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Review

## Tendon elasticity and muscle function<sup>☆</sup>

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### Abstract

Vertebrate animals exploit the elastic properties of their tendons in several different ways. Firstly, metabolic energy can be saved in locomotion if tendons stretch and then recoil, storing and returning elastic strain energy, as the animal loses and regains kinetic energy. Leg tendons save energy in this way when birds and mammals run, and an aponeurosis in the back is also important in galloping mammals. Tendons may have similar energy-saving roles in other modes of locomotion, for example in cetacean swimming. Secondly, tendons can recoil elastically much faster than muscles can shorten, enabling animals to jump further than they otherwise could. Thirdly, tendon elasticity affects the control of muscles, enhancing force control at the expense of position control.

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### 1. Introduction: properties of tendon and muscle

This paper shows how tendon elasticity affects muscle function, especially in locomotion. To do this, it is necessary to know something about the mechanical properties both of the tendons themselves, and of the muscles that pull on them.

With the exception of the ossified tendons in the legs of some birds (Bennett and Stafford, 1988), the tendons of vertebrate animals are remarkably uniform in properties (Bennett et al., 1986; Pollock and Shadwick, 1994). The tangent Young's modulus of elasticity (the gradient of a graph of stress against strain) is low at low

stresses, increasing to an almost constant value of approximately 1.5 GPa at stresses above 30 MPa. Tendon has low energy dissipation, returning in an elastic recoil approximately 93% of the work previously done stretching it, and dissipating only 7% as heat. Neither the modulus nor the dissipation is affected much by changes in the frequency of stretching, at least over the range 0.2–11 Hz. The ultimate tensile stress is not easy to determine because it is difficult to grip tendons for testing without setting up stress concentrations that may cause premature failure, but seems to be at least 100 MPa. The experiments by Wang and Ker (1995) suggest that it may be as high as 140 MPa. The one property in which unossified tendons are known to vary markedly is resistance to fatigue damage, a property that will not concern us in this paper but is discussed in the paper by Ker (2002) in this symposium.

Vertebrate skeletal muscles are generally capable of exerting maximum stresses of 200–300 kPa in isometric contractions, that is, in contractions in which they are held at constant length (see for

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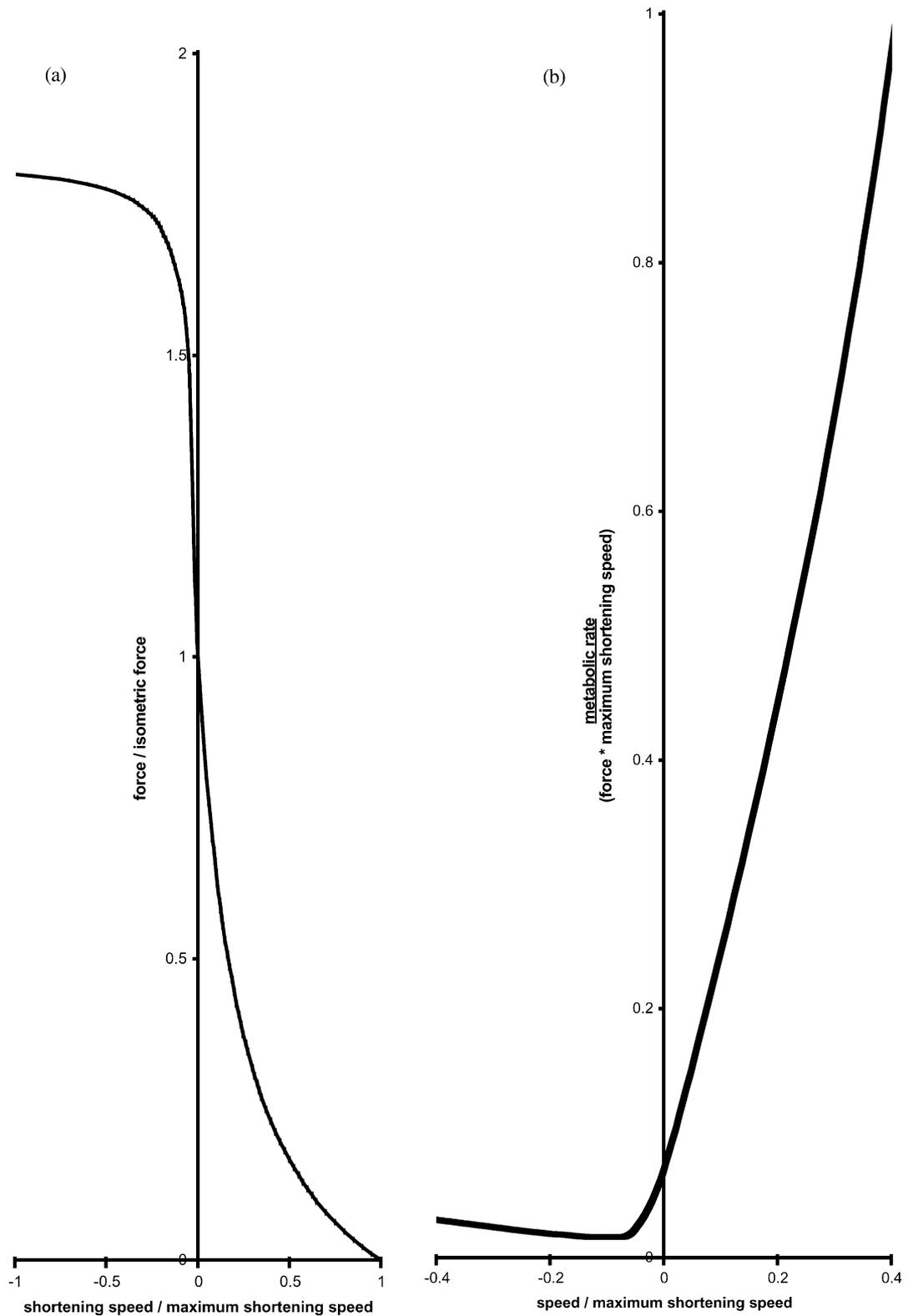


Fig. 1. Properties of vertebrate skeletal muscle, calculated from empirical equations given by Alexander (1997). (a) is a graph of the force exerted by a fully activated muscle (as a multiple of the isometric force) against shortening speed (as a multiple of the maximum shortening speed). (b) is a graph of metabolic rate per unit force against shortening speed (both as multiples of the maximum shortening speed).

example Marsh, 1994, on frog muscles and Wells, 1965, on mammalian muscles). These stresses can be exerted only over a restricted range of sarcomere lengths. When an active muscle is allowed to shorten it exerts less than the isometric stress (Fig. 1a). The stress falls as the rate of shortening increases, reaching zero at the maximum shortening speed of which the muscle is capable. The strain rate corresponding to this speed is generally represented by the symbol  $v_{\max}$ . When it is rapidly stretched (represented on the graph as a negative rate of shortening) it exerts up to approximately 1.8 times the isometric stress.

The isometric stress is fairly uniform in most vertebrate skeletal muscles, but is less in some fast muscles in which much of the space that would otherwise be available for myofibrils is occupied by unusually large proportions of mitochondria or sarcoplasmic reticulum (Rome et al., 1999). The maximum strain rate, however, varies enormously, for example from 0.2 to 3.8  $\text{s}^{-1}$  within a single muscle (the soleus muscle of horses tested at 15 °C; Rome et al., 1990). Even wider ranges of strain rate are found when different species are compared (Close, 1972).

Muscles have low metabolic rates when resting, and much higher rates when they are active. Alexander (1997) gave empirical equations both for the force that a muscle can exert when contracting at a given speed (Fig. 1a) and for its metabolic rate during that contraction. In Fig. 1b, these equations have been combined to produce a graph of metabolic rate per unit force, against shortening speed.

A muscle that develops force and shortens does work, which requires metabolic energy. If it exerts force without shortening, it does no work, but metabolic energy is nevertheless used. Suppose that the metabolic rate of an active muscle were the sum of two components, one proportional to the force and the other to the rate at which work was being done.

$$\text{Metabolic rate} = (a \times \text{force}) + (b \times \text{rate of doing work}) \quad (1)$$

where  $a$  and  $b$  are constants. The rate of doing work is the force multiplied by the rate of shortening, so this equation can be written

$$\text{Metabolic rate/force} = a + (b \times \text{rate of shortening}). \quad (2)$$

If this equation held, the graph in Fig. 1b would be a straight line. The fact that it is approximately straight over quite a wide range of shortening speeds suggests that it may be useful to think of the metabolic energy consumption of a muscle that is shortening as the sum of a cost of generating force and a cost of doing work. When an active muscle is forcibly stretched it does negative work, degrading mechanical energy to heat. Fig. 1b shows that the metabolic cost of negative work is low.

The graphs in Fig. 1 should be used with caution, in discussions of animal locomotion, because they have been derived from experiments in which muscles made single, isolated contractions under quasi-static conditions. They may not represent well the behaviour of muscles in repetitive cycles of lengthening and shortening, such as occur in locomotion (Askew and Marsh, 1998).

## 2. Running: springs in legs

The forces that the feet of running animals exert on the ground generally act more or less in line with the legs (see, for example, Alexander and Vernon, 1975). When it first hits the ground, a foot pushes downwards and forwards, slowing the animal down. Later in the step it pushes downwards and backwards, speeding the animal up again. Thus the animal loses and regains kinetic energy in each step. It also loses gravitational potential energy as it falls in the first half of the step, and regains it as it rises again. If the lost kinetic and potential energy can be stored briefly as elastic strain energy, and returned in an elastic recoil, very little work may be required from the animal's muscles.

Cavagna et al. (1964) measured these energy fluctuations for human runners. They added up all the increases in kinetic and potential energy and divided them by the metabolic energy cost of running, calculated from measurements of oxygen consumption. This gave an efficiency that was much higher than muscle efficiencies calculated from previous experiments in which subjects had walked up slopes or pedalled a bicycle ergometer. The most likely explanation was that kinetic and potential energy lost at one stage of a running stride was stored as elastic strain energy and returned later in a recoil. Cavagna and his colleagues concluded that elastic energy must be stored in the muscles. Cavagna et al. (1977)

similarly calculated efficiencies for running birds and non-human mammals. They obtained very high apparent efficiencies for kangaroos, which gave clear evidence for energy saving by elastic mechanisms, but the evidence from the other species was less clear.

Camp and Smith (1942) had shown that the digital ligaments of horses must stretch and recoil when the animals run. These 'ligaments' are actually the tendons of muscles whose muscle fibres have almost disappeared. Alexander (1974) showed that when a dog made a running jump, the forces on its gastrocnemius and plantaris tendons were large enough to stretch them substantially. My calculations indicated that the muscle fibres might contract almost isometrically, while the dog was taking off for the jump.

These observations showed that tendons must stretch enough to affect muscle function significantly. Alexander and Vernon (1975) used films and force plate records to calculate the forces in tendons and muscles in the hind legs of hopping kangaroos. We showed that a large proportion of the work, which muscles would otherwise have had to do, was saved by elastic stretching and recoil of tendons. Alexander and Bennet-Clark (1997) argued that tendon elasticity must be much more important than muscle elasticity, both in hopping kangaroos and in running people.

It has recently become possible to investigate tendon stretching and muscle function in locomotion much more directly. Roberts et al. (1997) glued strain gauges to the ossified part of the gastrocnemius tendon of turkeys (*Meleagris*), so that they could record the forces transmitted by the tendon while the bird was running. They also implanted sonomicrometry crystals at either end of a fascicle in the belly of the gastrocnemius muscle, so that they could record the length changes of the fascicle. They found that while the foot was on the ground in a running stride, the muscle fascicles contracted almost isometrically. The tendon stretched and recoiled as the ankle flexed and extended, but the muscle fascicles remained almost constant in length and did hardly any work. Biewener et al. (1998) performed a similar experiment with wallabies (*Macropus*), using a tendon buckle to measure the force. They found that the gastrocnemius and plantaris muscles both contracted almost isometrically, while the foot was on the ground in hopping.

These demonstrations of the importance of tendon elasticity contrast with the results of earlier experiments by Biewener and Blickhan (1988). They worked on kangaroo rats (*Dipodomys*), small rodents that hop like wallabies. The stresses that act in the gastrocnemius and plantaris tendons of these animals, in steady hopping, are much lower than in wallabies. Consequently the tendons stretch only a little, and the muscle fascicles have to lengthen and shorten substantially, as the ankle bends and re-extends while the foot is on the ground. These animals are capable of large jumps, involving much larger forces than steady hopping. Because the tendons have to be strong enough for jumping, they are not extensible enough to save much energy in hopping. It seems possible that only moderately large mammals and birds save much energy in running or hopping, by elastic storage in tendons. Wallabies and turkeys have masses of several kilogrammes, but kangaroo rats weigh only approximately 0.1 kg. There is scope here for research on other small mammals and birds.

Tendon elasticity can eliminate the work required from distal leg muscles, but metabolic energy is required to develop force in the muscles even if they do no work (Fig. 1b). This could be reduced in either of two ways: either by reducing the length of the fascicles and so the volume of muscle that has to be activated, or by using slower muscle fibres with lower  $v_{\max}$ . Reduction of fascicle length may be advantageous for running, but might be disadvantageous for some other activities. Short fascicles would not be a good design for animals that climb trees, because the uneven spacing of footholds obliges them to use their limbs in a wide range of positions. They could not do this, if the fascicles were too short (had too few sarcomeres in series) to be capable of exerting substantial forces over a wide range of lengths. Monkeys have relatively long fascicles in their distal leg muscles, much longer than in antelopes of similar body mass (Alexander and Maloiy, 1989).

Camels and horses have even shorter fascicles than antelopes, in distal leg muscles (Alexander et al., 1982; Dimery et al., 1986). The digital flexor muscles of the fore leg, and the gastrocnemius, plantaris and interosseous muscles, have fascicles only a few millimetres long. For example, the plantaris muscle of the camel consists mainly of a stout tendon 1.3 m long. The muscle belly is

represented by a small quantity of fascicles only 1–3 mm long. Contraction of fascicles as short as that could have only a trivial effect on joint angles. Thus, the length changes of each muscle-tendon complex, which occur in locomotion, must be almost entirely due to elastic extension and recoil of the tendon. Alexander et al. (1982) and Dimery et al. (1986) performed anatomical experiments on carcasses to discover how much the tendons must stretch, to allow the angular movements of joints that occur in locomotion. We found in the case of the horse that the tendons we investigated must stretch by 3–6% while the foot was on the ground in walking, 3–7% in trotting and 4–9% in galloping. Biewener (1998) made force plate records of horses galloping and calculated the forces in tendons. He found that stresses of 40–50 MPa must act in some of them, enough to stretch them by approximately 5%. He estimated that elastic recoil of tendons contributed up to 40% of the positive work required for galloping.

Until recently, it was generally assumed that these very short muscle fascicles were functionless vestiges. However, Wilson et al. (2001) have now made an interesting suggestion. They have shown by experiments with the legs of freshly-killed horses that these muscles are capable of damping the vibrations following impact with the ground. They suggest that this may protect bones and tendons from fatigue damage, a topic discussed by Ker (2002) in his contribution to this symposium.

Overheating is another potential cause of damage to tendons. We have already noted that only approximately 93% of the work done stretching a tendon is returned in its elastic recoil. The rest is dissipated as heat. Ker (1981) confirmed that tendons repeatedly stretched in a dynamic testing machine heated up at approximately the rate predicted from the mechanical energy loss. This heat is not easily dissipated even in the living animal because tendons have a poor blood supply. Birch et al. (1997) showed that the temperature of the core of the superficial digital flexor tendon in horses may rise to 45 °C during galloping. They found evidence of heat damage in this tendon. Low energy dissipation is an important property of tendons, not only because it ensures high energy return in an elastic recoil, but also because it minimises heat damage.

Even the most specialised running animals could not function with the fascicles reduced to vestiges in all their leg muscles. Substantial masses of

muscle are needed to accelerate and decelerate the animal, and to do the work of jumping. Antelopes, horses and camels retain substantial muscles in the proximal parts of their legs. Among these muscles, the triceps brachii and the quadriceps femoris have quite long tendons that may have a significant function as energy-saving springs. This possibility has not been adequately investigated.

### 3. Running: springs in backs

In this section, I will show how a sheet of tendon in the backs of mammals may serve as an energy-saving spring in galloping. For this purpose, it is convenient to distinguish two parts of an animal's kinetic energy. External kinetic energy is the energy associated with the movement of its centre of mass. It is  $1/2 m_{\text{body}} v_{\text{cm}}^2$ , where  $m_{\text{body}}$  is the mass of the body and  $v_{\text{cm}}$  is the velocity of the centre of mass. Internal kinetic energy is the energy associated with movements of parts of the body relative to the centre of mass. Consider the body as consisting of a large number of tiny particles, and let the  $i$ th particle have mass  $m_i$  and velocity  $v_i$ . The internal kinetic energy is  $1/2 \sum m_i (v_i - v_{\text{cm}})^2$ . Note that  $\Sigma$  indicates a sum including all the particles, and that the velocities are treated as vectors. The total kinetic energy of the body is the external kinetic energy plus the internal kinetic energy.

So far, we have discussed the energy fluctuations of running animals as if the whole mass of the body were concentrated at the centre of mass. We have ignored internal kinetic energy. Alexander (1977) used a very simple model of running to predict how work requirements would change with speed. I calculated separately the positive work done increasing the body's mechanical energy at some stages of the stride, and the negative work done reducing it at others. I showed that the positive work per unit distance travelled, associated with external kinetic energy fluctuations, could be expected to be independent of speed. The positive work per unit distance associated with fluctuations of gravitational potential energy should be smaller, falling as speed increased. And the positive work per unit distance associated with internal kinetic energy changes should increase with increasing speed. Internal kinetic energy fluctuations, due principally to movements of the limbs relative to the trunk, become important for the energy cost of running at high speeds.

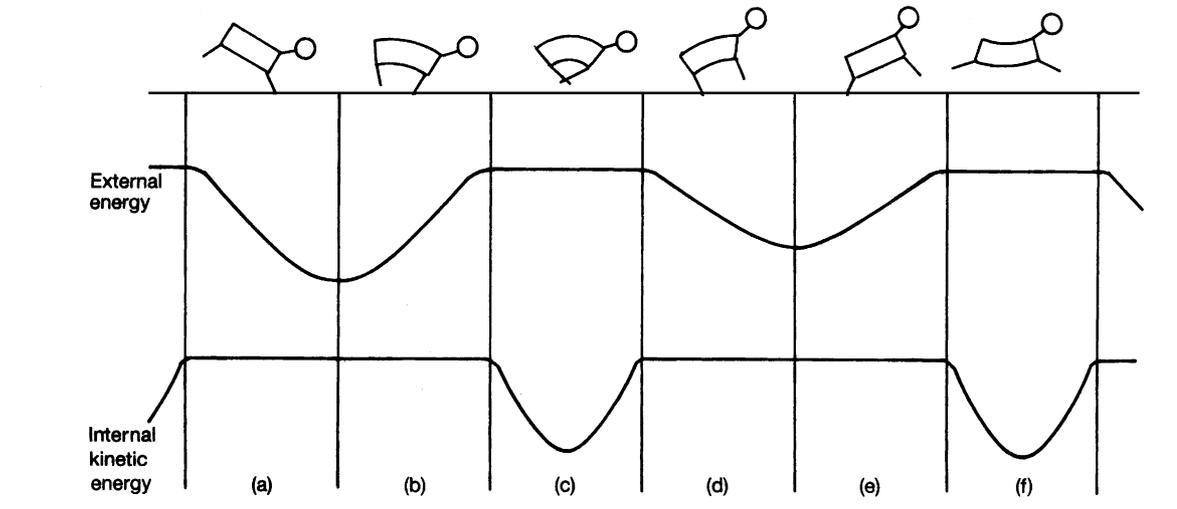


Fig. 2. Diagrams of successive stages of a galloping stride, with schematic graphs showing changes in the mechanical energy of the body. 'External energy' means external kinetic energy plus gravitational potential energy. From Alexander et al. (1985).

Fluctuations of external kinetic energy and of gravitational kinetic energy can be calculated from records of forces exerted on the ground. Using this method, Cavagna et al. (1977) and Heglund et al. (1982) showed that these energies fluctuate more or less as predicted by the simple model. Their data show that the work required to supply these energies, per unit body mass and distance, amounts to approximately 0.7 J/kg per m for a wide variety of running birds and mammals. Fluctuations of internal kinetic energy cannot be calculated from records of ground forces, but can be determined by analysis of films. Fedak et al. (1982) did this for four species of birds and three of mammals. They showed that the work required to supply internal kinetic energy, per unit mass and distance, is approximately  $0.5v^{0.5}$  J/kg per m, where  $v$  is the speed in metres per second. As predicted by my simple model (Alexander, 1977), internal kinetic energy fluctuations become increasingly important as speed increases.

The distal parts of limbs make much larger changes of velocity than the proximal parts, in the course of a running stride. Accordingly, fluctuations of internal kinetic energy can be minimised by making the distal parts of limbs as light as possible. This presumably saves metabolic energy, but an attempt to demonstrate this point empirically did not succeed (Taylor et al., 1974). We have already noted that the large muscles that are important for acceleration and jumping tend to be

in proximal limb segments. However, no limb design can prevent fluctuations of internal kinetic energy becoming important at high speeds.

The tendons in the distal parts of legs store elastic strain energy as the body loses external kinetic energy and gravitational potential energy in the first half of a step, and return this energy in the second half. They reduce the work required from the muscles on account of these energy fluctuations, but are not well placed to save work associated with internal kinetic energy changes.

Alexander et al. (1985) suggested that the aponeurosis (sheet-like tendon) of the longissimus muscle might serve as an energy-saving spring in galloping. This is the principal extensor muscle of the back. Galloping differs from slower quadrupedal ways in two important respects. First, instead of being set down alternately, the two fore feet are set down more or less simultaneously; and the same is true for the hind feet. Secondly, the back bends and extends in the course of a stride. In the gathered stage of a galloping stride (Fig. 2c) the fore legs end their backward swing and are about to swing forwards, and the hind legs end their forward swing and are about to swing back. At the extended stage (Fig. 2f) the reverse is the case. At each of these stages, internal kinetic energy is lost and regained. Also at each of these stages, the legs have angular accelerations that imply bending moments in the back. Alexander et al. (1985) pointed out that in the gathered stage the longis-

simus muscle must be active to counteract the bending moment, and that elastic strain energy must be stored in its aponeurosis. The force exerted by the muscle would cause axial compression of the vertebral column, storing additional strain energy there. We investigated the elastic properties of the aponeurosis and of the vertebral column in a dog and a deer, and concluded in each case that they were capable of storing and returning a large proportion of the lost internal kinetic energy. It would be possible to check our interpretation by using sonomicrometry to measure the length changes of the muscle fascicles and aponeurosis in galloping animals, but so far this does not seem to have been done.

There is scope for further energy savings by elastic storage at the extended stage of the stride (Fig. 2f). We have found no spring that seems likely to be as effective at this stage, as the aponeurosis seems to be at the gathered stage. However, Bennett (1989) suggested that the tendon of tensor fasciae latae (a muscle in the thigh) may make a useful contribution.

Experiments by Hoyt and Taylor (1981) with ponies showed that trotting cost less metabolic energy than galloping below a critical speed, and galloping cost less energy above that speed. The advantage of galloping at higher speeds seems to be that it enables the animal to benefit from springs that store and return internal kinetic energy. At lower speeds galloping is disadvantageous, probably because it increases fluctuations of gravitational kinetic energy. A trotting quadruped is like two bipeds running one behind the other. A galloping one is more like two kangaroos hopping one behind the other, and out of phase with each other. A hopping animal is unsupported for a larger fraction of its strides than a runner, so its gravitational potential energy fluctuates more for the same stride length (Alexander, 1977). Gravitational potential energy changes are relatively more important at low speeds, and internal kinetic energy changes at high speeds, so we can expect there to be a critical speed at which the balance of advantage shifts from trotting to galloping. There is scope for a mathematical model that would explore this point more rigorously.

#### 4. Springs in swimming and flight

In principle, springs can save energy in any movement in which parts of the body are repeat-

edly accelerated and decelerated. For example, swimming whales beat their tails up and down, swimming fish beat their tails from side to side and flying birds beat their wings. Alexander (1997) presented a general model of movements like these, using the physiological information shown in Fig. 1 to estimate metabolic energy costs. The model predicted optimal combinations of muscle speed ( $v_{\max}$ ) and tendon elasticity, which would minimise the metabolic cost.

The swimming muscles of dolphins insert through a very large number of long, slender tendons. Bennett et al. (1987) measured the elastic properties of these tendons and considered whether they might serve as energy-saving springs. We concluded that they were more extensible than would have been optimal. However, we failed to take proper account in our calculations of unsteady hydrodynamic effects. An improved calculation by Blickhan and Cheng (1994) led to the conclusion that the extensibilities of the tendons were close to the values that would eliminate the need for the muscles to do negative work to decelerate the tail at the end of each beat. However, according to the theory of Alexander (1997) the tendons should be rather less extensible than this, to minimise metabolic costs.

The swimming muscles of tunas also insert through long tendons. Their possible role as energy-saving springs does not seem to have been investigated. However, there is a little evidence suggesting that it may not be very important. Shadwick et al. (1999) used sonomicrometry to record the length changes of muscle fascicles in swimming skipjack (*Katsuwonus*). They found that muscle shortening on each side of the body coincides precisely in time with bending of the body towards that side. However, the inertial forces on the tail are greatest when it is at the extremes of its side to side movements. If these forces stretched the tendons much, the length changes of the muscle fascicles would be out of phase with the side to side movements of the tail.

It is possible that the tendons of the flight muscles of birds may be useful energy-saving springs, but the possibility does not seem to have been investigated. For example, the kinetic energy fluctuations of the wings of hovering hummingbirds are four times the aerodynamic work, implying substantial scope for savings (Wells, 1993; see also Alexander, 1997).

## 5. Springs for jumping

I have already referred to the role of tendon elasticity in running jumps by dogs (Alexander, 1974). In this section I concentrate on standing jumps.

The higher the take off speed of a jumping animal, the further it can jump. To take off at speed  $v$ , an animal of mass  $m$  must do work  $1/2mv^2$ . If the extended length of its legs is  $s$ , it must accelerate from rest to  $v$  over a distance  $s$ . If its acceleration is constant, its mean speed over this distance will be  $v/2$ , and leg extension must be completed in time  $2s/v$ . Thus take off requires a power output of  $mv^3/4s$ . If the leg muscles cannot supply this power, the animal cannot make the jump.

The faster a muscle shortens, the less force it can exert (Fig. 1a). Its power output (the product of force and shortening speed) is greatest when it is shortening at a moderate speed, typically approximately  $0.3v_{\max}$  for vertebrate skeletal muscles (Woledge et al., 1985). Stretched tendons can recoil elastically much faster than any muscle can shorten. The work done in the recoil is almost independent of the shortening speeds over a wide range of speeds (Ker, 1981). Consequently, tendons can function as power amplifiers, like catapults. A catapult that has been stretched slowly can recoil rapidly. The work returned in the recoil cannot exceed the work done to stretch the catapult, but it is done in a shorter time so the power is greater. Bennet-Clark and Lucey (1967) drew our attention to the potential of catapults as aids to jumping, in their classic paper on fleas. The flea's catapult has a catch mechanism that locks the legs in a flexed position until the muscle that supplies the energy for the jump has completed its contraction. No equivalent catch has been found in vertebrate jumpers, but elastic tendons may nevertheless serve as power amplifiers.

A simple mathematical model illustrates how this can happen (Alexander, 1995). The model represents an athlete or animal that jumps by extending a pair of legs. Its muscles have the physiological properties shown in Fig. 1a, and their tendons function as springs. I simulated several possible styles of jumping. In a catapult jump, a catch prevented leg extension until the muscle had stretched the tendon as much as it could, by exerting its maximum isometric force. In a squat jump there was no catch. When the

muscles were activated, they started shortening, stretching the tendons and building up force. At the same time, the legs started extending. In the early stages of takeoff, strain energy was stored as the tendons stretched. In the later stages, as the muscles shortened faster the force they could exert fell, and the tendons returned energy by elastic recoil. Take off speed was lower than in a catapult jump because the muscles shortened throughout take off, so were unable to develop their full isometric force. However, it was higher than in simulations in which the tendons were inextensible. Tendon elasticity made longer or higher jumps possible.

Another set of simulations were of counter-movement jumps such as human athletes make. The jumper starts with the legs straight. The body is allowed to fall passively, bending the legs. At an appropriate moment, the extensor muscles are activated, halting the fall and re-extending the legs. This strategy makes it possible for tendons to be stretched without muscle shortening, enabling the muscles to develop larger forces. Indeed, the muscles may be stretched at the bottom of the fall and so may develop greater-than-isometric forces (Fig. 1a). The simulations showed that for large mammals such as our selves, counter-movement jumps could be as effective as catapult jumps would be expected to be.

Bushbabies (*Galago*) make spectacular jumps. Aerts (1998) analysed high speed video and a force plate record of a 0.25-kg bushbaby taking off for a jump to a height of 1.74 m, and calculated the power output of the muscles. He assumed that only the leg muscles (25% of body mass) were involved, but I will make the more conservative assumption that all the muscle in the body (36% of body mass; Grand, 1977) may have played a part. With that assumption, the peak power output calculated by Aerts, just before the animal's feet left the ground, was 2200 W/kg muscle. The highest instantaneous power output known to me, measured in experiments with excised muscle fibre bundles, is approximately 1000 W/kg muscle (Askew and Marsh, 2001, on quail wing muscle). Thus, it seems likely that, in the bushbaby's jump, power was amplified by tendon elasticity.

Peplowski and Marsh (1997) presented a similar argument for a 1.44-m long jump by a small frog (*Osteopilus*). Their argument was more complete than that of Aerts in that they had measurements of the properties of one of the frog's leg muscles.

They found that the jump required a power output of approximately 800 W/kg muscle (averaged over the period of leg extension), implying a peak power output of approximately 1600 W/kg. However, in their experiments with the excised muscle they found that it was capable of only 240 W/kg. They concluded that a power amplifier must be involved. This research left a question unanswered. If the *mean* power output during leg extension was much greater than the maximum power available from the muscles, the muscles must have started doing work well before the legs started extending. That implies a catapult jump rather than a squat jump, but the lock that the catapult would need has not been identified. Either a lock remains to be discovered, or the muscles of the intact animal can generate more power than was obtained in the experiment with the excised muscle.

## 6. Low stress tendons

Large stresses act in tendons that are important as energy-saving springs. For example, as already noted, peak stresses of 40–50 MPa act in some of the distal leg tendons of galloping horses (Biewener, 1998). If the tendons were thicker, the stresses in them would be less, so they would stretch less and store less strain energy. However, high stresses are not essential for effective energy saving. If the muscles had smaller moment arms at the joints, larger muscle forces would be required to exert the same moments at the joints, so the tendons would not have to stretch so much to store the same energy. This would not require any change in muscle mass or peak muscle stress, if the muscle were composed of a larger number of shorter fascicles. Short fascicles with a short moment arm could produce the same angular movement at the joint as long fascicles with a long moment arm.

The stresses that can act in tendons are limited by the strengths of their muscles. Ker et al. (1988) used measurements of the cross-sectional areas of tendons, and of the physiological cross sectional areas of their muscles, to calculate the stresses that would act in the tendons if the muscles exerted their maximum isometric stress, which we assumed to be 300 kPa (Wells, 1965). The calculated tendon stresses were relatively high, most commonly 40–50 MPa, for tendons that are important as energy-saving springs. However, they were very much less, generally 10–15 MPa, for other tendons. Ker

(2002) discusses the differences between these two groups of tendons.

Tendons that experience only low stresses do not stretch very much in use, but their elastic extension may nevertheless be important for muscle function. Rack and Ross (1984) studied the long flexor tendon of the human thumb, which experiences a stress of only 11 MPa when its muscle exerts 300 kPa (Cutts et al., 1991). The muscle, contracting isometrically, is capable of stretching the tendon by 1.4 mm, enough to allow the distal joint of the thumb to rotate through 11° (Alexander, 1988). Rack and Ross (1984) anaesthetised the other muscles of a subject's thumb, and tested the reflex responses of the long flexor muscle to forced bending of the thumb. Their results showed that the elastic properties of the tendon must make the muscle much less able to hold the thumb in position against a fluctuating force, than if the tendon were inextensible. However, they make it easier to maintain a constant force on a vibrating surface.

The conclusion, that tendon elasticity makes position control more difficult and force control easier, applies not only to this thumb muscle, but to muscles generally. For some tasks such as writing or steering a car, position control is crucial. For others, such as picking up empty eggshells and similar delicate objects, force control is more important. The effect of tendon elasticity on position control is particularly severe when forces are low, because the tangent Young's modulus of tendon is low at low stresses. It is sometimes possible to alleviate this problem by activating antagonistic muscles simultaneously, so that higher stresses act in the tendons although the force exerted on the environment remains low.

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