

COMMENTARY

Flexible mechanisms: the diverse roles of biological springs in vertebrate movement

Thomas J. Roberts^{1,*} and Emanuel Azizi²

¹Department of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912, USA and ²Department of Biology, The College of New Jersey, Ewing, NJ 08628, USA

*Author for correspondence (roberts@brown.edu)

Summary

The muscles that power vertebrate locomotion are associated with springy tissues, both within muscle and in connective tissue elements such as tendons. These springs share in common the same simple action: they stretch and store elastic strain energy when force is applied to them and recoil to release energy when force decays. Although this elastic action is simple, it serves a diverse set of functions, including metabolic energy conservation, amplification of muscle power output, attenuation of muscle power input, and rapid mechanical feedback that may aid in stability. In recent years, our understanding of the mechanisms and importance of biological springs in locomotion has advanced significantly, and it has been demonstrated that elastic mechanisms are essential for the effective function of the muscle motors that power movement. Here, we review some recent advances in our understanding of elastic mechanisms, with an emphasis on two proposed organizing principles. First, we review the evidence that the various functions of biological springs allow the locomotor system to operate beyond the bounds of intrinsic muscle properties, including metabolic and mechanical characteristics, as well as motor control processes. Second, we propose that an energy-based framework is useful for interpreting the diverse functions of series-elastic springs. In this framework, the direction and timing of the flow of energy between the body, the elastic element and the contracting muscle determine the function served by the elastic mechanism (e.g. energy conservation vs power amplification). We also review recent work demonstrating that structures such as tendons remodel more actively and behave more dynamically than previously assumed.

Key words: elastic, locomotion, tendon.

Introduction

Most biologists are familiar with the idea that a kangaroo's hop is powered by spring-like tendons that allow it to literally bounce along the ground (Alexander and Vernon, 1975). This mechanism is obvious to any observer, so much so that the kangaroo's hop has become the iconic image of elastic mechanisms in locomotion. Yet in many ways this image sells springs short. It is becoming increasingly clear that the role of elastic mechanisms in movement extends well beyond obviously springy gaits such as hopping, influencing the mechanics, energetics and control of a wide range of activities. The springs are diverse as well, including not just tendons but connective tissue elements that bind muscles together and molecular springs within the muscles themselves. Although they may not always be as obvious as a kangaroo's bouncing gait, elastic mechanisms are likely to play a significant role in all vertebrate locomotor systems.

A spring element, by definition, follows a very simple behavior. Springs deform when a force is applied and recoil to their resting shape when the force is released. Materials can act like springs when loaded in tension, like a rubber band, or in compression, like a rubber ball. Both kinds of loading are important in nature. When springy materials deform, they store energy in the form of elastic strain energy, and when they recoil this energy is released. The amount of energy stored depends on the material stiffness and the deformation. Compared with many biological tissues, springs are 'dumb'; their behavior is determined by a single force-length relationship, and cannot be modified or controlled directly. Springs also cannot produce mechanical energy; they can only return energy loaded previously by an external source. By way of comparison, any given muscle can produce mechanical energy, and

can operate over a wide range of combinations of forces and lengths, all controlled and fine-tuned by intricate feed-forward and feedback signals from the nervous system. What is so fascinating about elastic mechanisms is that, from such a simple and arguably limited mechanism, nature has produced a remarkable variety of applications.

In this Commentary, we review some of the elastic mechanisms important in vertebrate movement. We propose an energy-based framework for categorizing the different functions of elastic mechanisms (Fig. 1). In Fig. 1, the functional role of tendons is categorized according to the directional flow of energy, with three possible patterns: (1) energy from the body or a body segment is temporarily stored in tendons, then returned to the body; (2) the mechanical energy produced by a muscle contraction is stored in a tendon, then released to increase mechanical energy of the body or a body segment; and (3) energy from the body or a body segment is temporarily stored in tendon, then released to do work on muscle that is actively lengthened to absorb energy. This conceptual framework is based on muscle-tendon interactions, but it is also applicable to many (but not all) other elastic mechanisms used in locomotion. Below, we consider the application of this framework to vertebrate movement, with an emphasis on the idea that in each case the elastic mechanism allows the locomotor system to function beyond the limits of the muscle motor.

Recycling energy: walking running and hopping

Although speculation about elastic mechanisms in animal movement dates back to The Renaissance period (e.g. Borelli, 1689), our current understanding of the importance of springs in running rests on the work of contemporary physiologists. Early

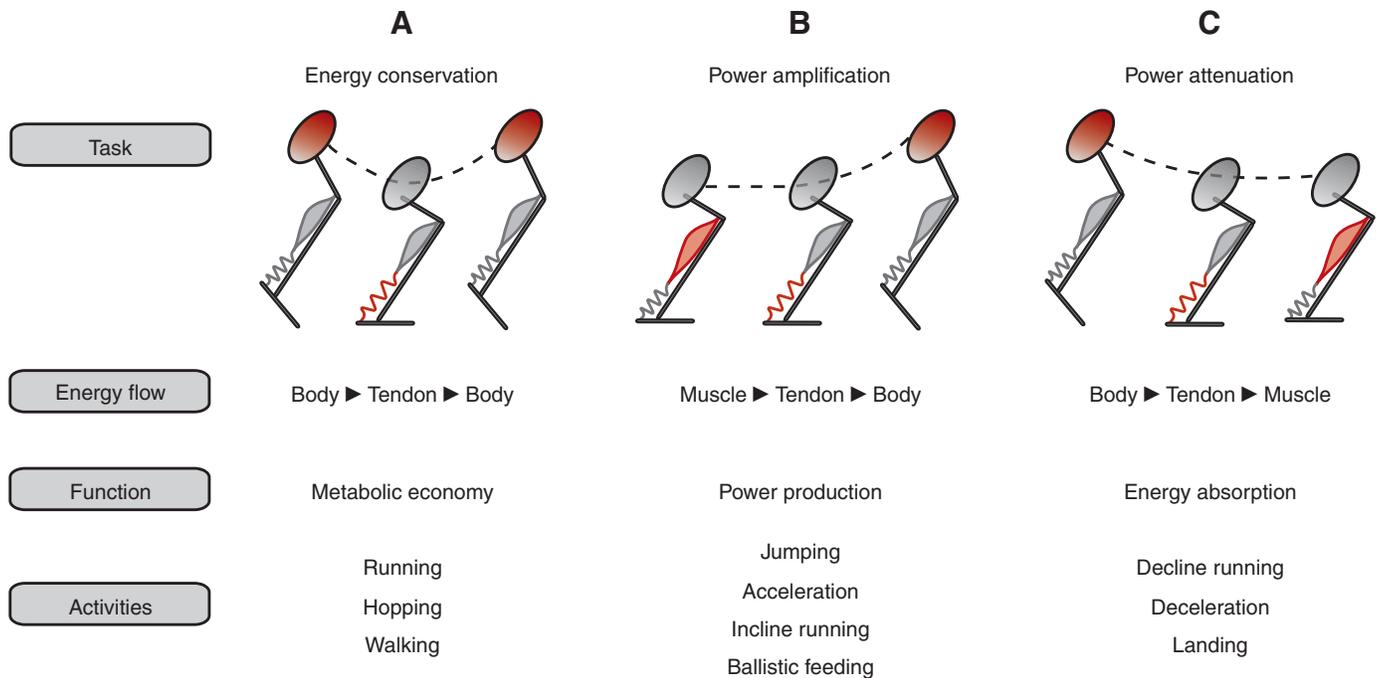


Fig. 1. A schematic illustrating how the directional flow of energy in muscle–tendon systems determines mechanical function. (A) Mechanical energy is conserved (i.e. muscle work is reduced) when elastic structures store and recover cyclic changes in the mechanical energy of the body or an appendage. (B) Tendons loaded directly by the work of muscle contraction can release that energy rapidly to the body. If the energy is released more rapidly than it is stored, muscle power can be amplified. (C) A rapid decline in the mechanical energy of the body or an appendage can be temporarily stored as elastic strain energy, followed by the release of this strain energy to do work on active muscles. This mechanism has the potential to reduce peak power input to muscles, thereby functioning as a power attenuator. In the figure, red indicates the flow of energy between active muscle contraction, tendon strain energy and body kinetic/potential energies.

studies of spring mechanisms in terrestrial locomotion proceeded on two fronts. First, studies combining careful anatomical (e.g. tendon dimensions), mechanical (e.g. force plate recordings) and mathematical approaches showed that a significant fraction of the work done in a step could be provided by the spring-like action of tendons, rather than by muscle work (Alexander and Vernon, 1975). In other studies, combined measurements of the mechanical work of running and the energy input necessary to sustain this work, as measured by oxygen consumption, resulted in very high efficiency values that could only be explained if elastic mechanisms contributed some of this work ‘for free’. These energetic studies began with human subjects (Cavagna et al., 1964) and later included broad and comprehensive comparative analyses (Cavagna et al., 1977; Heglund et al., 1982). The conclusion from both mechanical and energetic studies was that much of the cyclical work done during running could be attributed to the energy stored and released by elastic structures with each step (Fig. 1A).

Since then, the idea that running is a ‘bouncing gait’ powered by spring-like limbs has become a cornerstone for models of running mechanics and energetics (Dickinson et al., 2000). Key features of the dynamics of running, including ground reaction force patterns, the trajectory of the center of mass, and the change in foot contact time with speed, are consistent with a simple spring–mass model of running for humans (McMahon and Cheng, 1990; Blickhan, 1989), and for other runners and hoppers (Farley et al., 1993). Direct measurements of muscle function have demonstrated the importance of the stretch and recoil of tendons on the length changes and power output of active muscles during running (Roberts et al., 1997) and hopping (Biewener et al., 1998).

More recently, empirical and theoretical approaches have demonstrated that the use of elastic mechanisms is not limited to running but also occurs during walking. Historically, conceptual models of energy-saving mechanisms in locomotion have categorized walking as a ‘pendulum gait’, in which energy is conserved through the pendular exchange of kinetic and potential energy as the walker vaults over a strut-like leg with each step (Cavagna et al., 1977; Dickinson et al., 2000). The dichotomy between the spring mechanism of running and the pendular mechanism of walking was challenged by Lee and Farley (Lee and Farley, 1998), who used kinematic data to show that the compression of the leg (as measured by the distance from the hip to the toe) during walking in humans was only 26% less than that during running. Ultrasound data has provided direct evidence of the importance of tendon action during walking; triceps surae muscles in humans are able to operate nearly isometrically (i.e. at constant length) during walking owing to the stretch and recoil of the Achilles tendon (Fukunaga et al., 2001; Lichtwark et al., 2007). Recent models have also demonstrated that some key dynamic features of walking, such as the pattern of ground reaction force, are not consistent with a simple inverted pendulum model, but can be explained by a spring-loaded inverted pendulum (Geyer et al., 2006) (Fig. 2). Together, these studies suggest that elastic mechanisms are an essential part of both walking and running gaits.

Do all runners use an elastic mechanism to conserve energy? The literature is mixed on this question. In particular, the importance of elastic mechanisms in small animals has been questioned. A comparison of the elastic strain energy stored and recovered in the Achilles tendons of hopping kangaroo rats showed that the fraction

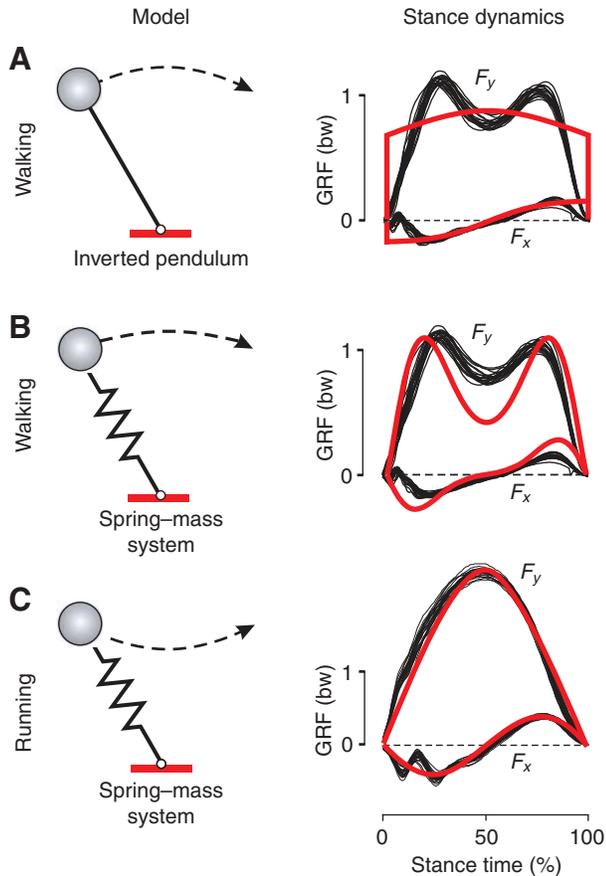


Fig. 2. Simple spring-mass models can reproduce key features of the dynamics of running and walking. Walking has historically been characterized as an inverted pendulum gait, in which the exchange of elastic and potential energy helps to power the motion of the body center of mass as it vaults over a rigid leg. (A) A simple inverted pendulum produces a ground reaction force (GRF) pattern (red) that is a poor approximation of the GRF observed in walking humans (black). bw, body weights. (B) Ground reaction forces developed during walking are consistent with an inverted pendulum model, if the model includes a leg spring. (C) The parabolic pattern of vertical ground reaction forces (F_y) and the sine-wave pattern of horizontal forces (F_x) in running are produced by a simple spring-mass model, and absolute values of forces can be matched with appropriate values for leg spring stiffness and angle of attack. Figure modified from figs 1 and 3 of Geyer et al. (Geyer et al., 2006).

of the mechanical energy oscillations of the body that could be provided by tendon springs was relatively small in kangaroo rats (14%–24%) when compared with the same values for kangaroos (21%–36%) (Biewener et al., 1981). A comprehensive comparative study also provided evidence that the tendons of small animals are relatively stiff and therefore have a lower capacity for energy storage when compared with large animals' tendons (Pollock and Shadwick, 1994a; Pollock and Shadwick, 1994b). However, a recent scaling analysis demonstrated that although small mammals' tendons can be relatively stiff, the scaling of muscle mechanical advantage indicates that they also experience higher forces (Bullimore and Burn, 2005). Scaling relationships also indicate that small animals do less work per stride, thus the absolute amount of energy that must be stored and recovered to contribute to the work of each step is reduced in smaller animals. Taken together, these scaling relationships predict that the fraction of locomotor work

that can be provided by tendon energy storage and recovery is greater in small runners than in large (Bullimore and Burn, 2005). Good evidence exists for the action of elastic mechanisms in running arthropods, suggesting that *size per se* is not a barrier to the effective use of springs (Dudek and Full, 2006).

What is the benefit of a springy gait? The most obvious answer is that work done by tendons does not have to be done by muscles, and muscle work is metabolically expensive. However, the utilization of tendon elasticity does not come completely without cost. Tendons operate in series with muscles, and can only act as useful springs when muscles generate force. Force generation by muscles requires metabolic energy, thus there is a cost to operating tendon springs. It has been proposed that the net metabolic benefit of tendon elasticity in walking and running is best understood in the context of two properties of skeletal muscle (Roberts et al., 1997; Roberts, 2002). The first is the 'Fenn effect', which states that active muscles use more energy when performing work than when only generating force (Fenn, 1924). Thus, to the extent that tendons allow muscles to generate force without doing work (or while doing less work), they reduce the rate of energy consumption of each active muscle fiber. Second and less well recognized is the influence that tendon mechanisms can have on the recruited muscle volume during walking and running. Regardless of the work performed, walkers and runners must produce enough force to support body weight. Owing to the force-velocity properties of muscles, force can be produced with fewer active muscle fibers if the muscle operates at low or zero (i.e. isometric) shortening velocity (Roberts et al., 1997). This effect of muscle shortening velocity on recruitment has been demonstrated in studies of turkey ankle extensors, in which the volume of muscle recruited to generate a unit force, as estimated from electromyography, is directly proportional to shortening velocity (Gabaldon et al., 2008) (Fig. 3). Human hopping experiments have also demonstrated a dramatic increase in muscle activity for a given force output when humans hop on extremely soft surfaces that undermine effective elastic-energy storage (Moritz and Farley, 2005).

Recently, interest in elastic mechanisms in walkers and runners has turned to the potential importance of springs in motor control and stability. Some of this interest has been stimulated by roboticists, who must make a robot that can walk without falling down before they can worry about its energy efficiency. Mathematical models support the idea that the elastic behavior of the leg can stabilize movement, meaning that an elastic system has some ability to recover from a perturbation with limited or no change in control strategies (Blickhan et al., 2007; Ghigliazza et al., 2005). Experimental work has demonstrated responses of human runners to perturbations, such as a sudden change in running or hopping surface stiffness, that appear to be due, at least in part, to the spring-like behavior of the leg. Moritz and Farley (Moritz and Farley, 2004) demonstrated that human runners faced with a surprise change in surface stiffness show changes in leg stiffness that are faster than typical reflex responses and that precede changes in electromyograph (EMG) activity. They concluded that this response was due to passive mechanical reactions of the spring-like limb (Moritz and Farley, 2004). These rapid feedback mechanisms might involve the elastic action of tendons, but the spring-like behavior of limbs might reflect the action of muscles as well as elastic structures. Muscles undergoing a stretch-shorten cycle could produce some of the spring-like function of the leg, and this action might provide some of the rapid mechanical feedback observed experimentally (Ferris et al., 1998). The response of guinea fowl hindlimbs to sudden perturbations support the idea that

some 'elastic' responses of the support limb are actually explained by active muscle function (Daley and Biewener, 2006), and a detailed forward-dynamics model of human hopping suggests that the elastic elements in series with muscles provide only one of several possible explanations for rapid stabilizing responses (van der Krogt et al., 2009). More work is needed to determine the extent to which elastic structures promote stability in terrestrial gaits.

Recycling energy: swimming and flying

Compared with terrestrial locomotion, examples of elastic mechanisms are relatively scarce in studies of swimming and flying vertebrates. This discrepancy may be explained in part by the relative number of studies of these different locomotor modes, but it is also possible that the nature of swimming and flying mechanics limits the usefulness of elastic mechanisms. Compared with running or walking, swimming and flying require a substantial loss of energy to the environment to provide propulsion and overcome drag. Work lost to the environment to overcome drag cannot be stored and recovered to help power cyclical movements. Nevertheless, at least two potential benefits of elastic mechanisms in flight and swimming have been identified.

In flying animals, it has been proposed that elastic mechanisms might aid in providing the inertial work required to accelerate and decelerate the wing with each wing beat. In birds, the down stroke to upstroke transition might be aided by the storage and recovery of elastic energy in the tendon of supracoracoideus, a wing elevator (Hedrick et al., 2004). Direct evidence for this mechanism is currently lacking, and it is also possible that the kinetic energy lost as the wing is decelerated is imparted to the environment to provide useful aerodynamic forces (Hedrick et al., 2004).

Swimmers and flyers may also potentially benefit from the temporal redistribution of muscle work via elastic elements. Such a mechanism might allow for relatively constant and efficient muscle power production, even at points in the locomotor cycle when there is a mismatch between available muscle power and the opportunity for generating useful propulsive forces (Gosline and Shadwick, 1983; Pabst, 1996). Alternatively, the release of energy stored elastically might allow for power development at points in the locomotor cycle when muscle operating lengths or velocities are unfavorable for producing power. It has been proposed, for example, that the release of stored energy in the skin of sharks occurs at the point at which muscles are stretched to long lengths and reduced in their capacity to produce force owing to the muscle's length-tension properties (Wainwright et al., 1978). These kinds of mechanisms would fall broadly under the category of energy flow depicted in Fig. 1B, because the timing of muscular work is decoupled from the timing of locomotor work by the temporary storage of muscle work as elastic strain energy (although power is not necessarily amplified).

Playing with power: amplification and attenuation

Elastic mechanisms can act as power amplifiers, by storing muscle work slowly and releasing it rapidly. This mechanism is distinct from the role of series elastic elements in walking and running because the source of the elastic strain energy is muscle contraction, rather than transient changes in the body's kinetic or potential energy (Fig. 1). Power amplification mechanisms work because springs and muscles have different intrinsic power limits. Skeletal muscles are limited in their maximum power output, ultimately by rate limits to enzymatic processes associated with actomyosin cross-bridge cycling. The mechanical function of tendons and other spring elements has a structural basis, and therefore is not subject

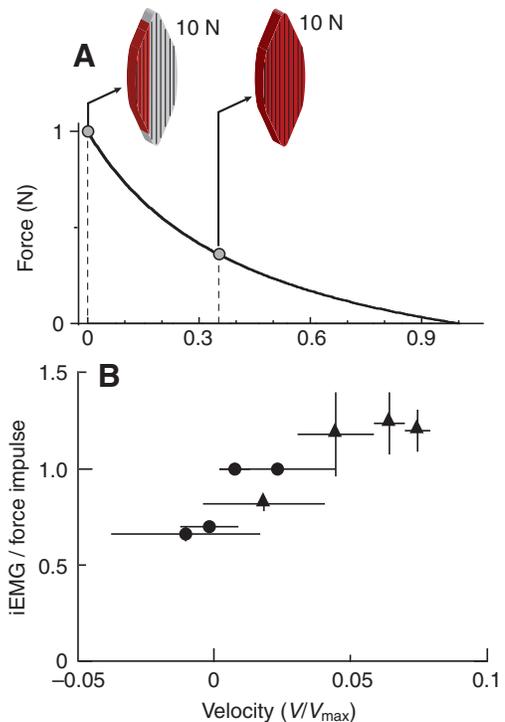


Fig. 3. Tendons can reduce the metabolic cost of muscle activity during running by reducing the volume of muscle that must be active to produce force. (A) A schematic to show how the shortening velocity of a muscle affects the muscle volume required to generate a given force. A hypothetical force-velocity curve is given for a single motor unit in a limb muscle composed of approximately 30 such units. Each motor unit is capable of producing 1 N of force, when isometric. If the muscle must develop 10 N of force (during stance phase support, for example), this force can be produced with 10 active motor units if the muscle is isometric. If the muscle contracts at an intermediate shortening velocity, at which muscle power is maximized, the force output of each active motor unit is reduced to ~0.30 N, and the entire muscle must be active to develop the same 10 N of muscle force. (B) Data from measurements of average muscle shortening velocity and recruited muscle volume required to generate force in running turkeys support the hypothesis presented in A. The rectified integrated EMG signal (iEMG) per unit force developed is used as a proxy for recruited muscle volume. The average iEMG for level (circles) and incline (triangles) running at various speeds is directly proportional to the average relative shortening velocity during stance (modified from Gabaldon et al., 2008).

to such limitations on power output. Muscle work applied to elastic elements over the course of a relatively slow muscular contraction can be released rapidly to produce transient power outputs that exceed the capacity of the muscle (Fig. 1B). The energy released by the tendon is equal to (or slightly less, given some tendon energy loss) the work done by the muscle, but it is released in a shorter amount of time to produce higher power outputs (power=work/time). This mechanism makes it possible to uncouple the work of the muscle from the work done on the body or limbs, and allows for power outputs that exceed the maximum power capacity of the muscle. It is important to note that the term 'amplification' is potentially misleading, in that familiar electronic power amplifiers work by adding energy to a power source. Elastic mechanisms in animals do not add energy to the system, but rather amplify power only in the sense that they release energy more rapidly than it is stored.

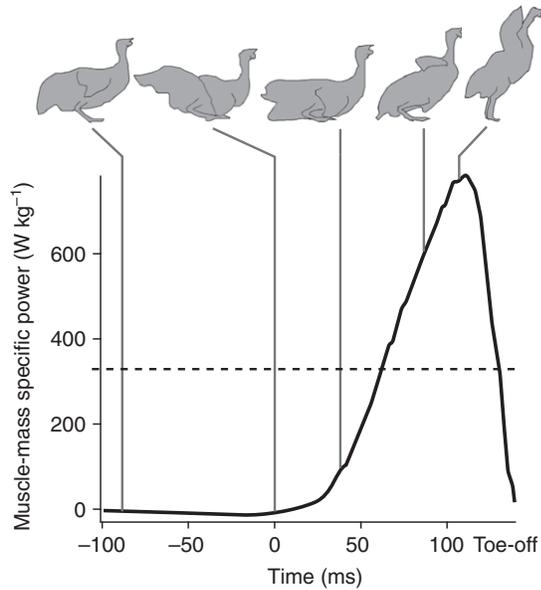


Fig. 4. Profiles of amplified power. Muscle-mass specific power output in a jumping guinea fowl. The power developed during a jump shows an asymmetric profile with peak power occurring late in the jump. In addition, the power achieved during the jump exceeds the estimated peak power output of the hindlimb muscles (dotted line) by more than a factor of two. Taken together, the patterns observed in this jump are consistent with the use of elastic mechanisms to amplify power output (modified from Henry et al., 2005).

Jumping is an activity for which power amplification is potentially beneficial because the time available to produce power once the acceleration of the body begins is limited, and the time available to generate power before the jump begins is not. Power-amplifying mechanisms are typically detected in jumpers by comparing the power developed during a jump, as measured by inverse dynamics or force-plate ergometry, to the total power available from the recruited muscles. Evidence for an amplifying mechanism exists when the peak power output of a jump exceeds the power-producing capacity of the muscles involved (Fig. 4). Systems using elastic-based power amplification also typically display an asymmetric power profile, with most of the power applied to the body late in the jump (Aerts, 1997; Roberts and Marsh, 2003; Henry et al., 2005) (Fig. 4). An elastic mechanism for muscle power amplification also appears to be essential to jumping success in bushbabies (Aerts, 1997) and frogs (Peplowski and Marsh, 1997; Roberts and Marsh, 2003), and even in animals not specialized for jumping, such as birds (Henry et al., 2005) (Fig. 4) and humans (Bobbert, 2001).

The shuttling of energy through tendon springs may provide a mechanism to decouple the timing of muscle work production and body movement that is useful for a wide range of activities. Hof proposed that the brief burst of power at the ankle late in the stance phase of walking in humans involves an elastic ‘catapult’ mechanism powered by elastic energy storage in the Achilles tendon (Hof et al., 1983). This idea is supported by a recent successful design for an ankle prosthesis, which incorporates elasticity both in series and in parallel with the ankle motor, in part to provide the necessary power density late in the stance phase of

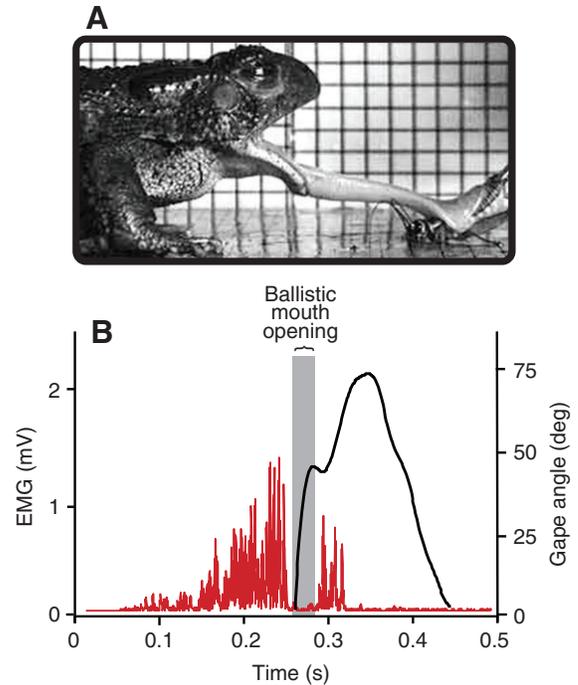


Fig. 5. Power amplification in ballistic tongue projection. The jaw depressor of toads is active for 250 ms prior to mouth opening. Ballistic mouth opening occurs in about 20 ms with no EMG activity. This observed pattern is consistent with the use of elastic mechanisms that are loaded slowly during the pre-activation phase and released quickly during the ballistic phase. Gape angle is indicated in black and EMG signal in red (modified from Lappin et al., 2006).

walking (Au et al., 2008). A particularly dramatic catapult-like mechanism also occurs during limb swing in horses. Power output of the biceps brachii is amplified by more than 50 times during a rapid burst of power to initiate limb protraction (Wilson et al., 2003). Accelerating animals may also benefit from the temporal redistribution of muscle work via elastic elements. For example, high power outputs in accelerating turkeys provide evidence of the use of elastic mechanisms (Roberts and Scales, 2002). These examples come from systems that are amenable to study or for which the amplification of power is particularly dramatic, but it is likely that elastic mechanisms resulting in modest power amplification are widespread.

Some feeding mechanisms also make effective use of elastic power amplification, and to our knowledge are the only vertebrate motions for which the kind of anatomical latch/trigger mechanism common to invertebrate catapult mechanisms (e.g. Bennet-Clark, 1975) has been identified. Some species of toads, salamanders and chameleons use catapult-like mechanisms to rapidly protrude their tongues during feeding. Ballistic tongue projection mechanisms in salamanders have evolved independently at least three times, and these systems are capable of power outputs that are an order of magnitude greater than that of the muscles associated with tongue projection (Deban et al., 2007). Toads also use an impressive amplification system associated with rapid jaw opening. The catapult-like action of the depressor mandibulae in toads is reflected in the decoupling of the timing of muscle activity, which begins in the 250 ms period before jaw movement, and the rapid jaw depression event that lasts only 20 ms (Lappin et al., 2006) (Fig. 5). Some very rapid feeding mechanisms in fish also appear

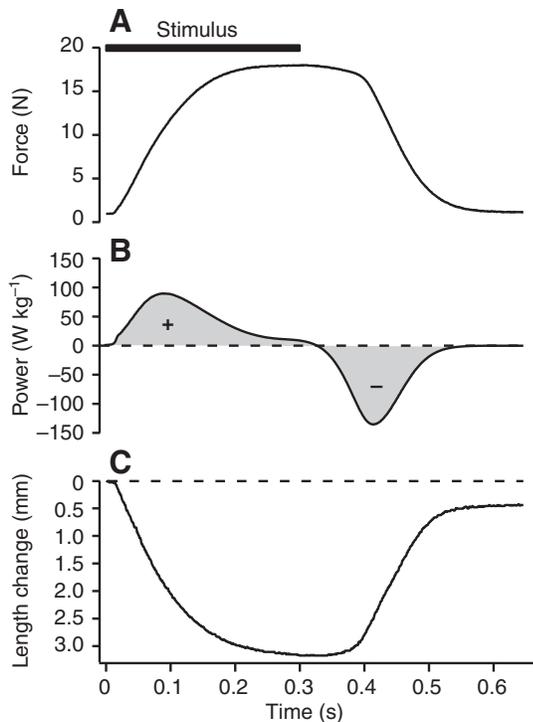


Fig. 6. Internal cycling of energy in a muscle–tendon unit. (A) Muscle force, (B) fascicle power and (C) fascicle length in a fixed-end contraction (i.e. the muscle–tendon unit is isometric) illustrate the possible negative consequences of internal energy cycling. The mechanical work produced by the muscle is loaded into the tendon (positive power phase) and then released back into the muscle fascicles (negative power phase). No external work is performed, but fascicles produce and absorb work. This type of futile energy cycling could occur *in vivo* if the timing and magnitude of muscle activity is poorly matched to the kinetics and kinematics of movement or relative to the timing of release of a catch mechanism. Measurements were taken on frog plantaris muscle, using sonomicrometry to measure fascicle length and a servomotor to measure muscle force (Azizi and Roberts, 2010).

to use an elastic power-amplifying mechanism. Pipefish generate muscle mass specific power outputs of more than 5000 W kg^{-1} to rapidly elevate their head towards prey (van Wassenbergh et al., 2008), and modeling evidence indicates that rapid jaw depression in a suction-feeding cichlid involves a catapult-like latch and trigger mechanism (Aerts et al., 1987). This kind of decoupling in the timing of muscle work and movement would seem to require a true catapult mechanism, in which the storage and release of energy is controlled by a latch/trigger mechanism.

What is the benefit of temporarily storing muscle work in elastic structures before releasing it to effect movement? The most obvious benefit, already described, is that energy storage and release in springs allows power outputs that exceed the power available from the muscle motors. However, there are several other less obvious potential benefits of the uncoupling of muscle work from work on the body. During locomotor movements, the storage of muscle work in elastic elements may allow muscles to perform work during a period (of a stride cycle, for example) when the application of power to the body or limbs is constrained by kinematics or kinetics. Alternatively, elastic mechanisms may allow muscles to produce power at lengths and/or velocities that are most favorable for performance given muscle force–velocity or length–tension properties (e.g. Wainwright et al., 1978). Finally, muscle power

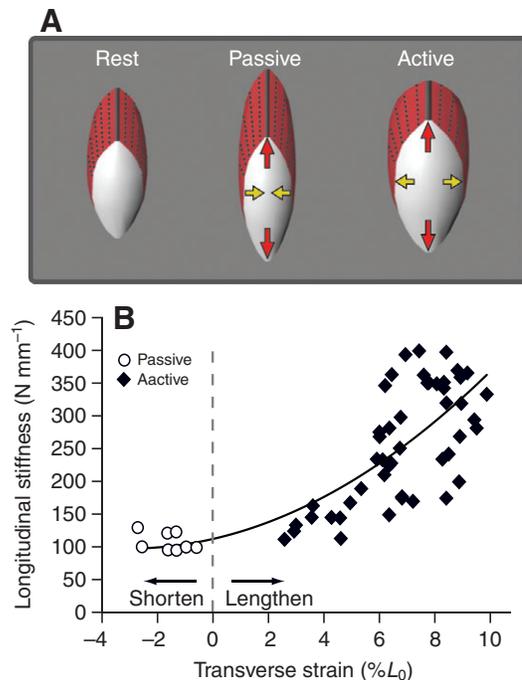


Fig. 7. Variation in aponeurosis stiffness with biaxial loading. (A) A schematic of aponeurosis behavior during active and passive force production. (B) The longitudinal stiffness of aponeuroses (along the muscle line of action) as a function of transverse strain. L_0 is the resting length of the aponeurosis. When the tissue is loaded biaxially during active force production the effective longitudinal stiffness of the elastic structure increases. This figure highlights the capacity of aponeuroses to function across range of stiffnesses dynamically (modified from Azizi and Roberts, 2009).

output is strongly dependent on temperature, with typical Q_{10} values of 2 or more (Bennett, 1985). For ectotherms, the temporal separation of muscle work from work done in movement may free performance from potential temperature constraints. This was demonstrated recently for the elastic tongue projection mechanism in chameleons (Anderson and Deban, 2010). The mechanical power developed to project the tongue decreased by only about 50% over a 20°C decrease in temperature, whereas the power developed by the tongue retractor mechanism decreased more than 600% across the same temperature range (Anderson and Deban, 2010). The use of thermally insensitive elastic mechanisms may provide organisms an expanded thermal niche for select behaviors (Anderson and Deban, 2010).

Muscles not only produce mechanical power, they also absorb it. The role of elastic mechanisms in energy absorption has received less attention than for power generation, but tendons may play an important role in activities that require the dissipation of mechanical energy. Studies on isolated muscle–tendon preparations (Griffiths, 1991) and *in vivo* studies have demonstrated that rapid stretches applied to muscle–tendon units can be taken up by the stretch of tendons, sometimes so effectively that the muscle remains isometric (Reeves and Narici, 2003) or shortens (Griffiths, 1991) during the ‘eccentric’ (muscle–tendon unit lengthening) event. Griffiths (Griffiths, 1991) proposed that this action provides a mechanical buffer against damage to muscles, which are particularly susceptible to damage when muscle fibers are actively lengthened (Proske and Morgan, 2001; Lieber and Friden, 2002). Of course, tendons cannot completely insulate muscles from active lengthening. The net

absorption of energy can only be achieved by active lengthening of muscle fibers, as the energy temporarily stored in stretched elastic elements must be released. Just as muscle fibers must be the ultimate source of energy in power-producing events, muscle fibers must be the sink for energy when muscle–tendon units act to reduce the energy of the body or a body segment. Thus, the initial stretch of tendon in an activity like a jump landing is followed by a period in which the tendon releases its potential energy by recoiling to stretch active muscle fibers (Fig. 1C). Is there an advantage to having the work done on the muscle by the tendon rather than direct absorption from the environment? This mechanism may be important in that it provides for attenuation of power input to muscle contractile elements (Roberts and Azizi, 2010). Just as power amplification by tendons allows for power outputs beyond a muscle's capacity, power attenuation via tendons may allow muscle–tendon systems to absorb energy at a rate beyond the muscle's maximum capacity for energy absorption. This elastic mechanism can result in reductions in the peak power input, lengthening velocity, and force experienced by lengthening muscles. These factors have been associated with muscle damage (Proske and Morgan, 2001; Lieber and Friden, 2002), thus the shuttling of energy through tendons before it is absorbed by muscles may provide a protective mechanism.

Challenges associated with biological springs

This Commentary, like most of the literature, focuses on the beneficial effects of elastic mechanisms. Yet the placement of passive springs in series with active actuators presents some potential challenges to locomotor control, energetics and mechanics. Human-engineered powertrains are typically designed to maximize stiffness in coupling the motor to the load in order to provide precision of position control, rapid force development, and to reduce the chance of unstable oscillations (Pratt and Williamson, 1995). In nature, some features of elastic systems must in part be designed to avoid some of these potential tradeoffs, and to minimize their consequences. To give one illustration of the potentially negative consequences of series elastic springs, Fig. 6 presents muscle power, force and length for a single fixed-end contraction. In this contraction the origin and insertion of the muscle are fixed, and therefore the entire muscle–tendon unit remains isometric. Upon stimulation, muscle fascicles shorten as the tendon is stretched, and subsequently lengthen as the tendon recoils. The pattern in Fig. 6 illustrates three potentially significant consequences of tendon action in this 'isometric' contraction. First, the rate of force rise is slowed by the fact that in the process of stretching the tendon, the muscle shortens and its force output is reduced by muscle force–velocity properties. Second, the muscle actually develops significant power and does work to develop force (Fig. 6B), even though the system does no external work. In the context of the schematic of Fig. 1, this example provides a fourth pattern of energy flow, from muscle to tendon and back to muscle again. Muscles consume more energy when they generate force while performing work, thus an 'isometric' contraction in a system with a tendon is presumably more costly than if the system operated without a tendon. A final effect is that the energy loaded into the tendon spring is released to stretch the muscle fascicles and do work on them. This illustrates a control challenge inherent in systems powered by muscle–tendon units. Energy loaded into tendons has the potential to backfire, recoiling against the muscle itself rather than unloading its energy to power movement. The pattern of muscle activation – for example, in power-amplifying mechanisms – is presumably tuned to ensure that energy flows in the desired direction in the muscle–tendon system.

The nature of the springs

As our understanding of the uses of springs in animal movement has advanced, so has our understanding of the nature of the springs. Familiar tendon springs, connective tissue elements (e.g. epimysium, perimysium) that hold muscles together, and the molecular constituents of muscles themselves all provide spring-like actions that may significantly influence muscle and locomotor function. Many of these springs are also quite dynamic, and key parameters, such as stiffness, can be modulated *via* both rapid and long-term mechanisms.

For tendon springs to operate effectively, their mechanical properties must be matched to their function. A key parameter for elastic mechanisms is tendon stiffness, and there is increasing evidence that the stiffness of a tendon is 'tuned' by remodeling to allow for the effective operation of the muscle–tendon-load system. Several studies have now documented significant increases in tendon stiffness in response to long-term exercise (Buchanan and Marsh, 2001; Arampatzis et al., 2007). There is not yet a consensus on whether such exposure to a loading regime results in changes in tendon dimensions (Kasashima et al., 2002), material properties (Buchanan and Marsh, 2001), or both (Seynnes et al., 2009). What is clear from these studies, however, is that tendon properties are more plastic than previously thought. The dynamic response of a tendon to loading has been demonstrated even in very short timescales. Recent studies have documented increased blood flow and metabolic energy consumption in tendons during periods of heavy exercise (Kjaer et al., 2005; Hannukainen et al., 2005), illustrating the robust metabolic infrastructure available to promote changes in tendon mechanical properties.

Variation in tendon stiffness over very short time scales, such as during a single muscle contraction, also appears to occur in some muscle–tendon systems. For many muscles, a significant portion of the tendon is an aponeurosis. Sheet-like aponeuroses are continuous with the free portion of the tendon and extend over the muscle belly to provide an attachment surface for muscle fascicles. Several studies have noted what might be considered unusual behavior for a structural spring: the stiffness of the aponeurosis (as measured by muscle force and aponeurosis longitudinal strain) appears to be different during active contractions when compared with passive loading (Zuurbier et al., 1994; Lieber et al., 2000; Azizi and Roberts, 2009) (Fig. 7). The explanation for this behavior appears to be that transverse (e.g. orthogonal to the line of action) expansion of the muscle during active contraction loads aponeuroses biaxially, which tends to alter their effective stiffness measured in the longitudinal direction (Azizi and Roberts, 2009) (Fig. 7). This mechanism provides for the possibility of rapid and dynamic changes in effective tendon stiffness during muscle contractions. The implications of this dynamic modulation of stiffness for the energetics and mechanics of locomotion have yet to be fully explored.

Relatively poorly understood is the extent to which the elasticity of connective tissue structures within the muscle has significance for muscle or locomotor function. The hierarchical organization of muscle tissue relies on organized connective tissue wrappings – epimysium, perimysium and endomysium – that together comprise an extensive connective tissue skeleton within muscles. The elasticity of intramuscular connective tissues is part of the 'parallel' elasticity of muscles that acts to resist passive stretch. Intramuscular connective tissues are considered crucial for the lateral transmission of force between adjacent fibers (Huijing, 1999), different heads of the same muscle (Huijing et al., 1998) or two synergistic muscles (Huijing et al., 2007). In addition, these structures can encapsulate muscle groups in tightly packed compartments and may serve an

important function in maintaining intramuscular pressure (Purslow, 2002) and controlling muscle shape changes (Azizi et al., 2008) during contraction. What is currently unclear is the degree to which intramuscular connective tissues utilize elastic mechanisms as they transmit and bear the loads generated by muscle.

Elastic function is also present in the molecular springs of the sarcomere. Recent biophysical studies have established the presence of elasticity in several regions of the actomyosin cross-bridge (Veigel et al., 1998). Myofilament stiffness has been shown to be non-linear (Edman, 2009), and to vary dynamically depending on the cross-bridge state (Brenner et al., 1982) or the pattern of length changes (Mantovani, 1999). Similarly, the mechanical behavior of the giant cytoskeletal protein titin has been characterized as spring-like (Granzier and Labeit, 2006). Early observations had suggested a largely passive role for titin's elasticity (Maruyama et al., 1977). However, titin stiffness has been shown to increase in the presence of calcium and may therefore contribute more dynamically to the force capacity of the sarcomere upon activation (Labeit et al., 2003). Changes in titin isoforms, which vary in their stiffness, may also occur in response to long-term exposure to loading in order to better tune this molecular spring to a muscle's mechanical function (Lindstedt et al., 2002). Our rapidly advancing knowledge of the molecular springs of muscles will provide exciting opportunities for future integrated studies that aim to reveal the function of these elastic structures during movement.

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