals in general.

These mathematical models and the other investigations described in this article all lead to a single conclusion: legs and leg movements are subtly adapted to minimize the energy costs of locomotion. If such studies improve our appreciation and understanding of human and animal movement, that in itself is worthwhile. If they are also useful to orthopedic surgeons, veterinarians, athletics coaches, and others concerned with human and animal movement, that is a bonus.

## References

- Alexander, R. M. 1980. Optimum walking techniques for quadrupeds and bipeds. *J. Zool. (London)* 192:97-117.  
 ———. 1982. *Optima for Animals*. London: Arnold.  
 Alexander, R. M., and H. C. Bennet-Clark. 1977. Storage of elastic strain energy in muscle and other tissues. *Nature* 265:114-17.

- Alexander, R. M., and A. S. Jayes. 1980. Fourier analysis of forces exerted in walking and running. *J. Biomechan.* 13:383-90.  
 ———. 1983. A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *J. Zool. (London)* 201:135-52.  
 Alexander, R. M., G. M. O. Maloij, R. F. Ker, A. S. Jayes, and C. N. Warui. 1982. The role of tendon elasticity in the locomotion of the camel (*Camelus dromedarius*). *J. Zool. (London)* 198:293-313.  
 Alexander, R. M., and A. Vernon. 1975. The dimensions of knee and ankle muscles and the forces they exert. *J. Human Mov. Stud.* 1: 115-23.  
 Brandell, B. R. 1973. An analysis of muscle coordination in walking and running gaits. *Medicine and Sports* 8:278-87.  
 Cavagna, G. A., and M. Kaneko. 1977. Mechanical work and efficiency in walking and running. *J. Physiol. (London)* 268:467-81.  
 Dyson, G. H. G. 1973. *The Mechanics of Athletics*, 6th ed. Univ. of London Press.  
 Flitney, F. W., and D. G. Hirst. 1978. Cross-bridge detachment and sarcomere "give" during stretch of active frog's muscle. *J. Physiol. (London)* 276:449-65.  
 Hoyt, D. F., and C. R. Taylor. 1981. Gait and the energetics of locomotion in horses. *Nature* 292:239-40.  
 Jenkins, F. A. 1971. Limb posture and locomotion in the Virginia opossum (*Didelphis marsupialis*) and in other non-cursorial mammals. *J. Zool. (London)* 165:303-15.  
 Ker, R. F. 1981. Dynamic tensile properties of the plantaris tendon of sheep (*Ovis aries*). *J. Exp. Biol.* 93:283-302.  
 Margaria, R. 1976. *Biomechanics and Energetics of Muscular Exercise*. Oxford: Clarendon Press.  
 Mochon, S., and T. A. McMahon. 1980. Ballistic walking: An improved model. *Math. Biosci.* 52:241-60.  
 Pugh, L. G. C. E. 1971. The influence of wind resistance in running and walking and the efficiency of work against horizontal or vertical forces. *J. Physiol. (London)* 213:255-76.  
 ———. 1974. The relation of oxygen intake and speed in competition cycling and comparative observations on the bicycle ergometer. *J. Physiol. (London)* 241:795-808.

