Research

The anatomical arrangement of muscle and tendon enhances limb versatility and locomotor performance

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The arrangement of muscles and tendons has been studied in detail by anatomists, surgeons and bio-mechanists for over a century, and the energetics and mechanics of muscle contraction for almost as long. Investigation of how muscles function during locomotion and the relative length change in muscle fibres and the associated elastic tendon has, however, been more challenging. In recent years, novel *in vivo* measurement methods such as ultrasound and sonomicrometry have contributed to our understanding of the dynamics of the muscle tendon unit during locomotion. Here, we examine both published and new data to explore how muscles are arranged to deliver the wide repertoire of locomotor function and the trade-offs between performance and economy that result.

Keywords: muscle; tendon; locomotion; biomechanics

1. INTRODUCTION

Consider a cat stalking a mouse, it will creep slowly forward, stand still, pounce and land, all with apparently great aptitude. The nervous system and its control is undoubtedly complex and sophisticated, but the final motor or force producer for these activities is the cross bridge, which has relatively fixed contractile properties and once arranged into fibrils has defined relationships relative to length and velocity. The properties of the cross bridge and how it is arranged into sarcomeres is covered in detail elsewhere and here we focus on how nature has arranged muscle from the level of the sarcomere up to the whole body. We consider how the locomotor system delivers the range of activities from performing mechanical work by shortening, where that shortening may be slow and finely controlled to a powerful movement where high velocities and forces are required. Furthermore, muscles need to be able to absorb energy when a segment or the body must be decelerated. While there is redundancy in the musculoskeletal system with several muscles crossing most joints and a range of muscle fibre types, many individual muscles need to contribute to all of these roles. The muscles therefore need to be versatile to meet the demands of a range of activities. The obvious pressures in terms of system configuration are to minimize the energy used by muscle (though in certain circumstances the waste heat is useful for an animal) and to minimize the volume of muscle an animal requires—as that mass must be carried around and incurs a cost to grow and maintain.

2. MUSCLE ARCHITECTURAL DESIGN

A classical anatomical observation is that muscles vary in architecture and that this architecture reflects their function. Figure 1a shows two examples of one particular aspect of muscle architecture. Muscle A is a longitudinal (parallel) muscle where the fibres run along the length and in the direction of force transmission of the muscle. Muscle B is a short-fibred bipennate muscle where the fibres are shorter and packed in at an angle that does not align along the main axis of force transmission. Both muscle architectures have the same volume and hence contain the same number of cross bridges (assuming that the tendinous volume is negligible).

If we assume that all sarcomeres have the same stress–strain properties on average [2], then the stress will also be the same in both types. Force will therefore scale as a direct function of the number of fibrils in parallel, which approximates to the cross-sectional area of sarcomeres corrected for fibre angle [3,4]. This value is commonly referred to as the physiological cross-sectional area (PCSA) of the muscle and is calculated as the ratio of muscle volume to muscle fibre length [5]. Therefore muscle B, which has shorter fibres but a larger PCSA, has a larger capacity for force.

The capacity for length change scales as a direct function of the number of sarcomeres in series, i.e. muscle fibre length. Maximum fibre strain will be the same in both muscles, but because the fibres are longer in muscle A, it will have a greater capacity for length change. If we assume that each sarcomere has

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(a) muscle A—parallel fibres

muscle B—pennate fibres

(b)

muscle B

muscle A

force

length

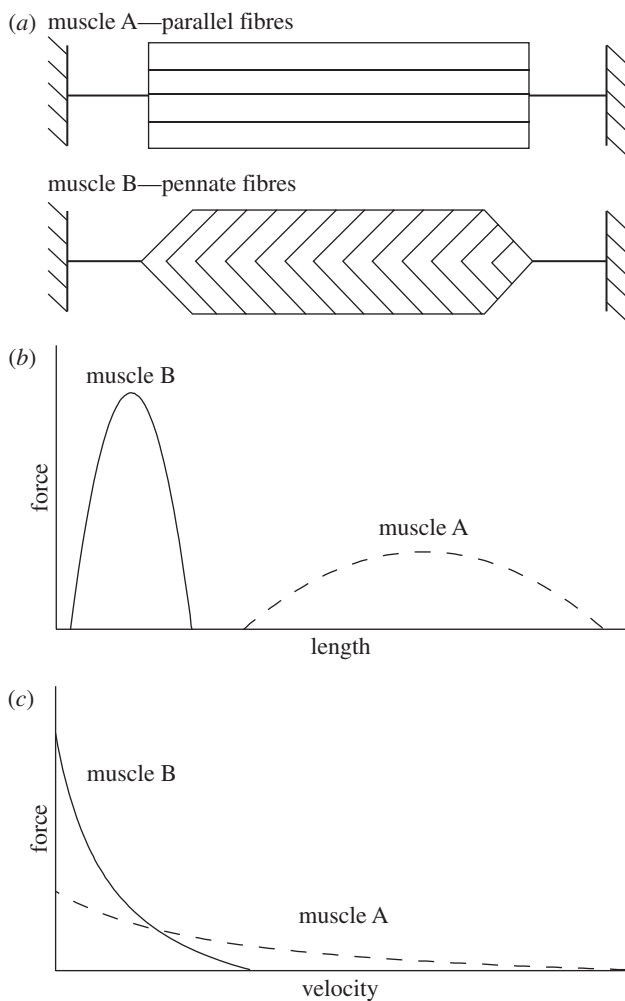(c)

muscle B

muscle A

force

velocity

Figure 1. The anatomical extremes of muscle architecture with appropriate force–length and force–velocity plots. (Based on plots in [1].)

the same force–velocity property, then peak strain rate and the strain rate for generating peak power will be the same in both muscle forms. Peak power will consequently be the same for both muscles as both contain the same number of cross bridges; however, muscle A has longer fascicles so muscle A can contract more rapidly and will generate peak power at a higher velocity. Therefore, muscle A can shorten quickly while muscle B will have a higher peak force. It would appear that muscle A is appropriate for eliciting rapid movement and that muscle B can generate near isometric force economically as a smaller volume of muscle needs to be activated to elicit a given force. This is discussed further in a number of the cited references including numerous texts [1,6,7]. Real animals have a range of muscle architecture types in part, presumably, for this functional specialization. Figure 2a shows the distribution of fascicle length (FL) and PCSA/maximum isometric force for different hindlimb muscles in the cheetah [9].

One of the primary tasks of a muscle is to shorten or lengthen while generating tension and hence perform (or absorb) mechanical work. The maximum rate of producing work (peak power) will be developed at around one-third of maximum contraction velocity and peak efficiency of performing mechanical work at

a slightly lower velocity [3]. The exact value is somewhat dependent on the shape of the power–velocity curve. It would therefore appear sensible that a muscle has a PSCA sufficient to generate force at appropriate velocities and sufficiently long fibres to operate at a strain rate around or below that corresponding to peak economy or peak power. In muscles, which must both generate high force and perform work, like the many limb extensor muscles that contribute to both resisting gravity and acceleration, there is a tradeoff that defines the optimum muscle fibre length. Short fibres would lessen the costs to generate the high forces needed, yet long fibres reduce the sarcomere shortening velocity for a given shortening speed and hence reduce the costs associated with performing work. A third constraint is that large muscle volumes increase limb inertia and body mass. In essence, the architecture and anatomy should match the required sarcomere velocity to that at which efficiency is greatest.

Most muscles cross joints and can elicit or resist movement, so the change in joint angle that occurs as a result of a muscle shortening or lengthening is important for it to fulfil its function. A long-fibred muscle with a short moment arm will produce a large angular displacement and a high angular velocity alongside a small torque and initial acceleration [10]. By contrast, a muscle with short fibres and long moment arms will result in large muscle forces (and hence joint torques) and less capacity for limb movement. We present data for the hindlimb of a cheetah in figure 2b,c, which shows the wide range of values observed in nature [8]. The relationship between sarcomere velocity and joint angular velocity will be modulated by stretching and recoiling of the series tendon (below).

3. MUSCLE–TENDON ELASTICITY
Muscles also contain elastic elements that can further enhance muscle versatility. The arrangement of this elasticity is classically represented using a three-component Hill muscle model [11–13], which comprises a contractile element (CE, muscle fibres), a series elastic element (SEE, elastic tendon/aponeurosis at either end of the muscle) and an elastic element in parallel with the contractile component (PEE, titin, perimysium). Muscle fibres also have inherent elasticity (what is represented within the SEE in the classical Hill model as Hill worked on fibre bundles [14–16]). Here, we focus on larger animals where the compliance of the tendon and aponeurosis will be much greater than that of the fascicles [13] and the fascicles can be approximated to be only contractile in nature.

There is a wide range of relative muscle and tendon properties observed in the mammalian body. One way of normalizing such data is to calculate how much the muscle fibres can shorten (taken as a relatively high 40% of resting length for this chapter) and compare that with how much the tendon would stretch if subjected to the maximum isometric force of the muscle. This can be determined by measuring the muscle volume, fibre length (and hence PCSA), tendon length and average tendon cross-sectional area (usually derived from tendon length and weight) and assuming constant material properties of the muscle and tendon
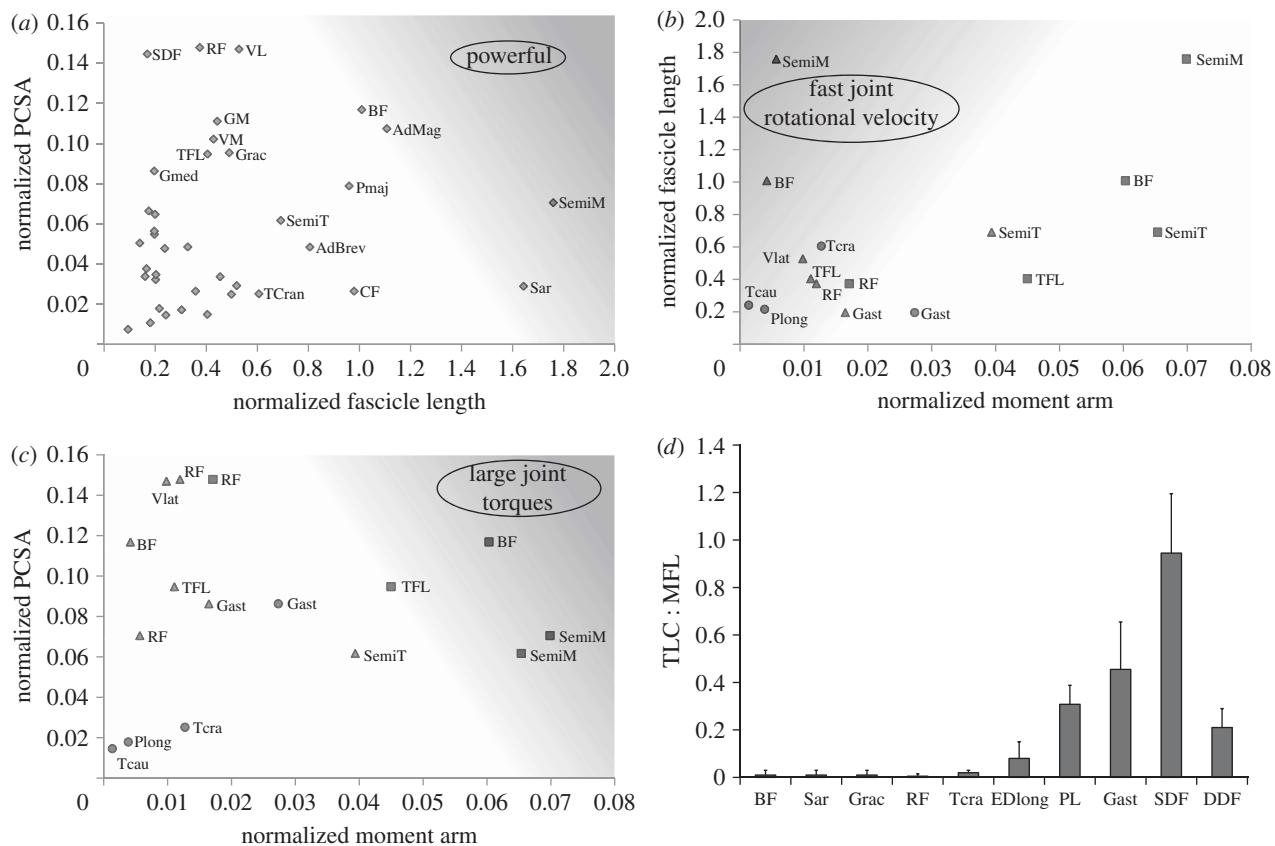
Figure 2. (a) Physiological cross-sectional area (PCSA) against fascicle length (FL) to illustrate the balance between force, range of motion/velocity and power output for different muscles in the cheetah hind limb. (b) Moment arm against FL to illustrate the muscle's ability to rotate the joint rapidly. (c) Moment arm against PCSA to illustrate the muscle's ability to produce joint moment. Darker shaded areas of the graphs represent increased (a) power output, (b) fast joint rotational velocity and (c) large joint torques. In (b,c) muscles acting at the hip are represented by squares, those acting at the stifle by circles and those acting at the tarsus by triangles. Some muscles cross two joints and appear twice. Muscle name abbreviations are given in the original reference. (d) Ratio of tendon elongation (estimated length change elicited by muscle maximum isometric force) to muscle FL (TLC : MFL) for selected pelvic limb tendons in the hare (*Lepus europeus*). Architecture was scaled isometrically to body mass and, because the limb bone lengths did not scale with body mass, the moment arms were scaled to segment length (femur for hip and stifle and tibia length for the tarsus). Figure (a–c) from Hudson *et al.* [8] and (d) reproduced from Williams *et al.* [9].

(e.g. maximum muscle stress of 0.3 MPa and a tendon elastic modulus of 1 GPa) [3,17,18]. This does not take into account aponeurosis elongation, and arguments can be made as to why the material properties should be larger or smaller in different muscles, but the general principles will not change. Figure 2d shows such a plot for the muscles of a hare's hindlimb and demonstrates that, for instance, the superficial digital flexor (SDF) and gastrocnemius (G) muscles are predominantly elastic in nature. In these muscles, the force length and velocity will largely depend on the external loads applied to the muscle while the force length velocity properties of say biceps femoris (BF) and rectus femoris (RF) are inherently more controllable through changes in muscle activation. This trade-off is discussed in greater detail in Biewener & Roberts [10].

4. MUSCLE WORK OUTPUT AND ITS RELATION TO TENDON STIFFNESS

For a muscle to perform work, it needs to shorten against an external force. During tasks such as locomotion, muscles perform cyclical contractions where they are activated to generate tension. This tension is applied across a joint to generate a torque, which has a subsequent effect on joint motion and hence a change in muscle length. The work performed (or absorbed) by a muscle in a single cyclical contraction is the area between the lengthening and shortening portions of the length versus force curve (or joint torque— moment curve for angular movements), commonly referred to as a work loop [19,20]. Because it takes a finite amount of time for a muscle to both activate and deactivate owing to the excitation–contraction coupling process, the timing of muscle activation relative to its length change is important in determining how much work is performed. If we consider the length changes of a muscle as being sinusoidal, then to maximize work per cycle, a muscle must typically be activated just prior to the shortening phase and stay activated until just before the muscle begins to lengthen to prevent any work being absorbed [21,22].

Owing to the force–velocity properties of muscle (which predict that force declines with increasing shortening velocity), the peak power output achievable by a muscle is limited by the cyclical length change. As such, to maximize power output with increasing cycle frequency, it is necessary to reduce the amplitude of the length change to maintain optimum shortening velocity [23]. At increasingly higher frequencies of

cyclical contraction, the ability to generate power also depends on the rate at which muscles can be activated and deactivated.

Addition of an elastic element in series with the muscle (analogous to adding a spring to the system) has a substantial benefit for two possible reasons: (i) some of the length change can occur in the spring rather than in the muscle, reducing the need for positive and negative work of the muscle fibres themselves [24,25]; (ii) the muscle can activate earlier when the muscle–tendon unit (MTU) is still lengthening, resulting in a high force before the muscle starts to shorten [26,27]. This increases the area of the work loop and hence the work done in each stroke [28]. Furthermore, the CE can shorten more slowly than the MTU as the tendon recoils, meaning that the muscle fibres can potentially act at velocities where they are more powerful and more efficient than if there were no SEE [29,30].

We have demonstrated experimentally [22] that both power output and efficiency can be enhanced with a compliant tendon during sinusoidal contractions, providing that sufficient amplitude of stretch is applied to the MTU and that the muscles are activated appropriately. While the muscle fibres are required to perform all of the net mechanical work, uncoupling the muscle fibre length changes from the MTU allows the muscle to act at lengths and velocities which maximize power output of the muscle throughout the cycle and this can be achieved with shorter periods of activation. While these experiments are highly constrained by the imposed length change trajectory (sinusoidal), the general principle that tendon compliance can be of benefit in enhancing muscles' power output and efficiency during stretch–shorten cycles is evident.

5. MODELLING THE INFLUENCE OF MUSCLE AND TENDON DESIGN ON POWER AND EFFICIENCY

It is possible to explore in more detail the capacity of tendons to maximize average muscle power output per cycle using a Hill-type muscle model [28,31,32]. Such models allow us to vary the parameters of the cyclical contraction (e.g. the amplitude of length change, timing and duration of activation, cycle frequency) as well as the muscle properties themselves (e.g. maximum shortening speed, optimum length, rate of activation and series elastic compliance) and examine how muscle performance varies under different conditions. We have previously shown using such a model that a suitably adjusted SEE compliance can allow muscles to operate with near-maximum efficiency while generating maximum power under certain conditions. This is not possible in muscles with stiff tendons [21].

Using the same model as reported in Lichtwark & Wilson [28,31], here we will explore how changing the frequency of contraction might theoretically influence muscle power output in muscles with varying SEE compliance. We set the model force–length and force–velocity properties to represent typical mixed fibre-type mammalian muscle (e.g. length range of 40% of resting, maximum shortening velocity of 8 length s^{-1}, activation rise and fall time of approx. 0.1 s), but varied the relative series elastic compliance to explore the influence on

muscle power output at a range of cycle frequencies. For each frequency and series elastic compliance condition, we used an optimization routine to determine the length change amplitude, timing of activation and duration of activation, which maximized the average MTU power over a single cycle.

The results from this simulation are shown in figure 3. In this simulation, SEE compliance is described as the length change of the SEE relative to the FL when maximum isometric force is applied, which is similar to the concept of fixed-end compliance [30]. It is apparent that increasing tendon compliance can have a positive influence on muscle power output at frequencies below 3 Hz provided that optimal conditions are used. Examination of the work loops, which achieve maximum power in a stiff and compliant tendon (figure 3b,c), highlights the mechanism by which tendon compliance can achieve more work. Using conditions reflecting a stiff tendon, the force rises rapidly just prior to muscle shortening and then drops to a value of approximately 30 per cent of the maximum isometric force for the majority of the shortening phase, before the muscle is deactivated. In contrast, the compliant tendon scenario requires a larger amplitude of MTU length change to achieve maximum power and requires a period of apparent negative work (active lengthening). During this period of negative work (figure 3c), the muscle CE is actually performing positive mechanical work, which acts to store energy in the elongating series elastic element. The force is then able to stay high through most of shortening, which generates considerably more average power than with conditions representing a stiff tendon.

6. MUSCLE AND TENDON INTERACTIONS IN THE HUMAN TRICEPS SURAE

So how does tendon elasticity influence the function of muscle during movements like locomotion? Some elasticity would appear beneficial but too much is likely to be detrimental. For instance, if a muscle has to go through most of its length change to stretch the tendon before peak force is achieved then controlling position, movement and timing of work release would become challenging and difficult to modulate. It is useful to review the dynamics of what is probably the most studied muscle tendon system—the human triceps surae and Achilles tendon. This muscle group consists of muscle fibres across three muscle groups, which range in length from 30 to 70 mm. The MTUs span the length of the tibia (approx. 400 mm in a full grown man) and hence the elastic connective tissue (tendon and aponeurosis) comprises the majority of each muscle's length. Tendons can stretch by up to 10 per cent, so this gives the tendon a large potential for stretch relative to the length range of the muscle fibres. While the material properties of the Achilles tendon are within the typical range for tendinous material [33,34], the Achilles tendon does seem to have a large capacity for high strains, with values above 8–10% reported during high stress activities [29,33,35,36]. This is normally in the realm of strains which cause tendon failure; however, the unusual structure of the Achilles tendon (fanned and
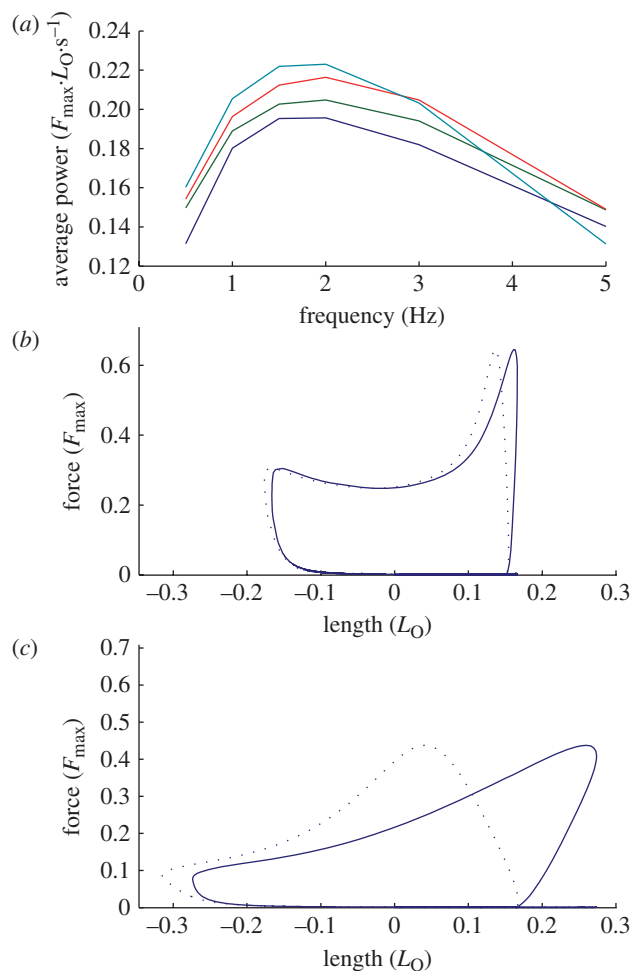
Figure 3. (*a*) Maximum average power predicted by a Hill-type muscle model with different values of relative SEE compliance (indicated by different colours) as a function of frequency of sinusoidal length changes. The force–length and force–velocity properties of the muscle are chosen to be similar to that of a mixed fibre type mammalian muscle. The power values used here are the maximum found when amplitude of length change, activation duration and activation timing were optimized to find the maximum work per cycle (violet line, 4%; green line, 10%; red line, 20%; light blue line, 50%). (*b*) Force output as a function of muscle–tendon unit (MTU, solid line) and contractile element length (CE, dotted line) for a single cycle with a relatively stiff tendon (compliance, 4%; frequency, 2 Hz). The area under these curves is the total work performed by the muscle. (*c*) Force output as a function of MTU and CE length for a single cycle with a relatively compliant tendon (compliance, 50%; frequency, 2 Hz). The CE shortens while the MTU lengthens during force development because of stretch of the tendon. The larger amplitude of length change able to be achieved as a result of the stretch of the tendon enabled a greater power output to be achieved in compliant condition when compared with the stiff condition.

Figure 4. (*a–c*) Predicted muscle FL (*a*), muscle fascicle velocity (*b*) and muscle activation level during the stance phase of running for different ratios of tendon stiffness relative to the approximate measured Achilles tendon stiffness ($\sim$180 N mm^{-1})—0.5 (dashed line), 1 (solid line), 2 (dashed-dotted line), 4 (dotted line). A comparison with the experimental measures (grey area) is also shown. (*d*) Predicted muscle efficiency during the stance phase of running as a function of Achilles tendon stiffness and medial gastrocnemius muscle FL. The predictions assume that the MTU length changes and force generated by the muscle remain constant across different tendon stiffness values. The predicted FL and tendon compliance combination that maximize efficiency (approx. 38%) is indicated by the X. White regions outside of the contours are combinations where the muscle is incapable of generating the required power without a greater muscle volume. Figures adapted from Lichtwark & Wilson [38,39].

spiralled architecturally) may help to prevent this from occurring as the arrangement could mean that tendon fascicle strain is lower than tendon strain.

During hopping, the gastrocnemius MTU undergoes a length change of about 20 mm (approx. 8%), the majority of which occurs in the tendon itself [33]. This is achieved by the Achilles tendon having a relatively low safety margin and the long human foot enabling the ground reaction force (GRF) to have a substantial moment at the ankle joint. Typically,
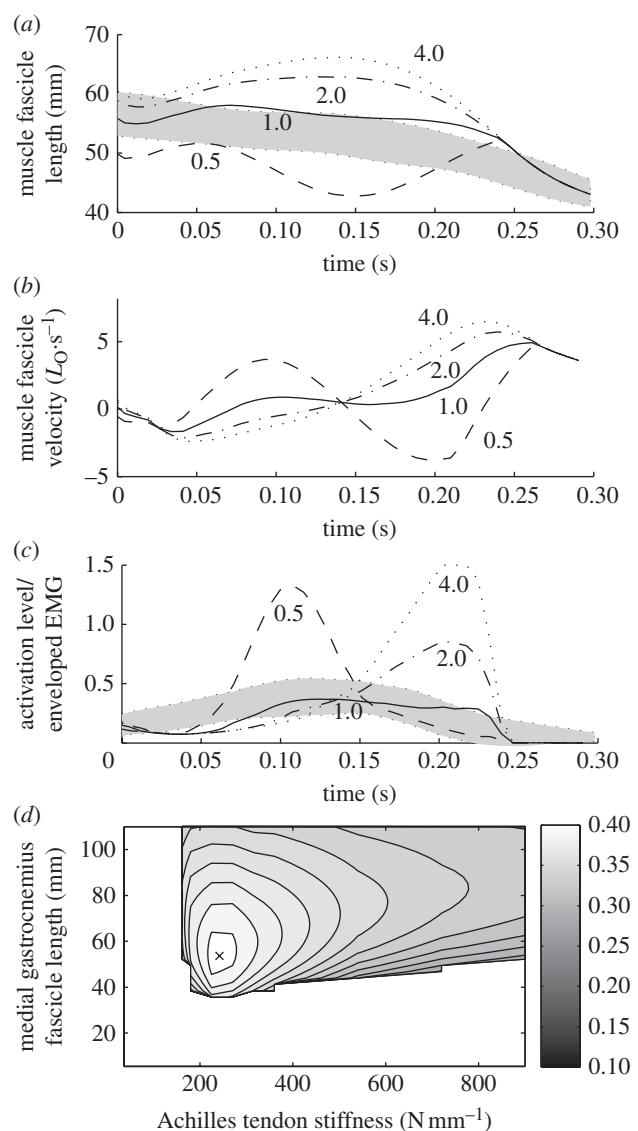
tendon force is about five times the body weight (BW) during hopping and about two to three times the BW during running [37].

In running, the body moves over the foot and the gradual plantar flexion of the ankle moves the tendon insertion distally, lengthening the MTU throughout stance. In late stance, the heel leaves the ground allowing the MTU to shorten. The gastrocnemius muscle fibres however shorten slowly throughout stance so
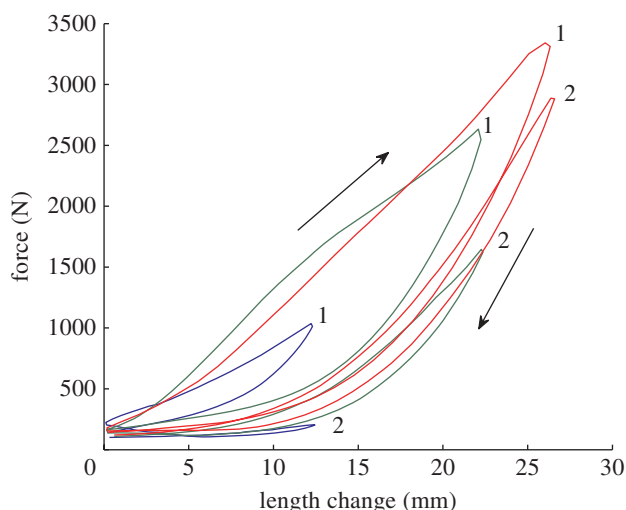
Figure 5. Biceps brachii force versus extension during *ex vivo* experiments on excised pony muscles at three different excursion lengths at a frequency of 1 Hz. At each muscle excursion, the muscle was stretched both actively (1) and passively (2). Violet line, 12 mm; green line, 22 mm; red line, 26 mm. Figure adapted from Lichtwark *et al.* [44].

that the fibre velocity is around 3 lengths s^{-1}, while MTU velocity peaks at around 10 lengths s^{-1}—around fibre maximum shortening velocity [29]. It would appear that a stiffer tendon would be less susceptible to overload injury but what would be the effect on MTU dynamics? The outcome of exploring this question is presented in figure 4*a–c*, which is adapted from Lichtwark & Wilson [38].

Increased tendon stiffness requires the gastrocnemius muscle fascicles to follow a trajectory much more similar to the MTU during running. This therefore requires higher shortening velocities after heel off, which in turn requires an increased volume of muscle to be activated, primarily owing to moving to the right on the force–velocity relationship. This in turn increases the metabolic energy required by the muscle with a stiff tendon. It is also apparent that decreasing the tendon stiffness to values well below that of the Achilles tendon would not be beneficial because the muscle fascicles would have to shorten at high speeds early in the stance to stretch the tendon to an appropriate length to permit the required force output. Hence, it seems that the tendon stiffness is tuned to optimize fibre shortening velocity and minimize muscle activation. Using an energetic model [31], we have also demonstrated that the tendon stiffness is appropriate to maximize muscle efficiency [38].

It is apparent that if tendon stiffness was different, it would be possible for this to be compensated by a change in fibre length. To further investigate this, we optimized both gastrocnemius fibre length and tendon stiffness to achieve maximum economy, assuming that the muscle volume is held constant. Our energetic model predicts optimal muscle FLs and tendon stiffness values for walking and running (figure 4*d*) that are very close to those measured in humans [39]. This therefore suggests that muscle and tendon design are indeed appropriate to minimize the energy consumption and that tendon compliance is central to this mechanism. There is an interplay between MTU anatomy, limb

anatomy and gait, but the examination of the natural world and gait dynamics suggests that locomotion and limb anatomy are much more constrained than what one might imagine—consider for example, the relationship of size and effective mechanical advantage (EMA) discussed below [40] and also the relative segment lengths between different cursorial animals, especially the larger ones.

An additional question is how tendons of different stiffness could be accommodated within the limb if the material properties of tendon are relatively consistent? A tendon that has to withstand the same force but only have half the stiffness must be the same thickness and twice the length. To accommodate this added length within a segment, the muscle fibres would need to be shorter (no major effect feasible in gastrocnemius as muscle fibres are a very small fraction of segment length) or the segment be longer. Alternatively, such a change could be achieved by changing MTU moment arm or EMA, although that would result in a higher tendon force and therefore require a higher tendon CSA and therefore a longer tendon. One could imagine a system where either tendon or GRF moment arm (i.e. EMA) changes through stance in a manner that is advantageous for tendon mechanics and energy storage, effectively a cam, but this does not seem to be common, at least in the literature to date, though the horse biceps has some of these features.

There is some specialization in certain muscles, especially in the distal limb, where short-fibred muscles exist that have low mass-specific work outputs [41,42]. Even in inclined locomotion work by these distal muscles seems low [25,29]. These distal muscles usually cross more than one joint and they will function as series elasticity altering the relationship between proximal muscle length change and the distance between the foot and the hip/centre of mass (COM). It may therefore be incorrect to consider the large proximal muscles as having minimal SEE. The role of the muscle component of these distal muscles may therefore not be to directly perform work but to modulate the power production of proximal muscles by functioning as a tuneable series elasticity or 'tendon'. The role of pennate muscles as tuneable springs is discussed further below.

7. TUNING ELASTIC ENERGY RETURN
While many animals use elastic strain energy to minimize the muscular work of locomotion, some animals have developed highly specialized muscle–tendon design, whereby the tendons are responsible for much of the positive mechanical work. Many large terrestrial animals, including horse, camels and kangaroos, have developed muscles with short muscle fibres and long tendons, ideally suited for storage and return of elastic energy. Such muscle design may reduce muscle metabolic work; however, it may also hinder versatility of the muscle. These muscles are often required to absorb energy, which is stored in the tendon, to modulate subsequent movement. Therefore, it is necessary for the muscle to be able to control the amount of energy that is returned to the mechanical system.

When energy is stored in a spring, it is returned at a rate dependent on the inertia that is being accelerated. Larger masses are accelerated more gradually and the spring therefore takes longer to reach its slack length and zero strain energy. Changing the system dynamics therefore requires the capacity to change the rate of energy return by the spring—i.e. the effective stiffness of the spring during unloading or the shape of the unloading curve. Simple tendon returns about 93 per cent of the energy stored in it [43], but the energy return for an MTU can be considerably lower (figure 5). If the muscle fibres in series with an SEE are allowed to lengthen while the SEE spring is shortening, then they will absorb energy from the spring and the inertial load will be accelerated as if connected to a less stiff spring—i.e. a more rapid drop in force through time or displacement. This control can be achieved using a relatively small volume of muscle tissue as muscle stresses can be high, thus eccentric lengthening absorbs a very high power.

To put some numbers on this, consider 1 kg of muscle (volume approx. 900 ml) with length of 10 cm (PCSA, 90 cm^2). If we assume a high peak isometric stress of 0.3 MPa, then this muscle will be able to generate a maximum isometric force (F_{MAX}) of approximately 2700 N. Assume that it will contract by 30 per cent of resting length (0.03 m) at a force that is one-third of F_{MAX} throughout the length change (900 N). The work done would therefore be 27 J. In lengthening, with the same length change but a force that is 1.5 F_{MAX}, the 1 kg muscle could absorb 4.5 times as much energy, or 121 J [6].

By comparison, tendon can store a remarkable energy density owing to the high strains it can withstand and its high elastic modulus. The energy stored in a perfect elastic tissue or elastic potential energy per unit volume is:

$$\frac{\text{elastic modulus} \times \text{strain}^2}{2}.$$

Taking 1 GPa for the elastic modulus of tendon and a strain of 0.1 gives a value of 5 MJ m^{-3}.

For spring steel, the elastic modulus would be 207 GPa and the failure stress (strength) 2070 MPa. A helical steel spring would have a safety or fatigue factor (SF) of about 2.5, and a form coefficient (CF) that captures how uniformly stress is applied to the spring. This would be 1 for a rod in tension 0.9 for a tube in torsion but only about 0.36 for a helical spring [45].

Using these figures in a formula for energy stored (E) in a helical steel tension spring:

$$E = \frac{CF \times (\text{strength/SF})^2}{2 \times \text{elastic modulus}}$$
$$= \frac{0.36 \times ((2070 \times 10^6)/2.5)^2}{2 \times 207 \times 10^9} = 600 \text{ kJ m}^{-3}.$$

This is approximately 1/8th of the energy stored in the same volume of tendon material. Considerably more than half of the volume of a helical spring is the space between coils and the core, so the energy density of the complete spring envelope will be between 30 and 300 kJ m^{-3} [45].

The big difference in energy stored is because the steel can only safely deform to a strain of about 0.003 compared with the 0.1 of tendon compensating for the high stress steel can withstand. An effective energy-storing material should withstand high stress and reach a high strain.

Taking into account that tendon has a density of about 1100 kg m^{-3} and steel 7850 kg m^{-3}, strained tendon stores about 60 times as much energy per unit mass than a helical steel spring.

Some synthetic polymer fibres composed of materials like carbon fibre, aramid and glass have much higher (10–30 times) energy densities than steel because they have higher failure stress and strain but they can be difficult to fabricate into an effective spring and can have significantly lower energy returns than tendon [46]. To conclude, a strained tendon is a remarkably energy-dense spring structure.

In more familiar terms, consider a 10 cm long tendon of cross-sectional area 1 cm^2 (10^{-4} m^2) with a stress of 100 MPa and an elastic modulus of 1 GPa. It would have elongated by 10 per cent (0.01 m) with an external force of 10 kN. The energy stored will be $0.5 \times 0.01 \times 10\,000 = 50$ J in 10 cm^3 or 11 g of tendon or 4500 J kg^{-1}. Using the above figures, approximately 1 kg of muscle tissue is therefore required to completely absorb the energy from 37 g of highly strained tendon.

The three tendons that resist metacarpo-phalangeal joint extension in the horse have a total length of about 2 m and each has a cross section of between 1 and 2 cm^2. It is estimated that they store about 1000 J of elastic strain energy in each leg in each stance of gallop [47]. From the above calculation, around 5 kg of muscle would be required to dissipate that energy completely—considerably more than what exists in those MTUs. We have speculated previously that the digital flexor muscles serve as vibration dampers [47], absorbing a few joules per cycle of vibration, and it would appear that damping is either also performed by other muscles within the limb or there is only limited capacity to control energy return from these tendons.

While it is apparently wasteful to dissipate the mechanical energy stored in the tendon, eccentric muscle contraction provides a means of controlling the dynamics of the tendon spring and the attached inertial loads. This may be worthwhile if energy can be accumulated more cheaply or delivered by a smaller muscle mass (a benefit in a non-aquatic animal) than by performing the movement by direct muscle work. This dissipation provides a second means of modulating an apparently passive structure.

One example of a specialized MTU design of this type is that of the biceps brachii in the horse, which is responsible for protraction of the forelimb during locomotion [48]. In summary, as the horse moves over the foot through stance, the moment arm of the GRF at the shoulder gradually rises stretching the biceps muscle, which has a substantial internal tendon and is highly pennate in structure. Through most of stance, the GRF exerts an extensor moment on the carpus holding the leg in extension and

balancing the flexor moment of the stretched digital flexor tendons. In late stance, the balance of forces at the carpus means that this joint starts to flex at which point there is nothing to prevent the digital flexor tendons from flexing the carpus and digits folding the leg. The leg is then free to be swung forward by elastic shortening of the biceps flexing the elbow and extending the shoulder. The observed kinematics of leg swing (accelerations and joint angles) can be accounted for by this largely passive system. We propose that the role of the muscle fibres within the spring is to modulate storage and return of elastic energy by changing the force length properties of the biceps MTU [44]. Examples of why this would be useful include when the foot breaks away from the surface earlier or later affecting energy stored in tendons at catapult release, changes in foot weight owing to dirt or a horseshoe and if a horse needs to lift its feet higher to jump an obstacle.

To store energy in a tendon, a muscle is required to generate tension, which can be achieved either passively or actively. There are conceptually different ways through which the nervous system can control how much energy is firstly stored and then returned, which ultimately depends on the interaction with the environment and whether the goal is to perform or absorb mechanical work at any instant. The nervous system can control how much volume of muscle is activated and hence the force produced and energy stored in the tendon and it can also control the timing of the activation and deactivation relative to some movement, which will influence the amount of energy firstly stored and then returned. We have addressed the question of how the nervous system can control energy in muscles with elastic tendons using both experimental and modelling approaches.

One of the primary roles of muscles with compliant tendons is to perform stretch–shorten cycles. The stretch part of this cycle is ultimately important for the amount of energy stored in the tendon and this is determined by the dynamics of the body (e.g. deceleration of the trunk) coupled with the force produced by the muscles. To increase energy stored in the tendon, it is beneficial to have the muscle doing a little negative work (actively stretching). In this scenario, the tendon can buffer the muscle from excessive stretch and store elastic energy which can subsequently be used to enhance the ability of the muscle to shorten rapidly. Therefore, the amount of energy that is put into stretching the MTU (and hence absorbed) is critical to determining the potential for energy return. However, as a consequence of the force–velocity properties of muscle, a muscle has greater capacity for energy absorption than energy return (higher forces can be achieved during eccentric stretch). This can be seen in figure 5, which shows the influence of length change on the work loop. In this case, the muscle was active throughout the entire stretch–shorten cycle and energy is ultimately absorbed as the work loop runs clockwise in time [44].

To vary the amount of energy absorbed, the timing and duration of the muscle stimulation relative to the length change is important. Muscles take a relatively long time to activate once stimulated and to deactivate after stimulation ceases. Short duration stimulations would not fully activate muscle fibres and hence the force will stay lower and less energy will be absorbed by the MTU. Longer duration stimulations may allow the muscle to generate greater tension, but may come at a higher energetic cost. The slow relaxation time of muscles may also be critical in maintaining tension in the muscle so that the tendon can recoil and perform as much positive work as possible.

These principles are demonstrated in figure 6, which shows example work loops achieved by electrically stimulating an excised extensor carpi radialis (ECR) muscle of a goat during a stretch–shorten cycle (G. Lichtwark & A. Wilson 2010, previously unpublished data). The goat ECR is a bipennate muscle with relatively short fibres (approx. 35–55 mm), which attach to a long internal tendon (approx. 145 mm). In this experiment, both the duration of stimulation (and hence timing of deactivation) and the stimulation intensity were varied to examine the influence on energy absorbed and returned during the stretch–shorten cycle.

As can be seen in figure 6c, as stimulation time increased, more energy was both stored and returned by the MTU until some specific duration (cycle 4) where no more work was achieved for longer durations of stimulation. Changing the timing of the activation, e.g. later in the stretch cycle, can also have a significant influence on how force is developed and may allow for net positive work during the stretch–shorten cycle [44]. Therefore, the timing and duration of activation is critical to absorbing and performing mechanical work; however, in the biological system this depends largely on the interaction of the muscle with its mechanical load.

While the timing and duration of activation are certainly important for tuning the spring-like properties of muscle, an easier way of finely controlling the forces produced by the muscles is to change the volume of muscle that is activated. The greater the volume of activated muscle, the greater the force and hence the more energy is stored in the tendon for subsequent shortening. This is demonstrated experimentally in figure 6d, where we have changed the number of active motor units by varying the stimulation voltage (and hence current, assuming a constant resistance) applied directly to the goat ECR (25, 50 and 100 V).

Very little is known about how the elastic properties of muscle change with activation level. Hof [49] presented data on the human triceps surae SEE stiffness, which suggested that the SEE stiffness increases with the activation level (the proportion of activated muscle). He proposed a model where a group of fibres is associated with a portion of the SEE (e.g. proportion of aponeurosis); so higher level of activation results in a stiffer SEE. Although this conclusion has been challenged over the experimental techniques used to demonstrate this variable SEE stiffness [50], the theoretical concept and potential effects are worth exploring.

We demonstrate this effect by modelling two scenarios: (i) the SEE stiffness is constant, regardless of the proportion of muscle fibres recruited and (ii) the SEE stiffness is dependent on the number of activated units. In the second model, each contractile subunit of
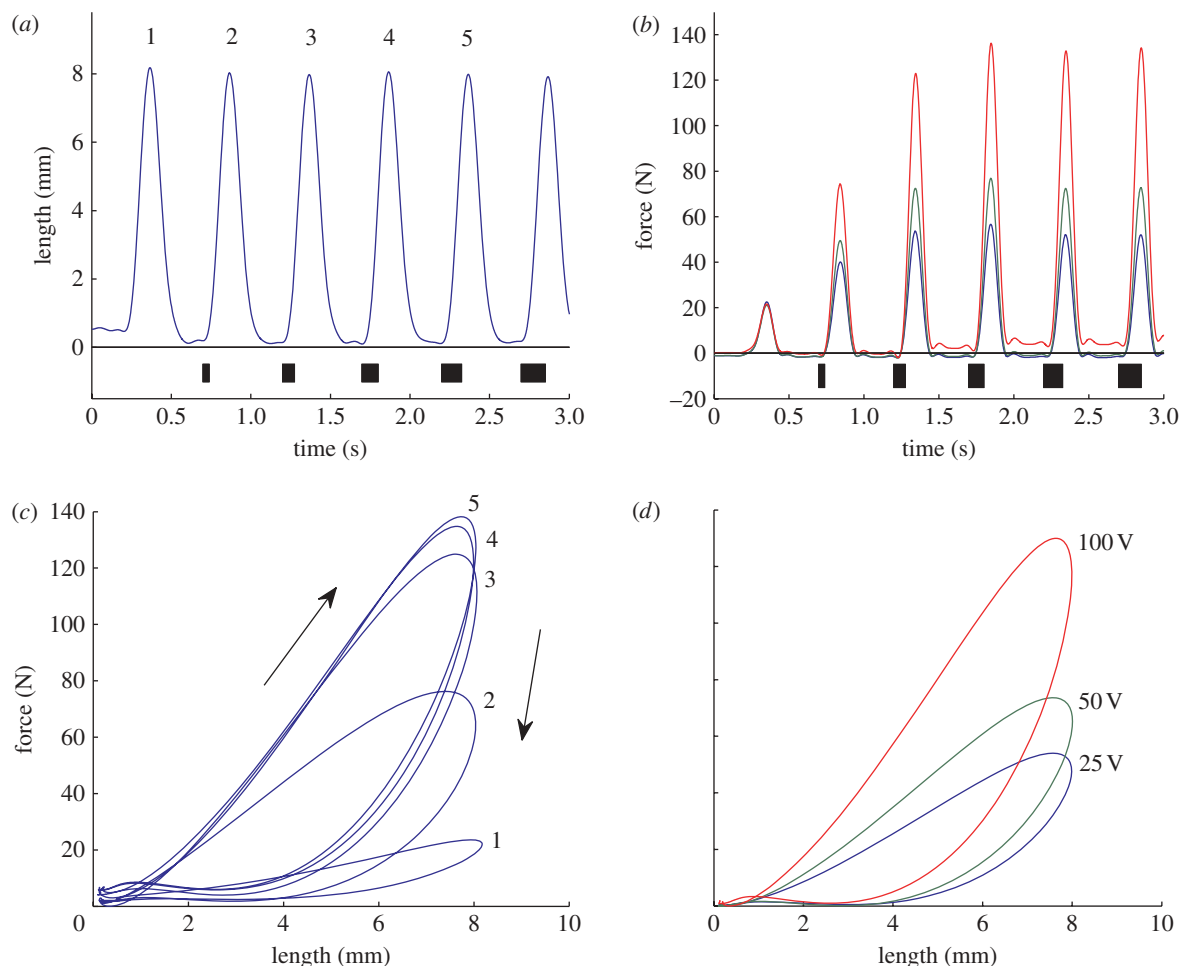
Figure 6. (*a*) Stretch–shorten length changes (2 Hz) of excised extensor carpi radialis muscles of goat with the timing and duration of stimulation represented by black bars. Durations of stimulation were 0, 15 30, 40, 50 and 60% of the cycle duration. Cycle numbers are shown above each cycle. (*b*) Force output corresponding to length change and stimulation pattern shown in (*a*) for three different stimulation intensities applied by adjusting the electrical voltage applied to the muscle (blue, 25 V, green, 50 V and red, 100 V). (*c*) Workloops for the maximum stimulation intensity and different durations of activation and corresponding cycle numbers. (*d*) Workloops for an individual cycle stimulation pattern at three different stimulation intensities, which change the number of active motor units.

the muscle has its own series elastic element and this is attached to a common SEE with the same stiffness as in model 1. The activation parameters of this model are important. In the first model, the activation and deactivation curve magnitude is linearly scaled by the proportion of fibres recruited with no change in time constant (which might occur owing to different activation of different muscle fibres). In the second model, each unit that is recruited will maximally activate, however the proportion of units activated can be changed to represent submaximal intensity contractions.

Using such a model, we can theoretically examine the effects of varying SEE stiffness during submaximal stretch–shorten contractions. Figure 7 demonstrates how changing the level of activation (which in this case represents the active volume) influences the work loop during a contraction where the muscle is activated at the beginning of stretch and begins deactivating at the commencement of shortening. While both models are equivalent at 100 per cent activation, reducing the activation alters both the negative and positive work performed by the muscle, resulting in less energy absorption in model 2. This is because of the decreased

apparent SEE stiffness, which acts to reduce the amount of stretch of the CE (muscle fibres) and also stores more energy in the SEE. Such models are of course highly sensitive to the stiffness of the common SEE (which may be thought of as the tendon) and the stiffness of SEE of each element (presumably the aponeurosis). In a real muscle, which applies will depend on the arrangement of motor units across the muscle. Certainly, muscles with different heads are likely to have distinct innervation patterns but it is uncertain if similar heterogeneity exists within a muscle. Determining the arrangement and function of individual motor units is time-consuming and challenging even in a small muscle [51].

8. TENDON COMPLIANCE AND ATHLETIC PERFORMANCE
A number of studies have attempted to relate tendon compliance to athletic performance and discipline but the results are not particularly clear-cut. Comparison of distance runners and sprinters demonstrates that sprinters have stiffer Achilles tendons but they also have stronger gastrocnemius muscles and it is
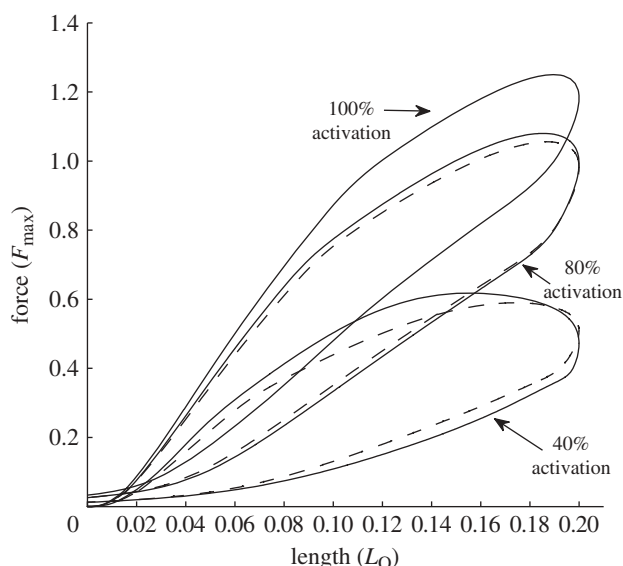
Figure 7. Comparison of the influence of the proportion of active fibres (termed activation) for two models of muscle contraction (previously unpublished data). In model 1 (solid lines), the series elastic stiffness is constant. In model 2 (dotted lines), the series elastic stiffness of the contractile component is dependent on the proportion of active fibres and hence activation level.

not clear if this is an athletic attribute rather than a simple hypertrophy [52,53]. A study of runners demonstrated that more economical runners had a smaller moment arm at the calcaneous [54], but that study did not report joint moments, GRF moment arm at the ankle (which could compensate for the anatomy). Elongating the foot of sprinters by using a rigid soled shoe does have an advantage which could, in part, enable a lower muscle contraction velocity and a longer contact time in push off [55].

9. LIMB DESIGN

It is apparent that MTU force is a function of posture and limb EMA [40,56]. It would appear that there is an infinite range of postures and arrangements of MTUs, but animals demonstrate a number of striking similarities with segment lengths in similar proportions and more tendinous MTUs in the distal limb suggesting a more limited range of configurations are appropriate for effective locomotion.

We will confine our thoughts to running type or higher speed gaits. Running appears like a spring-loaded inverted pendulum (SLIP) [57,58]. At top speed, the limb contacts the ground at an angle of about 30° relative to vertical after a period of air time. The COM is moving downwards so it must follow an approximately circular/sinusoidal path with the limb shortening and then extending. GRF rises up to mid-stance and then drops again in an approximately sinusoidal manner [59].

As an animal moves more quickly, the limb contact angle with the ground increases a little, contact time drops owing to the COM moving more rapidly over the foot and peak force increases [60], while vertical impulse remains approximately constant [61]. Since the leg contacts the ground at a greater angle, the

horizontal impulse increases and the leg compresses more so the animal slows down more and there is something of a dwell period around midstance, which increases the vertical force and impulse.

The SLIP model assumes steady state and no net energy losses of the COM. Energy must however be fed into the system to account for the real world energy losses or to increase the mechanical energy of the COM (increasing speed or potential energy). If we consider acceleration, there is a need for the net impulse to have appropriate horizontal and vertical components and for the horizontal force to never be so high a fraction of vertical force that it exceeds the coefficient of friction of the foot on the surface (or the foot will slip). Vertical impulse is defined by duty factor (and weight) and the GRF curve shape is approximately sinusoidal in running animals. If propulsion is limited by grip, then the ratio of horizontal to vertical forces should be just below the coefficient of static friction throughout the stance. Maximum propulsion will therefore occur when vertical and horizontal forces are in proportion (and both probably sinusoidal) throughout the stance. In this situation, mean acceleration over a stride would be equal to the coefficient of friction (μ) times gravity (g). For animal feet on a smooth surface μ is likely to be around 0.6 [62], though claws or running spikes may enable values approaching or even exceeding 1.0.

There are two conceptual mechanisms whereby the impulse/work on the COM required to meet these energy losses or increased system mechanical energy can be achieved. Here, we consider the impulse to be mainly horizontal in nature though the concepts can be extended into a scenario like jumping with appropriate alignment of the COM to the GRF vector.

The first mechanism is that the leg extends in late stance hence performing work. How much work can be undertaken is limited by limb force, which is predefined by duty factor and the approximately sinusoidal GRF profile associated with SLIP mechanics, and by how much the leg extends (as work is integral of force and displacement). Increasing limb force will increase work but only to the extent that the body will accelerate more rapidly and muscle power will drop (the inertial catch of Galantis & Woledge [63]) At first consideration, the leg is compressed up to midstance, so leg extension for propulsion could occur only in the second half of stance. This is not actually the case because in acceleration the leg sweep and length may become asymmetrical so that the leg contacts the ground at a smaller angle to the vertical and it is shorter and it then can extend for more than half the stride. Additionally, if a muscle is in series with a tendon, it is feasible for the muscle to be shortening and doing work while the MTU as a whole is elongating—seen, for instance, in turkey and human gastrocnemius [25,29]. Other examples of this include a hopping frog [64], but not a jumping insect where there is a mechanical catch enabling gradual storage of energy without COM acceleration [65]. One would envisage that an accelerating animal could crouch more enabling a greater leg extension and hence more work being performed. Crouched posture, however, results in a lower EMA and necessitates a

joint torque that may exceed the capacity of the leg extensor muscles (particularly if muscles are in full extension). This is especially significant if the muscles are shortening around peak power (one-third of maximum shortening velocity), where higher forces will slow muscle shortening and power output. In this scenario, the muscle experiences a force that is approximately in proportion to the leg force through stance, geared by changes in EMA, and must function under these imposed force time conditions. This could preclude lowering EMA when moving at higher speeds as the duty factor will be low and peak limb force high. So, leg extension can be used for COM work and appears to be the predominant mechanism in smaller animals, which already have a lower EMA, and especially those that jump.

The second way that energy can be delivered is by retracting the limb relative to the trunk. The benefit of hip torque propulsion is that the leg can appear as a largely tendinous passive compression spring of properties appropriate for running like a SLIP. This means limb load is not limited by the force capacity of serial extensor muscles. This has been proposed as a benefit that quadrupeds can exploit for enhanced turning performance [66]. Work can be performed throughout the stance phase and the hip extensor or forelimb retractor muscle (mainly latissimus dorsi) does not experience the predefined GRF profile (although trunk inertia is still required for the muscle to work against). An animal that exclusively propels itself using this mechanism and achieves the maximum feasible grip limited acceleration would need to provide a torque that changes the SLIP sinusoidal horizontal GRF trace to a horizontal force that is in proportion to the vertical force throughout the stance. This would result in a torque/horizontal force profile as shown in figure 8—i.e. a torque that rises up through early stance and drops from midstance onwards. It is easy to visualize this mechanism in a quadruped, where trunk inertia minimizes any pitching movement though a biped could change the posture and lean forward to permit acceleration by this mechanism and experience no net pitch impulse through a stride. Figure 8 shows that the required torque for maximum acceleration is high (which is matched by most of the propulsive musculature being arranged around the hip in horses and dogs) but it is still likely that animals use a combination of asymmetrical contact angles, limb torque and leg extension.

An interesting question is whether the dependence on these two mechanisms differs between small and large animals. Small animals have a more crouched posture in stance [40,56] and as such have more scope for extending their limbs, while large animals like horses have a more upright posture and limited scope for leg extension. They do, however, have longer legs and higher stance times, so more work can be done by muscle in a stance than for a small short-limbed animal. This is offset, but not completely, by the short-limbed animal having a higher stride frequency. Comparing the data of Witte *et al.* [67], a racehorse at $17 \, \text{ms}^{-1}$ has a hindleg stance length of 1.60 m (0.094 s stance time $\times \, 17 \, \text{ms}^{-1}$) and a stride frequency of 2.38 strides s^{-1}. Each hindfoot is therefore on the ground for $17 \, \text{ms}^{-1} \times$ duty factor (or 1.60×2.38), i.e. 3.81 m in each second. A racing
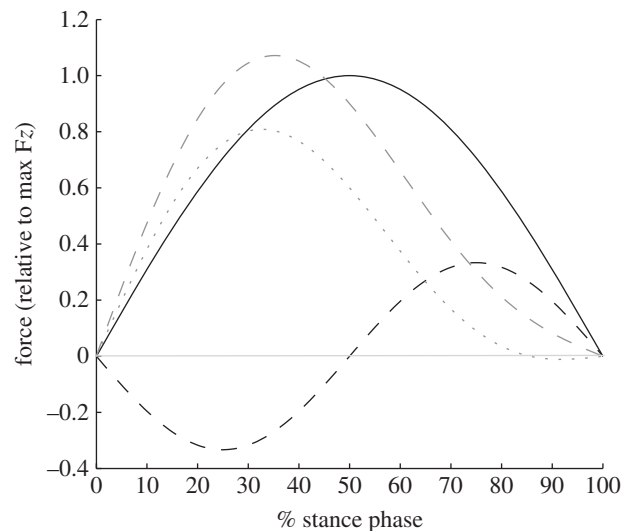

Figure 8. In black, the vertical (solid) and horizontal (dashed) forces for a stylized SLIP leg. The two grey lines are the horizontal force that would need to be added, for instance through hip torque, to convert horizontal force to one that is 0.6 (grey dotted) or 0.9 (grey dashed) times vertical force throughout the stance phase. The assumption is that for maximum propulsive effort, the ratio of horizontal force to vertical force (Fx/Fz) should be just below the coefficient of static friction for the foot–ground interface (0.6 and 0.9 for the two examples given here). In this context, the ratio of horizontal and vertical impulses and hence the horizontal and vertical accelerations (accounting for g at $9.81 \, \text{ms}^{-2}$ in most cases) should also be in proportion.

greyhound at the same speed has a stance length of 0.85 m (0.050×17) and a stride frequency of 3.3 strides s^{-1}, so the hind feet are only on the ground for 2.80 m in each second. The larger animals may therefore be forced towards and better placed for propulsion by limb torque.

The maximum work that can be performed by hip torque is constrained by stance length (the distance moved by the COM relative to the foot during stance), which is approximately leg length $\times$ sweep angle in radians. The maximum torque that can be delivered is constrained by either grip, muscle force velocity properties or the propensity for the animal to pitch like a motorcycle. Williams *et al.* [68] found that in polo horses and racing greyhounds avoiding pitch accounts for low-speed acceleration capacity and muscle power the limit at higher speed. Tan *et al.* [69] demonstrated that when horses are cornering their acceleration performance in the direction of travel is reduced, suggesting that a grip limit exists. The coefficient of friction for a foot on a hard surface is around 0.6 but can be much higher (over 1.0) on soft surfaces, especially if the animal has claws or hooves that will penetrate the surface.

So both methods can, in theory, permit maximum horizontal impulse as constrained by grip. In scenario 1 (SLIP), the muscle must function within the limb force profile and hence muscle force will increase with speed. The SLIP model can benefit from using SEE strain of the limb tendons to disconnect muscle shortening velocity from MTU velocity and the forward motion of the trunk can load the MTUs rapidly in early stance, which benefits muscle function. In contrast, the muscle in scenario 2 (limb retraction with joint torque) is isolated

from limb force (presumably a benefit) but the muscle is not automatically loaded in early stance. There may however be scope for the inertia of the trunk, limb or abdominal contents to preload muscles in an advantageous manner. The muscle contraction velocity will vary in direct proportion to speed and there appears to be little SEE or other mechanism to allow the muscle to shorten more slowly or with a longer contraction time than the MTU shortening.

Performing work by leg extension is limited by the scope for leg extension. If an animal's leg was completely extended at foot off, then work could be done only by increasing the force in the second half of the stance. It is possible that work can be performed on the leg spring in early stance, which is then returned. It is, of course, likely that real animals depend on a combination of both mechanisms and that biarticular muscles transmit hip extension down the leg to extend distal joints (for instance, the horse reciprocal apparatus). Consideration of the relative importance and interaction of these two mechanisms would be of considerable value in understanding animal design.

10. FUTURE DIRECTIONS

— To understand how the proximal and distal MTUs interact in power flow along the limb and the extent to which the properties of passive elastic structures in the distal limb can be modulated by more proximal muscular elements.

— To build on the work of Van Leeuwen & Spoor [70] and others, to create a three-dimensional finite element model of a pennate muscle that combines knowledge of motor unit arrangement with fibre type distribution and aponeurosis arrangement to explain the function and roles of pennate muscles in controlling and modulating dynamic movement through control of energy storage and return, and the strategic absorption of energy through active lengthening.

— To examine how system dynamics and reflexes enable expected and unexpected perturbations and manoeuvres to be achieved without instability or falling [41].

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