



SYMPOSIUM

Some Challenges of Playing with Power: Does Complex Energy Flow Constrain Neuromuscular Performance?

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Synopsis Many studies of the flow of energy between the body, muscles, and elastic elements highlight advantages of the storage and recovery of elastic energy. The spring-like action of structures associated with muscles allows for movements that are less costly, more powerful and safer than would be possible with contractile elements alone. But these actions also present challenges that might not be present if the pattern of energy flow were simpler, for example, if power were always applied directly from muscle to motions of the body. Muscle is under the direct control of the nervous system, and precise modulation of activity can allow for finely controlled displacement and force. Elastic structures deform under load in a predictable way, but are not under direct control, thus both displacement and the flow of energy act at the mercy of the mechanical interaction of muscle and forces associated with movement. Studies on isolated muscle-tendon units highlight the challenges of controlling such systems. A carefully tuned activation pattern is necessary for effective cycling of energy between tendon and the environment; most activation patterns lead to futile cycling of energy between tendon and muscle. In power-amplified systems, “elastic backfire” sometimes occurs, where energy loaded into tendon acts to lengthen active muscles, rather than accelerate the body. Classic models of proprioception that rely on muscle spindle organs for sensing muscle and joint displacement illustrate how elastic structures might influence sensory feedback by decoupling joint movement from muscle fiber displacements. The significance of the complex flow of energy between muscles, elastic elements and the body for neuromotor control is worth exploring.

Introduction—a downside to complex energy flow?

In the fall of 2018, the company Rethink Robotics closed its doors. This was a disappointment to the research community, because the company produced the robot Baxter, a popular platform for exploring control algorithms for robotic movement, primarily positioning and placing. News reports suggested that a significant and possibly fatal challenge for the platform was the use of series elastic actuators. Actuators in series with elastic elements endowed the robot with a flexibility that was desirable for safe human–robot interaction, but possibly at the cost of precision of movement. One roboticist was quoted as saying “It is extremely difficult to control a flexible manipulator, especially when trying to minimize cycle times. Thus, Rethink probably spent too much effort trying to fix hardware problems

through software” (<https://www.therobotreport.com/rethink-robotics-shutdown/>).

Human engineered systems are of course different from biological systems, but the challenges faced by engineers can inform our understanding of challenges that biological systems may have overcome. Biologists have long been interested in the role of elastic elements in animal movement, and the consensus, as reflected by contributions to this symposium, is that the relatively complex flow of energy between elastic elements, actuators, and the body is beneficial and reflects selection for locomotor performance. In the engineering literature, it is common to find arguments against compliance and in favor of a direct transmission of actuator power to movement. Such arguments in the biological literature are rare. The goal of this review is to assess our current understanding of the challenges that the complex flow

of energy may place on organismal movement and design, to review where these challenges have been recognized, and to explore where they have not.

Patterns of energy flow and their function in biological systems

Researchers have identified a number of features of elasticity associated with biological actuators that appear to be beneficial for a wide range of movements. Previously, my coworkers and I considered the particular case of muscle-tendon systems, and offered the idea that the task accomplished by elastic tendons in muscle powered systems varies, and can be categorized by the path and direction of energy flow between three elements: the body, muscle, and tendon (Fig. 1; Roberts and Azizi 2011). Power amplification, for example, occurs when muscles contract relatively slowly to stretch tendons, and the subsequent recoil of this tendon rapidly accelerates the body or a body part. The flow of energy is muscle \rightarrow tendon \rightarrow body. A less familiar example, which we called power attenuation, involves a flow of energy in the direction body \rightarrow tendon \rightarrow muscle. That is, energy (potential or kinetic) is converted to elastic strain energy, followed by tendon recoil acting to stretch active muscle, which forcibly lengthens, ultimately converting this energy to heat. Power attenuation occurs in activities like landing from a jump, or in walking down stairs. As the flow of energy varies, so does the potential benefit. Power amplification allows for power outputs that exceed the capacity of isotonic muscle alone, and can therefore significantly improve performance for movements like jumping. Power attenuation reduces the power input to muscles as they dissipate energy, and it has been suggested that this reduces the risk of muscle injury (Griffiths 1991; Reeves and Narici 2003; Roberts and Konow 2013; Konow and Roberts 2015). Muscles are particularly prone to damage when they actively lengthen (Proske and Morgan 2001).

In the context of the pathway for energy framework outlined above, the benefits of spring-driven systems are proposed to be: (1) Energy cycling: springs do not consume metabolic energy when they cycle mechanical energy, and therefore have the potential to operate more cheaply than muscle (though this assumption has been challenged (Holt et al. 2014)); (2) Power amplification: springs may ultimately have a power limit (Ilton et al. 2018), but this limit is many times greater than the maximum power output of muscle and so springs can power movements that muscle alone cannot; and (3) Power

attenuation: high rates of loading do not appear to be particularly harmful to tendons, while they are to muscles (Armstrong et al. 1983; Proske and Morgan 2001). These are all quite different benefits, but all relate ultimately to the fact that tendon elastic function does not involve a complex and somewhat delicate cellular machinery or enzymatic processes, while muscle contraction does.

The potential benefits of elastic mechanisms in movement have received more attention than their potential costs. In the case of biological springs, the cost, as the benefit, may rest in the simplicity of their function. According to Hooke, “as the extension, so the force” (Hooke 1678). The implications of this law for biological movement are two-fold: (1) springs do what they do, their displacement and force cannot be directly prescribed by the nervous system; and (2) the coupling of extension and force results in constraints on movement dynamics. Below I explore the implication of these features of biological springs, with the goal of identifying challenges that may be worth further exploration, as well as documenting instances where challenges have already been demonstrated.

Challenges to complex energy flow—constraints on dynamics

A load driven through oscillating movements by a spring will fall naturally into a rhythm that is defined by the mass and the stiffness of the spring. This idea that a spring-mass system has a natural frequency suggests a possible constraint for spring-driven movements like running, and indeed it has played a significant role in the development of our understanding of how running works. McMahon and Cheng (1990) developed a model of a runner as a simple spring-mass system to determine whether the dynamics of running could be described if the leg is modeled as a simple spring (Fig. 2). On a first look, some features of the dynamics of running seem inconsistent with spring-like function of the leg. The stride length and stride frequency increase with running speed, and the time of foot contact decreases. A change in frequency across speed seems at first inconsistent with a spring-driven system, because a spring-mass system should have only one natural frequency. The insight of McMahon and Cheng (1990) was that the geometry of limb loading allowed for a single leg stiffness but a variable effective stiffness in the vertical direction. The model predicts mathematically that by varying the angle of the leg at landing and takeoff (and therefore the total angle swept), the effective vertical stiffness

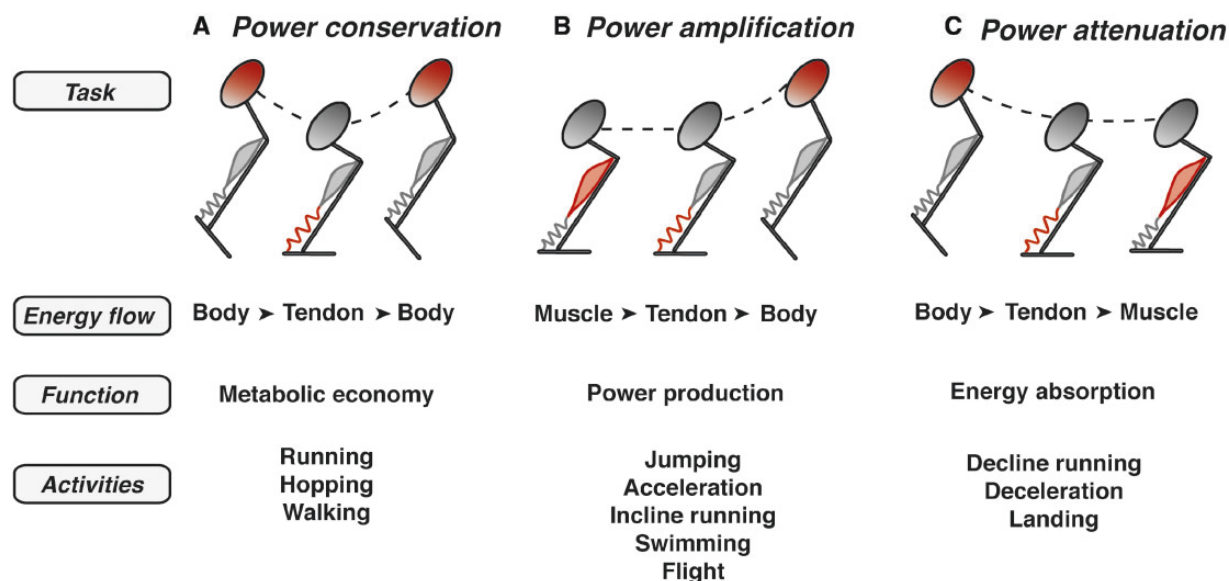


Fig. 1 The tasks that muscle-tendon systems perform can be categorized by the pathway that energy takes during locomotion. Each set of drawn figures represent a time sequence, where the flow of energy is indicated by the element drawn in red. For example, in the power conservation example, kinetic and gravitational potential energy of the body are converted to elastic strain energy in tendon, which is then converted back to kinetic and potential energy. Modified from [Roberts and Azizi \(2011\)](#).

(k_{vert}) could vary even as the leg stiffness (k_{leg}) remained constant. The variable vertical stiffness could explain changes in stride length and frequency with running speed. Data from a variety of animals supported the model, showing that leg sweep angle followed the predictions of the model ([McMahon and Cheng 1990](#)). [Blickhan \(1989\)](#) also modeled the leg as a spring, and was able to show that such a model explains dynamic features of both running and hopping.

The classic studies of [Blickhan \(1989\)](#) and [McMahon and Cheng \(1990\)](#) formed a foundation of many subsequent studies in both biological and robotic systems showing that runners are well-explained by a simple spring mass model. An alternative lesson to be taken from this work is that spring-driven systems can impose constraints on dynamics. The model suggests that the kinematics of leg motion is constrained by the need to load the limb spring effectively to provide the motion we observe during stance. Departing from the stride kinematics prescribed by spring-mass dynamics comes at a cost of increased metabolic energy consumption. ([McMahon et al. 1987](#); [Snyder and Farley 2011](#)). [Blickhan \(1989\)](#) emphasized this constraint by pointing to the relatively small range of hopping frequencies that humans can maintain, from a preferred frequency of about 2 hops s^{-1} to a maximum of about 6 hops s^{-1} . It is also illustrated effectively with measurements of the metabolic cost of running at different stride frequencies. At a given speed, the

cost of running increases at frequencies above and below the freely chosen frequency ([Hogberg 1952](#); [Cavanagh and Williams 1982](#); [Snyder and Farley 2011](#)). This suggests an energetic cost associated with moving away from a frequency determined by spring-like mechanics. Spring-mass systems can operate at frequencies other than the natural frequency if there is a driver (such as muscle), but this departure from the natural frequency comes at a cost.

Studies of human hopping also provide evidence that cyclic movements are constrained by the spring-like behavior of the limb and spring-mass dynamics. When humans hop at frequencies above their preferred frequency, their virtual leg stiffness (the ratio of peak force to peak body displacement) increases, suggesting that this stiffness is modulated to keep the system near its natural frequency ([Farley et al. 1991](#)). Modulation of leg stiffness is also a mechanism humans use to maintain similar center of mass movements when hopping on surfaces of different stiffnesses ([Farley et al. 1998](#)). Changes in knee geometry and ankle stiffness have been identified as mechanisms for changing leg stiffness on different surfaces ([Farley et al. 1998](#)). It should be pointed out that humans do appear to depart from spring-like limb behavior under some conditions. At hopping frequencies below preferred, body mass dynamics depart from the tight correlation between leg displacement and force that is expected for spring-like behavior ([Farley et al. 1991](#)). And, when hopping on very compliant surfaces, the leg engages in

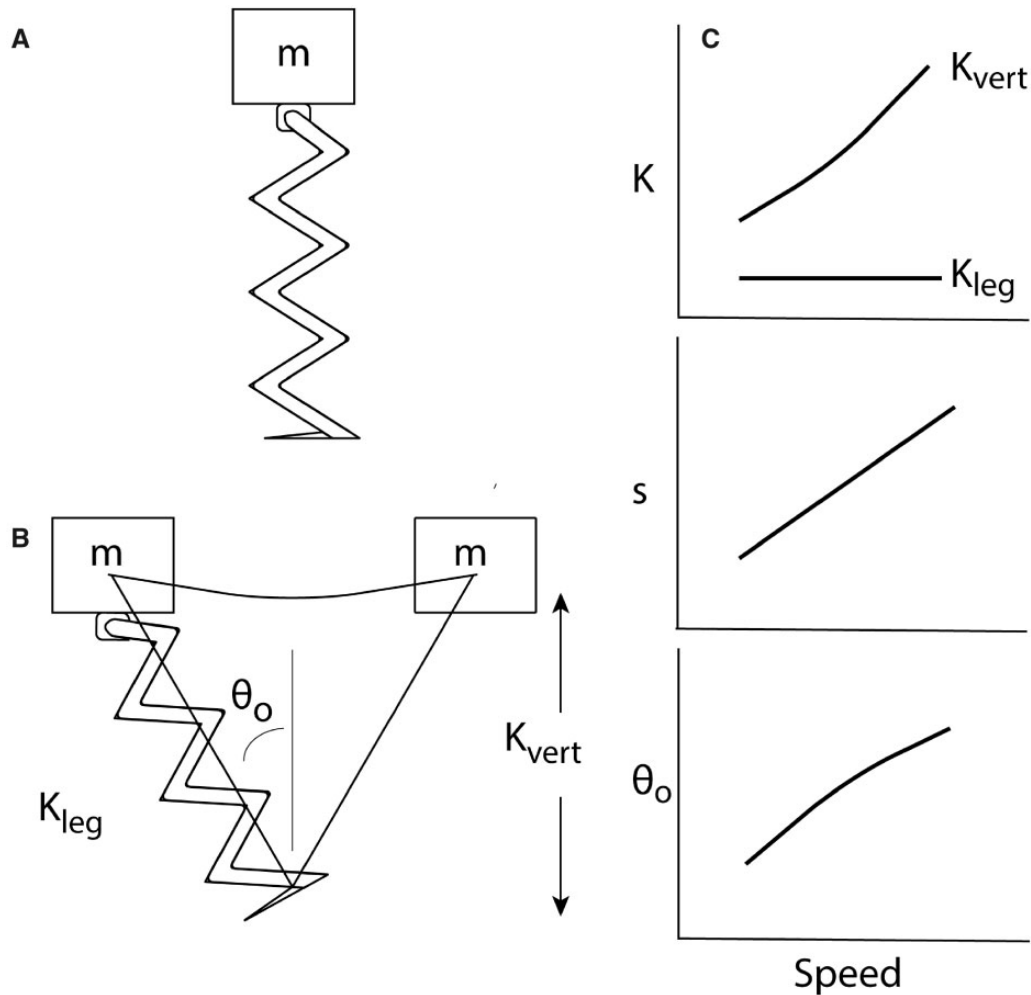


Fig. 2 Schematic representation of McMahon and Cheng's model of the leg spring in running. The limb is modeled as a simple spring and the body as a mass (A). In running, this spring is compressed and follows an arced trajectory (B). Two stiffnesses can be defined. The leg stiffness (K_{leg}) is the ratio of the ground reaction force to the compression of the leg spring. The vertical stiffness (K_{vert}) is the ratio of the displacement in the vertical direction to the ground reaction force. (C) Results from a model where K_{leg} is held constant. Under these conditions, K_{vert} and the initial contact angle (θ_o) are outputs of the model that match empirical data for stride frequency (s) from running dogs, rhea, and humans (not shown). Figures based on those in McMahon and Cheng (1990).

distinctly nonspring-like behavior, extending before compressing (Moritz and Farley 2005). Such action comes at a cost, as indicated by the greater muscle activation observed on compliant surface hopping (Moritz and Farley 2004).

Time constraints related to elastic mechanisms have received less attention in ballistic movements compared to cyclic movements. Rosario et al. (2016) used a muscle-tendon simulation to ask whether the time course of elastic energy storage during pre-loading influenced the ultimate power in a ballistic, catapult-like system. They asked whether the observed values for tendon stiffness in two hoppers, bullfrogs and grasshoppers, reflected demands on the time course of elastic energy loading. Agreement between the predicted optimal tendon stiffness given time constraints on loading and

the observed stiffness in frog and grasshopper elastic structures supported the idea that timing influences morphology and ultimately the maximal performance that can be achieved in catapult like systems (Rosario et al. 2016).

Challenges to complex energy flow II—directing the flow

Most analysis of the flow of energy through biological springs takes for granted that the flow will occur in the intended direction. However, evidence from both *in vivo* measurements and isolated muscle measurements and modeling suggest that this is not always the case, and that controlling the direction of flow may pose challenges. In power attenuation, energy stored temporarily in elastic elements is

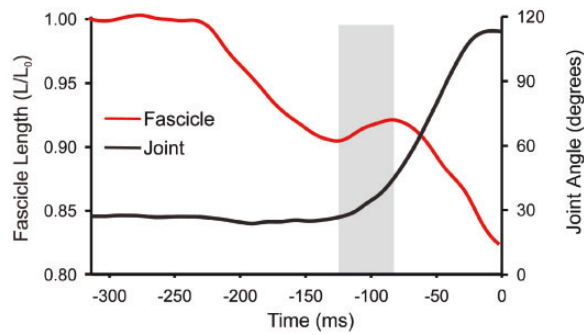


Fig. 3 Motion of the plantaris fascicles (red) and the ankle joint (black) during jumping in a bullfrog. Muscle fibers shorten before joint movement, indicating preloading of elastic elements. The period of “elastic backfire” is highlighted in the gray rectangle. During this period, the fascicles lengthen even as the joint extends, indicating that the recoil of stretched elastic elements acts to lengthen contractile elements. Modified from [Astley and Roberts \(2012\)](#).

then released to do work lengthening contractile elements, where the energy is then dissipated. This is desirable in situations where energy dissipation is required, such as in landing from a jump, but in other situations the release of energy from elastic elements to contractile elements is presumably counterproductive and wasteful. Some studies suggest that in systems where power is required, such wasteful energy cycling can occur. [Astley and Roberts \(2012\)](#) measured length changes in frog plantaris muscle fibers while also measuring ankle extension. Early shortening of muscle fibers, before ankle extension, indicated a pattern of elastic preloading. This preloading was followed, as expected, by rapid extension of the ankle, powered in part by elastic energy release. However, in many of the jumps, there was also a brief period of muscle fiber lengthening during ankle extension ([Fig. 3](#)). This lengthening appears to represent the backflow of elastic energy from tendons or other elastic structures to the contractile element. Such “elastic backfire” presumably represents a loss of power, and is therefore counterproductive ([Astley and Roberts 2012](#)). The amount of lengthening observed in frog jumping was quite small, but the observation highlights that ensuring that energy flows in a desirable direction is a challenge that power amplifying systems must meet. In frogs, the muscle firing pattern as indicated by electromyography suggests that control throughout the jump is modulated to maintain a muscle activation pattern that provides for proper energy flow. In most jumps, a burst of electromyography (EMG) coincident with the period where muscle fiber lengthening is sometimes observed suggests that force is modulated throughout the jump to control the flow of energy from loaded

elastic elements to the body ([Azizi and Roberts 2010](#)).

Modeling and *in vitro* muscle studies also suggest that elastic backfire, or the undesirable flow of elastic energy to muscle contractile elements, may pose a challenge to cyclic muscle actions. [Richards and Sawicki \(2012\)](#) simulated muscle-tendon function in swimming frogs and showed that series elastic elements could improve power output under the right conditions, but for many combinations of muscle properties, tendon properties, and mechanical advantage, the system performed worse than when there was no series elasticity. In many cases, this reduced performance was explained by the release of significant elastic energy back to the contractile element. Power flow was determined by the combination of muscle dynamics and forces due to fluid dynamics, and under many conditions, this interaction dictated that energy stored in the elastic element would flow back into the contractile element, thus wasting previous muscle work and reducing total power output ([Richards and Sawicki 2012](#)).

[Sawicki et al. \(2015\)](#) drove a muscle tendon unit through sinusoidal lengthen-shorten cycles meant to mimic the behavior expected during activities like running, with the goal of identifying the stimulation phasing that allowed for tendon to do most of the cyclic work. In an “ideal” energy conserving system, the tendon would store and recover all cyclic work while the muscle contractile element remains isometric. In an isolated muscle-tendon system under phasic maximal activation, getting even close to this ideal was difficult ([Sawicki et al. 2015](#)). In many cases, the muscle shortened to stretch the tendon, and in others the tendon did work on the contractile element to stretch muscle fibers. Isolated muscle studies have some shortcomings when it comes to mimicking the pattern of muscle action that occurs *in vivo*, and in particular the fact that these studies used symmetric (sine wave) lengthen-shorten cycles, and maximal muscle activation may present a limitation. Modulation in motor unit recruitment, asymmetric lengthen-shorten cycles, and possibly morphological features such as variable muscle moment arms or gearing may all contribute to allowing for near-isometric muscle function that has been observed during running and hopping ([Roberts et al. 1997](#); [Biewener et al. 1998](#); [Bohm et al. 2018](#)). But the observations on isolated muscle-tendon systems demonstrate at least that achieving the proper flow of energy to allow for isometric muscle function is not trivial.

The dynamics of the interaction between muscle, tendon, and load may also play a role in “tuning”

muscle-tendon systems to allow for effective power flow. Robertson and Sawicki (2015) used a similar muscle-tendon preparation to that of Sawicki et al. (2015), and stimulated it cyclically, but instead of prescribing the motion they simulated the load imposed by an inertial mass. Under these conditions, they found that the system produced maximal forces when stimulation was timed to drive the mass at the spring-mass natural frequency. The observation of control that allowed for effective elastic energy storage and recovery without feedback (i.e., open loop) suggests that the dynamics of muscle-tendon-mass systems may have properties that simplify control (Robertson and Sawicki 2015).

Challenges to complex energy flow III—timing the flow

A potential issue that involves both timing and direction of energy flow is in the role of tendons in attenuation of power. It is hypothesized that a key benefit of attenuation of power by tendons is that it reduces the rate of energy absorption by muscle contractile elements, which in turn reduces peak power input, peak contractile element velocity, and peak forces (Roberts and Azizi 2010; Roberts and Konow 2013). For such attenuation to be effective, the tendon must release energy to the contractile element more slowly than it stores it. Does this pose a control challenge, and therefore a risk that a control error could allow for muscle damage? We have speculated that the normal dynamics of muscle contraction might safeguard against the rapid release of energy from tendon to the contractile element. Muscle deactivation requires an active process of Ca^{2+} pumping and this process is slower than the inflow of Ca^{2+} during activation associated with voltage-gated channels. This is evident in the asymmetric shape of the force curve for a muscle twitch. The release of elastic energy requires a decline in force, which in an activity like landing from a jump is likely determined by the process of muscle deactivation. Might the slow rate of muscle deactivation limit the rate of force decay, and therefore the rate of energy flow from tendon to muscle contractile element?

As a first pass at this question, we can compare a twitch from a muscle for which power attenuation has been studied, the turkey gastrocnemius, to the time course of force decay in the same muscle during a jump landing (Fig. 4). The twitch curve is asymmetric, showing the expected slower relaxation compared with activation. However, the jump landing involves a decline in force that is much slower than observed in a twitch, suggesting that the rate of

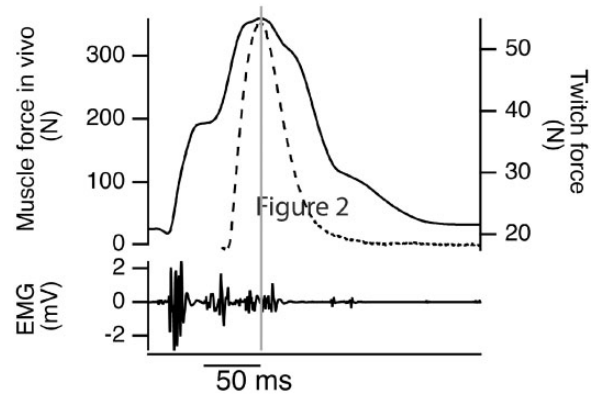


Fig. 4 Force developed in the turkey lateral gastrocnemius (top panel) during a landing (solid line) and during a twitch (dotted line, right-hand axis). The two force traces are aligned to match the timing of peak force. The twitch force profile indicates an upper limit to how quickly the muscle can relax following contraction. Force decay during landing is slower, indicating that the rate of muscle relaxation does not set a limit to the rate of force decay. An obvious EMG burst near the peak of force suggests modulation of muscle force to limit the rate of force decay. For measurement methods, see Konow and Roberts (2015).

decline of force is actively modulated by the timing of de-recruitment of motor units. The EMG signal for the landing shown Fig. 4 shows evidence of this motor control strategy, as the EMG signal lasts into the beginning of the period of force decay, and also shows evidence of additional recruitment over the period of force decay. This is just one trial, but the pattern suggests that the path and rate of energy flow requires active modulation by the nervous system, at least in this system.

It is tempting to speculate that a tuning of motor control patterns during eccentric activities may play a role in well-known phenomena related to muscle damage and delayed onset muscle soreness in humans. A number of different experimental approaches have demonstrated that eccentric exercise, such as walking downhill, can result in significant muscle soreness, but that just a single bout of such exercise confers a protective effect, so that subsequent bouts result in significantly less soreness (McHugh 2003; McHugh and Pasiakos 2004). Given the rapidity of this adaptation, it has proven difficult to identify a mechanism to explain it based on physiological mechanisms (e.g., tissue remodeling). Some changes in motor control patterns, as measured by EMG, have been detected from first to repeated bouts of eccentric exercise (McHugh 2003). It would be interesting to determine if a refined control of the flow of energy from series elastic elements to contractile elements might provide some explanation for the repeated bout effect.

Do elastic mechanisms simplify or complicate neuromotor control?

Mechanisms of neuromotor control in animals account for the complex flow of energy between the body, skeletal muscles, and elastic elements. This conclusion is sound; even if we do not know the mechanisms, because we know that coordinated movement happens under circumstances of complex energy flow. Previous examples in this review demonstrate several instances where complex energy flow requires a motor control strategy that accounts for the behavior of elastic elements, the dynamics of the load, and the nonlinear behavior of the actuator itself. What does not seem to be clear given the current state of understanding is whether the inclusion of elastic elements in muscle-actuated systems represents a cost with respect to neuromotor control, or a benefit. Do the mechanisms of power flow described above require additional computational overhead (as in the Baxter robot), are they less fault-tolerant (e.g., susceptible to an error in descending signals or environmental variability), or less accurate (e.g., in a positioning task)? Or is the opposite true, that elastic mechanisms simplify control, protect from errors and perturbations, and can improve positioning accuracy. To borrow a framework from computer engineering, from the standpoint of neuromotor control, is elasticity a bug, or a feature? The reason this is an interesting question is that researchers have made a case for both the idea that elasticity is beneficial for control and that it is detrimental. These arguments usually occur in isolation of one another. Below these isolated ideas, and their possible intersections, are discussed.

The idea that elasticity is a “bug” (i.e., it may decrease movement accuracy or increase computational overhead) is implicit or explicit in many studies of muscle-tendon system morphology. A primary concern is that the stretch of series elastic elements reduces the accuracy of fine position control, such as in dexterous fingertip positioning, because the stretch of the series elastic element may present an “error” in the translation of muscle length change to joint position. Ker et al. (1988) speculated that the need for accurate position control might explain why many mammalian muscles have tendons that are much thicker than necessary to avoid mechanical failure. Ward et al. (2006) loaded two human wrist flexors to the maximum force they would expect to see in life, and found that the strains under these conditions were quite low (0.7–1.7%). They suggested that this suits them well for fine positional control, because contractile

element length changes are faithfully transmitted to the skeleton.

In addition to concerns about the influence of elasticity on neuromotor output, a number of studies have highlighted the potential challenges that elasticity poses for sensory input. Muscle spindles provide position information by sensing muscle fiber length, and any stretch of series elastic elements potentially represent an error in translation from muscle fiber length to joint position (Griffiths 1991; Ward et al. 2006; Kistemaker et al. 2013). This challenge is perhaps best illustrated by the observation that during activities like walking, hopping, and landing, muscle fibers can shorten during early stance, just after foot contact, even though the muscle-tendon unit lengthens (Griffiths 1989; Griffiths 1991; Konow and Roberts 2015). Such observations call into question the assumption from early models that stretch of fibers immediately following foot contact modulates force during stance through reflexes triggered by the stretch of muscle spindles. Several mechanisms have been proposed to account for the lack of correspondence between muscle fiber length change and joint motion. Outflow through fusimotor efferents can act to define an expected movement, and deviations from this movement can provide information about position and movement that may be more accurate than a simple measure of muscle stretch (Hulliger 1984). It has also been proposed that the combined action of Golgi tendon organs and spindles can determine joint position because the Golgi tendon organs provide information from which tendon stretch can be determined and accounted for (Kistemaker et al. 2013).

The idea that elasticity is a “feature” is arguably intrinsic to many theories of motor control. Many models of motor control posit that tasks such as accurate positioning (e.g., as in manipulandum experiments) rely on a regulated joint compliance, that this compliant joint behavior is tunable to different tasks, and that it reduces sensitivity to perturbations (Houk 1979; Hogan 1985; Gottlieb 1994). The equilibrium-point theory of motor control, for example, models muscle actuation as a spring and posits that joint trajectories can be characterized by a neural signal that controls the equilibrium length of that spring (Feldman 1986; Gottlieb 1994). A challenge of interpreting what these models mean for the role of elastic structures in neuromotor control is that the structural basis for the joint spring-like behavior is unknown. The fact that joint compliance is tuned by different levels of muscle activation tells us that joint compliance under these circumstances must be largely due to muscle behavior that mimics

spring-like compliance, not necessarily that structural compliance is important (or constructive).

Models and measurements on individual muscles have provided evidence for some motor control benefits resulting from elastic structures. Rack and Ross (1984) studied the tendon of the flexor pollicis longus in humans under conditions of rapid oscillation, and also imposed measurements at the joint in a human subject. They suggested that the elastic tendon might reduce the accuracy of position control, but argued that series elasticity might benefit force control, such as occurs during a gripping task. Their data suggested that a small error in muscle activation, or a perturbation of limb position, would lead to a smaller change in force if a compliant tendon were present (Rack and Ross 1984).

The nervous system is slow, due to limits to nerve conduction velocities. In locomotion, this potentially limits an animal's ability to respond to a perturbation, such as a trip during running, because in some cases the mechanical response required to prevent a fall must occur in a time course that is too short for even the fastest reflexes (More et al. 2010; More and Donelan 2018). It has been recognized that the intrinsic properties of muscles, such as the length–tension and force–velocity properties, provide a rapid, dynamic response to perturbations that does not involve neural feedback. Loeb (1995) coined the term “preflexes” and defined such rapid responses owing to the properties of the actuators as “the zero-delay, intrinsic responses of a neuromusculoskeletal system to a perturbation” (Brown and Loeb 2000). Perturbations to running cockroaches demonstrate rapid responses that seem too fast to attribute to a reflex, and thus provide evidence of reflexes (Jindrich and Full 2002). This response can be modeled as a visco-elastic system (Jindrich and Full 2002), and thus is arguably spring-like.

It is difficult to know the extent to which structural elasticity (e.g., tendons or elastic elements within muscles) contributes to phenomena such as reflexes or noise rejection. Many of the theories described above emphasize muscle contractile element properties as providing the mechanism for rapid responses, for example, the length–tension and force–velocity properties of muscle can provide zero-delay responses to a perturbation, and in some cases can result in spring-like behavior (Feldman 1986; Brown and Loeb 2000). In robots, it has been demonstrated that compliant structures can provide reflex stabilization in running (Cham et al. 2004). It is more difficult to determine whether the spring-like behavior observed in controlled movements or responses to perturbations results

from actual elastic stretch and recoil. A controlled lengthen-shorten cycle of a muscle can produce joint behavior that is well-represented by a spring model, even if there is no actual spring involved (Alexander 1991). In studies of guinea fowl running over rough terrain Daley et al. found that the leg maintains spring-like behavior following a perturbation, even while individual joints were not spring-like (Daley and Biewener 2006; Daley et al. 2007). The study authors suggested that the limb's spring-like behavior may represent a control target, rather than necessarily a sign of an elastic response (Daley and Biewener 2006). However, they also noted that some of the rapid response seen in particular at distal joints may have been attributable to tendon function (Daley et al. 2007).

The fact that good arguments have been made both for the idea that elasticity is beneficial for neuromotor control in locomotion and the idea that it is detrimental suggests that this area is worthy of further study. It is interesting that this debate is ongoing in the world of legged robots, with good cases being made for the control benefits of series elastic actuators (Pratt and Williamson 1995) as well as for systems that minimize compliance (Seok et al. 2013). Future work will hopefully shed more light on the possible challenges and benefits that playing with power presents for animal locomotion.

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