

COMMENTARY

Beyond power amplification: latch-mediated spring actuation is an emerging framework for the study of diverse elastic systems

S. J. Longo^{1,*}, S. M. Cox², E. Azizi³, M. Ilton⁴, J. P. Olberding³, R. St Pierre⁵ and S. N. Patek^{1,*}

ABSTRACT

Rapid biological movements, such as the extraordinary strikes of mantis shrimp and accelerations of jumping insects, have captivated generations of scientists and engineers. These organisms store energy in elastic structures (e.g. springs) and then rapidly release it using latches, such that movement is driven by the rapid conversion of stored elastic to kinetic energy using springs, with the dynamics of this conversion mediated by latches. Initially drawn to these systems by an interest in the muscle power limits of small jumping insects, biologists established the idea of power amplification, which refers both to a measurement technique and to a conceptual framework defined by the mechanical power output of a system exceeding muscle limits. However, the field of fast elastically driven movements has expanded to encompass diverse biological and synthetic systems that do not have muscles – such as the surface tension catapults of fungal spores and launches of plant seeds. Furthermore, while latches have been recognized as an essential part of many elastic systems, their role in mediating the storage and release of elastic energy from the spring is only now being elucidated. Here, we critically examine the metrics and concepts of power amplification and encourage a framework centered on latch-mediated spring actuation (LaMSA). We emphasize approaches and metrics of LaMSA systems that will forge a pathway toward a principled, interdisciplinary field.

KEY WORDS: Elastic mechanism, Springs, LaMSA, Locomotion, Mechanical power output, Kinematics

Introduction

The power amplification framework was introduced when small insects, such as fleas and locusts, were discovered to jump with greater mechanical power output (see Glossary) than possible with muscle alone (Bennet-Clark and Lucey, 1967; Bennet-Clark, 1975). Instead, springs and latches (see Glossary) enable the enhanced power output of jumping insects. In the 50 years since the inception of this field, a great diversity of organisms have been discovered that use elastic mechanisms and latches to generate fast movements in small systems, including many that do not have muscles, such as plants and fungi (Edwards et al., 2005; Forterre et al., 2005; Noblin et al., 2009; Singh et al., 2011; Vincent et al., 2011; Deegan, 2012; Marmottant et al., 2013; Sakes et al., 2016; Liu et al., 2017; Poppinga et al., 2017; Roper and Seminara, 2019).

Biologists have historically used a mathematical inference to assess whether a given system uses elastic structures to enhance mechanical power output. This inference, called power amplification, applies a simple calculation that is centered on muscle power limits to infer the presence of elastic mechanisms, specifically by calculating the ratio of a movement's mechanical power output relative to maximum muscle power (Box 1) (Bennet-Clark, 1975; Gronenberg, 1996a; Patek et al., 2011; Roberts and Azizi, 2011).

Even though the power amplification inference focuses on the power limits of muscle, springs also experience an upper limit to mechanical power output, as do any actuators (see Glossary), whether biological or synthetic (Box 1) (Hill, 1938; Ilton et al., 2018; Rome and Lindstedt, 1998). Therefore, a cascade of mechanical power limits emerges when motors (see Glossary), springs and latches are integrated (Ilton et al., 2018; Galantis and Woledge, 2003). Crucially, studies of the mechanisms that circumvent power limits (i.e. power limits on muscle or other mechanisms that load energy into the system) are therefore more illuminating if the flow of energy through integrated systems of springs, latches and muscles/motors is analyzed, rather than focusing primarily on the constraints of one component, as has been the case for the focus on muscle in the power amplification framework.

We are now at a key juncture for establishing the fundamental principles of diverse biological and synthetic systems that actuate movement with springs, control energy release through latches and are integrated into diverse systems with tunable outputs. In this Commentary, we build on the historic power amplification framework to propose a framework based on the shared mechanics of these systems, which we term latch-mediated spring actuation (LaMSA) (Box 2). We consider the benefits and limits to the classic power amplification inference, and then examine approaches for the analysis of spring and latch dynamics. We conclude by recommending measurements of components and system outputs, with the goal of providing a pathway to rigorous analysis of latch-mediated spring-actuated systems.

Benefits and limits of the power amplification framework

In this section, we provide guidance for biologists interested in applying and correctly interpreting the power amplification framework. Power amplification provides researchers with a clever inference: if the mechanical power output of a movement exceeds that of muscle, then muscle should not be able to generate the movement (Box 1). Many biologists query systems in this way in order to infer whether or not the system relies on an elastic mechanism as the primary actuator (Evans, 1973; Bennet-Clark, 1975; Gronenberg, 1996a; Aerts, 1998; Burrows, 2003; Patek et al., 2004, 2011; Deban et al., 2007; Van Wassenbergh et al., 2008; Roberts and Azizi, 2011; Burrows and Dorosenko, 2015a,b).

Given that the power amplification inference discerns animal movements that are not directly powered by muscle, it requires comparisons of power outputs against a baseline and is most

¹Department of Biology, Duke University, Durham, NC 27708, USA. ²Department of Kinesiology, The Pennsylvania State University, University Park, PA 16802, USA.

³Department of Ecology and Evolutionary Biology, University of California Irvine, Irvine, CA 92697, USA. ⁴Department of Physics, Harvey Mudd College, Claremont, CA 91711, USA. ⁵Department of Mechanical Engineering, Carnegie Mellon University, Pittsburgh, PA 15213, USA.

*Authors for correspondence (sarah.longo@duke.edu; snp2@duke.edu)

© S.J.L., 0000-0001-5429-2473; S.M.C., 0000-0002-9704-0716; M.I., 0000-0002-2439-3940; J.P.O., 0000-0001-5426-9986; S.N.P., 0000-0001-9738-882X

Glossary**Actuator**

An actuator produces a movement or force. Springs, muscles and motors can all function as actuators.

Contact latch

A latch with the interaction of two or more structures that physically touch or move against one another. Contact latches include systems in which one component obstructs another, as well as systems in which friction or adhesion between parts mediates the storage and release of energy.

Fluidic latch

A latch mediated by the movement and properties of fluid within a system, including cohesion, coalescence and pressure.

Geometric latch

A latch with state-dependent behavior based on geometric configuration, forces, moment arms, location of the center of mass, etc. Subcategories of geometric latches include mechanical advantage latches, torque reversal (over-center) mechanisms, buckling (snap-through) mechanisms and other systems with bistable states.

Jerk

The rate of change of acceleration.

Latch, latch mediation

Any mechanism that mediates potential energy to kinetic energy transitions through, for example, physical contact, fluidics, shifts in center of mass and geometric instabilities. 'Latch' is often used synonymously with 'catch' in the literature.

Launch

Any time period when a mass is accelerated by a muscle, motor or elastic mechanism. Launch begins with first movement and ends when the movement is no longer actuated, at which point it typically transitions to ballistic or unpowered (e.g. when a jumping organism leaves the ground).

Launch acceleration

The acceleration of mass during spring actuation (a , m s^{-2}).

Launch distance

Distance that the accelerated mass moves during spring actuation (d , m).

Launch duration

The duration of spring actuation (t , s).

Launch kinetic energy

Kinetic energy (KE) of mass during spring actuation [J , $0.5 m (dt^{-1})^2$].

Launch speed

The speed of mass during spring actuation (v , m s^{-1}).

Mass of accelerated object

The mass of the part of the organism that is being accelerated during launch (for example, the whole body or a single limb) (m , kg).

Motor

A mechanism that actuates movement using stored chemical or electric potential energy (e.g. muscles, engines, shape memory alloy and piezoelectric actuators).

Muscle mass

Mass of the muscle that actuates a motion directly, or actuates it indirectly by loading a spring that later actuates the movement (m_m , kg).

Muscle mass-specific power

The power generated during launch relative to the mass of the underlying muscle involved in the movement (either directly actuating the movement or loading a spring that actuates the movement) (Pm_m^{-1}).

Power, mechanical power output

Energy of movement per unit time (P , W ; J t^{-1}). Energy can be calculated as work (force $\times$ distance) or as kinetic energy ($0.5mv^2$).

Spring mass

Mass of the spring mechanism that actuates the movement (m_s , kg).

Spring, spring actuation

A mechanism that actuates movement primarily using potential energy stored from the deformation of a material or structure (e.g. stresses within a material), such that another system must load energy into the elastic mechanism.

Spring mass-specific power

The power generated during launch relative to the mass of the spring mechanism that actuated the movement (Pm_s^{-1}).

Torque reversal latch

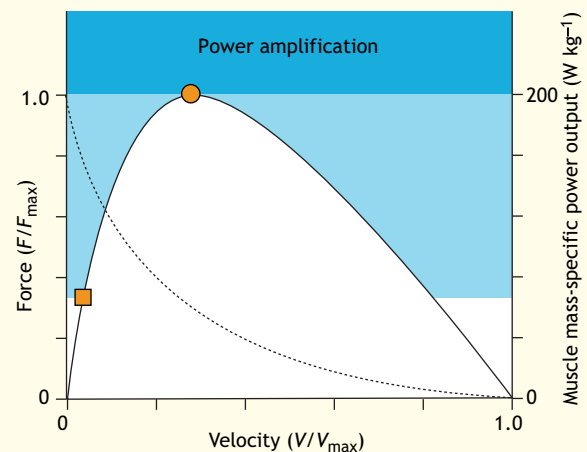
A geometric latch in which the sign of the output torque changes depending on the specific arrangement of linkages.

effectively applied to animal systems for which maximum muscle power limits are known. An unintentional outcome of this calculation is a perception that elastic mechanisms arose in animals that reached the limits of muscle power output and evolved springs and latches to enhance power output. This would seem to suggest that animals with elastic mechanisms use high-power muscles to load springs, and that elastic mechanisms evolved to surmount these constraints. In fact, as archers know, spring-driven systems are typically loaded with muscles operating slowly

Box 1. Testing for power amplification

Muscle exhibits a trade-off between force and velocity (dotted line, left y-axis) that limits peak mechanical power (solid line, right y-axis) (Hill, 1938; Huxley, 1957). The test for power amplification is based on the null hypothesis that muscle directly generates the observed power output of a movement. The alternative hypothesis is that muscle is insufficient, so an elastic mechanism is required. To test this, muscle mass-specific power output (or power density, W kg^{-1}) is calculated as follows. The maximum (sometimes calculated as peak instantaneous) power output of the movement is divided by the mass of the muscle(s) that either directly generates the movement or, alternatively, loads energy into a spring. The resulting power density is then compared against a baseline, either with the known maximum mass-specific power of the focal system's muscle or, more conservatively, with the highest known value for any muscle (e.g. bird flight muscle; Askew and Marsh, 2002). If the power density is above the baseline (dark blue region), then the null hypothesis is rejected, and the system is designated as power amplified.

Through this inductive logic, it is therefore possible to identify spring-actuated animal movements without specifying the underlying elastic mechanism at the outset. However, as discussed in the main text, it is important to note key limitations of this approach. Most importantly, it is not clear how to perform this test in systems that do not use muscle, as a useful baseline is unknown. In addition, muscle power densities for latch-mediated spring actuation (LaMSA) systems are based on dividing by the 'wrong' actuator in order to infer power amplification relative to muscle, and therefore do not provide meaningful insight into features underlying performance variation when compared across systems with different types of springs and spring masses (see Glossary). While the power amplification approach is a useful diagnostic tool, it is important to realize that its logic stems from an idealized concept of the power limits of muscle. For example, it is possible to miss a diagnosis of power amplification if the muscle is operating with high force (orange square) and not high power (orange circle) – as is the case for many LaMSA systems – and the power output of the movement is enhanced (light blue region) but below the maximum power output of muscle (dark blue region).



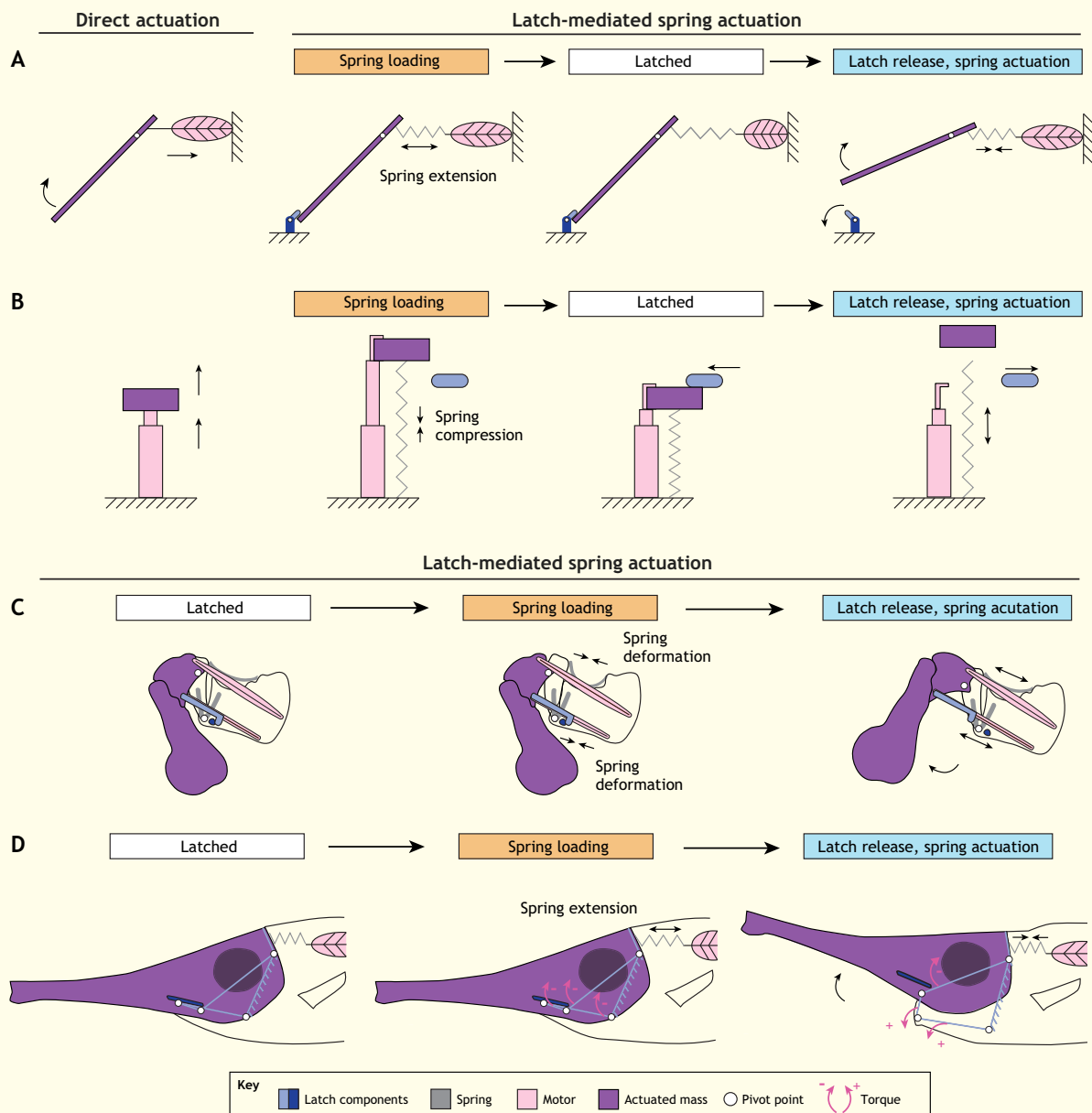
Box 2. LaMSA: operational definitions and biological examples

LaMSA encompasses systems that generate movements actuated by springs and mediated by latches. Here, we operationally define springs and latches in the context of the LaMSA framework.

Springs are structures that are capable of both storing energy when they deform and releasing that stored energy with some level of efficiency when they return to their original shape. Springs serve as actuators when they release energy and transfer it to kinetic energy of another structure. The potential energy stored in a spring is distinct from other forms of potential energy, such as gravitational or electromagnetic. The system that loads energy into the spring need not be a motor or muscle: it could include forces such as gravity. Elastic or spring mechanisms include traditional coiled springs, as well as beams in flexion, compression or extension, shells and other deformable surface geometries, liquid surface deformation and gas compression or rarefaction.

Latches, also sometimes called catches, are necessary for controlling the amount of energy stored in the spring and the timing and rate of elastic energy release. Latches are any feature of the integrated mechanism that mediates the transition between energy storage and release from the spring. Therefore, a latch includes the physical interaction between two surfaces (A–C), but can also encompass fluidic interactions or state-dependent behavior based on geometric configuration (D).

Compared with idealized diagrams (A,B), biological LaMSA mechanisms integrate a rich array of springs and latches. Rapid raptorial strikes by mantis shrimp (C) are driven by elastic energy stored via deformation of the exoskeleton. Their latches are composed of mineralized structures embedded in muscle apodemes that interact with the exoskeleton, acting as contact latches that keep the appendage from rotating during spring loading. Once released, the latches mediate energy transfer from the spring to the appendage (Burrows, 1969; Patek et al., 2007). Rapid head rotation in snipefish is driven by tendon-based spring actuation mediated by a torque reversal latch (D). In the latched conformation during spring loading, the head cannot be raised. With a slight shift in geometric conformation, the torque reverses on the lower linkages, and enables the release of stored elastic energy to drive rapid head elevation (Longo et al., 2018).



with high force, not with high power. Likewise, many spring-driven systems in animals have evolved muscles with modifications to enhance force, such as the long sarcomere, spring-loading muscles of mantis shrimp and trap-jaw ants (Blanco and Patek, 2014; Gronenberg and Ehmer, 1996).

In spite of the emphasis on muscle power constraints in the inference of power amplification (Box 1), spring-loading muscles often do not operate at, and are therefore not constrained by, their maximum power output. Furthermore, it is possible to miss elastic mechanisms when using this calculation. For example, one would not detect an elastic mechanism if the movement produces elevated, yet not exceptional power outputs (i.e. above the output for the muscle loading the elastic structure, but below the maximum muscle mass-specific power requirement, see Glossary; Box 1 figure, light blue area).

Even though mechanical power is the focus of the power amplification inference, this is not synonymous with discovering that the system actually generates high power, or even that the high performance or effective use of the system relates to its mechanical power output. Instead, an elastic mechanism improves performance by allowing the loading mechanism, such as muscle, to contract more slowly, generate more force and put more work into an elastic system (e.g. Alexander and Bennett-Clark, 1977; Roberts and Marsh, 2003; Roberts and Azizi, 2011; Rosario et al., 2016). This method of loading energy into a system is, in fact, a pathway to using a spring and latch to achieve a wide range of movement performance outcomes, which is distinct from inferring that high mechanical power output of a movement is the primary goal.

Comparison and quantification of the diversity of these systems requires metrics that apply regardless of the particular loading mechanism (Box 1). Mechanisms in biological systems without muscle, such as in plant and fungal dispersal systems (Edwards et al., 2005; Noblin et al., 2009; Sakes et al., 2016) and plant suction traps (Singh et al., 2011; Vincent et al., 2011; Poppinga et al., 2017), use latches combined with storage and release of energy in deformable structures. Likewise, synthetic jumpers are actuated with springs and latches, but not muscle (Burdick and Fiorini, 2003; Kovac et al., 2008; Aguilar et al., 2012; Gerratt and Bergbreiter, 2012; Zhao et al., 2013; Zaitsev et al., 2015; Haldane et al., 2016). To include these systems in our comparisons requires us to reframe the traditional focus of power amplification on muscle power limits.

While recognizing the utility of the power amplification inference, a key rationale for looking beyond this classic paradigm is to enable rigorous comparisons across diverse systems. Even though the concept of power amplification was originally established solely to assess whether or not muscle could generate a movement, the field has edged toward comparing power amplification ratios across diverse systems, which was never the intent of the power amplification inference. Power amplification calculations allow biologists to infer the presence of elastic mechanisms without needing to locate or solve the actual mechanism. Therefore, it is possible, yet unwise, to use a power amplification calculation for comparisons across diverse systems without a consistent or meaningful baseline power limit.

Whether a researcher has discovered a system actuated by springs and controlled by latches through the power amplification inference or through observations of rapid movement after a comparatively long loading process (the case for many non-muscle systems), the exciting challenge is to examine the mechanics and integration of springs and latches. Next, we will address how the dynamics of LaMSA have already yielded cross-disciplinary insights, explained aspects of biological diversity and inspired synthetic design.

LaMSA

LaMSA encompasses systems that use springs for generating movement and latches to mediate energy flow (Box 2). We operationally define spring actuation as the transformation of potential energy stored in material deformation (elastic energy) into kinetic energy that is used for generating movement. We define latch mediation as any mechanism that affects energy transformations in the spring, and therefore includes the function of latches to control (1) how energy is stored in the spring and (2) how that energy is transferred from the spring to movement and the environment. These definitions (see Glossary and Box 2) allow the materials, structures and mechanisms that constitute springs and latches to be broadly encompassed, such that diverse systems can be unified by shared features. These definitions do not require the presence of muscle and are agnostic about how energy is loaded in the spring. LaMSA includes mechanisms that exhibit power amplification, as well as others that result in less extreme performance outcomes, such as power attenuation, the reduction of jerk (see Glossary) or energy conservation. LaMSA neither replaces the power amplification paradigm nor encompasses all systems that use elastic elements, perform fast movements and enhance motor power output.

LaMSA systems can be highly sensitive and tuned to the properties and dynamics of springs, latches and motors/muscles. Scientists often assume that springs are Hookean (i.e. linear, massless, ideal springs), and that latches have infinite capacity for opposing spring loading, function as strict on-off switches, and can release (unlatch) instantaneously (Heitler, 1974; Roberts and Marsh, 2003). However, when springs and latches are parameterized more realistically to reflect the small size of many biological LaMSA systems, fundamental principles emerge, such as the mathematical delineation between systems best driven by a motor or muscle versus a spring and latch (Ilton et al., 2018; Sutton et al., 2019). Furthermore, changes in a system's output, such as takeoff velocity or launch duration, can be achieved by adjusting the relationships between the accelerated mass, motor or muscle behavior, and spring-latch dynamics (Ilton et al., 2018), which expands the capabilities of these systems well beyond previous idealized models of muscle, spring and latch systems (Galantis and Woledge, 2003).

LaMSA encourages cross-disciplinary connections alongside the advancement of comparative, experimental and theoretical studies. For example, LaMSA modeling and experiments can explore the dynamics of energy flow through the integration of different actuators, such as coupled motors and springs. Likewise, the material deformation inherent to spring actuation aligns LaMSA investigations with the burgeoning fields of mathematical and synthetic material geometries and energetics (Evans et al., 2015; Dudte et al., 2016; Gladman et al., 2016; Levin et al., 2016). In sum, the concept of LaMSA unifies a diverse array of biological and synthetic mechanical systems, opens the field to rigorous understanding of the remarkable diversity of these systems, enables quantitative, comparative analyses across species, and rigorously informs novel engineering design.

Metrics and measurements for LaMSA

A field focused on LaMSA requires clear metrics and approaches for accurate measurements comparable across diverse systems. Here, we provide recommendations for measuring LaMSA, beginning with spring actuation, then latch mediation and concluding with whole-system performance.

Spring actuation

Finding and characterizing elastic mechanisms in biology is difficult, because they are often small, hidden within the organism or monolithic (i.e. distributed over three-dimensional structures) (Rosario and Patek, 2015). Therefore, it is deceptively simple to state that the first step in identifying a spring is to isolate the structure that is capable of storing and releasing energy as it deforms and recoils.

If an elastic mechanism can be identified, then the next step is to study its spatial and temporal behavior using direct measurements, ideally as the organism actually performs the behavior. This approach reveals which structures deform, by how much, and the duration of loading and recoil. For external elastic mechanisms, such as deformable exoskeletons or cell walls, deformation can be tracked using high-speed imaging of natural landmarks on the organism or a grid of applied landmarks (e.g. Forterre et al., 2005). For internal mechanisms, radio-opaque markers can be inserted and then tracked as the organism moves (e.g. Astley and Roberts, 2012). Ideally, direct measurements are made on live animals, but sometimes it is necessary to artificially stimulate euthanized animals or isolated appendages (e.g. Burrows and Sutton, 2012). If these direct measurements are still not feasible, computational or analytical approaches can pinpoint the spatial distribution and dynamics of elastic energy storage that can be later validated in the actual organism (e.g. Deegan, 2012; Liu et al., 2017; Rosario and Patek, 2015).

Spring actuation depends on the material and geometric features that affect the storage and release of energy, including how fast a spring can recoil and the forces that it generates during rapid recoil. The mechanical work generated by elastic mechanisms can be inferred from the above approaches, and it can also be measured experimentally using a materials testing machine, also called a universal testing machine (UTM). UTMs are effective for establishing elastic potential energy capacity through the calculation of work during deformation; they also allow one to characterize spring stiffness or the failure limits of the system. Therefore, UTMs enable a more thorough exploration of spring properties under a variety of conditions – properties that could not be extrapolated from *in vivo* observations. UTMs have been used to amass a vast literature on the properties of biological materials that can be aligned with comparable measurements of synthetic structures (Wegst and Ashby, 2004; Barthelat et al., 2016).

Many biological spring-actuated systems are so small and rapid that standard materials testing devices cannot measure spring actuation at biologically relevant scales under realistic conditions. Dynamic material analysis systems (DMAs) are a good example of this. DMAs apply stresses of different frequencies and amplitudes to a material, and then measure the resultant resistive force. DMAs can go fast with a low force or vice versa, but not both. Ironically, they face the same force–velocity trade-offs that limit motors and may lead to the evolution of LaMSA. Consider that a mantis shrimp spring (meral-V) recoils roughly 0.5 mm in 0.9 ms. One of the best DMAs on the market (TA Instruments Discovery DMA 850) with high spatial and force resolution is limited to a period of 200 Hz (5 ms period). These sampling and acquisition rates are not sufficient to resolve a single meral-V unloading event. Such tests are also challenged by imposing realistic forces on the elastic mechanism that would occur in the natural contexts for the movement, such as fluid dynamic forces on rotating appendages of mantis shrimp (McHenry et al., 2012, 2016).

Moving beyond the assumption of ideal springs opens a trove of questions about their capabilities. Biological elastic structures exhibit diverse geometries, ranging from stiff, chitinous ant heads to

stretchy strap-like tendons (Larabee et al., 2017, 2018; Siwanowicz and Burrows, 2017). Although currently studied in relatively slow movements, simple geometries can potentially yield potent and controlled spring actuation in small, fast biological systems (Forterre et al., 2005; Lee et al., 2010; Marmottant et al., 2013; Gladman et al., 2016). Typically, pieces of material are removed for material testing, such that deformation of whole structures with intact geometry is rarely measured (but see Patek et al., 2013; Rosario and Patek, 2015; Zack et al., 2009). Testing whole structures is important, as biological springs are typically composite materials with complex geometries. For example, the arthropod elastic protein resilin operates in conjunction with stiff exoskeleton in the elastic storage devices of small jumpers (Burrows and Sutton, 2012; Siwanowicz and Burrows, 2017).

To our knowledge, force–velocity relationships during spring actuation in real time and *in situ* have yet to be measured in small, fast, biological LaMSA systems. Although measuring real-time spring mechanics of whole structures (rather than simply materials) under conditions that are comparable to the natural unloading of the spring presents a significant experimental challenge for high-velocity, high-acceleration systems, this approach is crucial given the importance of mass and spatial deformation for effective actuation, especially at small scales (Ilton et al., 2018). A growing interest in the energetics of latches and springs will hopefully spur the field to design solutions to the current technological limitations, which link back to motor limitations for small systems with high acceleration. In the meantime, engineers and scientists are applying cutting-edge visualization and materials testing techniques to uncover new insights into the structural basis for effective spring actuation (Burrows and Sutton, 2012; Tadayon et al., 2015, 2018; Siwanowicz and Burrows, 2017).

Latch mediation

Spring-actuated systems need a latch to control the timing and rate of energy storage and release (Box 2). The disparate forms of latches – from friction between two surfaces to linkage systems with state-dependent dynamics – make this search uniquely challenging. Latches are broadly organized into three basic types – contact, fluidic and geometric (see Glossary; Ilton et al., 2018) – and by whether or not they require external activation (Gronenberg, 1996a). As with springs, the goal is to identify the latch and to connect the action of the latch to its effect on energy flow into and out of the spring; however, few studies have correlated latch properties with the flow of energy through elastic mechanisms.

Latches have been described using a diverse array of terminology and have been recognized as important for power amplification (Gronenberg, 1996a; Galantis and Woledge, 2003; Roberts and Marsh, 2003; Patek et al., 2011; Astley and Roberts, 2014). As mentioned above, implicit in many studies is the assumption that latches function as simple, ideal switches. However, adding simple latch dynamics can dramatically transform the flow of energy through a system, altering both the amount of elastic energy stored and the rate of energy release (Ilton et al., 2018). Non-ideal latches potentially enable tuned and controllable energy release in systems previously thought to simply function as open-loop systems (e.g. Kagaya and Patek, 2016). Dynamic latch mediation could allow for robust performance across a range of substrates based on their compliance (Reynaga et al., 2019).

As with springs, initial hypotheses for latch mechanisms emerge from direct observations of moving structures in or on the organism. This is often coupled with morphological descriptions, ranging from dissections to micro-computed tomography (Evans, 1972;

Patek et al., 2007; Larabee et al., 2017; Longo et al., 2018). While these descriptive approaches can be compelling, additional evidence is required to discriminate among hypothesized latch mechanisms. For example, experiments can perturb latching dynamics, such as through modification of contact surfaces or severing or denervation of muscles that could engage latches (e.g. Ritzmann, 1973).

To identify latch mechanisms, it can help to demonstrate a sequence of states during latching and unlatching. Latches are typically in one state during spring loading (and often prior to loading) and must change state in order for spring actuation to begin (Fig. 1, Box 2 figure). The means by which the sequence of latch actions can be determined differs by latch type. For example, contact latches may be identified by using high-speed imaging or radiography to visualize the interaction of components (Gronenberg, 1996b; Patek et al., 2007; Burrows and Sutton, 2013). Some fluidic latches can be detected as a pressure increase prior to movement followed by a rapid decrease once movement begins (Singh et al., 2011). Geometric latches can be inferred by demonstrating shifts in mechanical advantage or the direction of torques that occur during different phases of movement (Astley and Roberts, 2014; Kaji et al., 2018; Longo et al., 2018).

Physical or mathematical modeling can be used to evaluate different latching hypotheses (Galantis and Woledge, 2003; Koh et al., 2013), particularly for geometric latches. For instance, despite strong evidence for the presence of an elastic mechanism, an anatomical latch has not been identified for frog jumping (Marsh

and John-Alder, 1994; Olson and Marsh, 1998; Peplowski and Marsh, 1997; Roberts and Marsh, 2003; Astley and Roberts, 2012). Instead, inverse dynamic modeling reveals that latching in frogs arises from the proximal to distal progression of joint activity and rapid increase in effective mechanical advantage that occurs during limb extension (Roberts and Marsh, 2003; Astley and Roberts, 2014; Olberding et al., 2019).

Modeling can also reveal unexpected dynamics among components that can function as latches under certain conditions. For example, depending on the relative mass of spring and projectile, the projectile itself can mediate energy delivery when its own inertia is sufficient to delay the release of energy from a spring; in this way, the changing mechanical advantage of frog limbs during a jump functions as a geometric latch (Galantis and Woledge, 2003; Roberts and Marsh, 2003; Ilton et al., 2018).

More than one latch can be operating in a given system, or different latching mechanisms can appear based on the scale of inquiry. For instance, torque reversal latch mechanisms (see Glossary; example in Box 2) are geometric latches; depending on their arrangement, the linkages will respond differently to an input torque, such that the system can be latched in one arrangement and unlatched in another (Bennet-Clark and Lucey, 1967; Kaji et al., 2018). Components of geometric latches can also interface with or contact each other and other structures. In some cases, the latch and spring may be closely integrated or even exist in the same structure (e.g. snap-through elastic structures such as the Venus fly trap; Forterre et al., 2005). In some engineered systems with torque

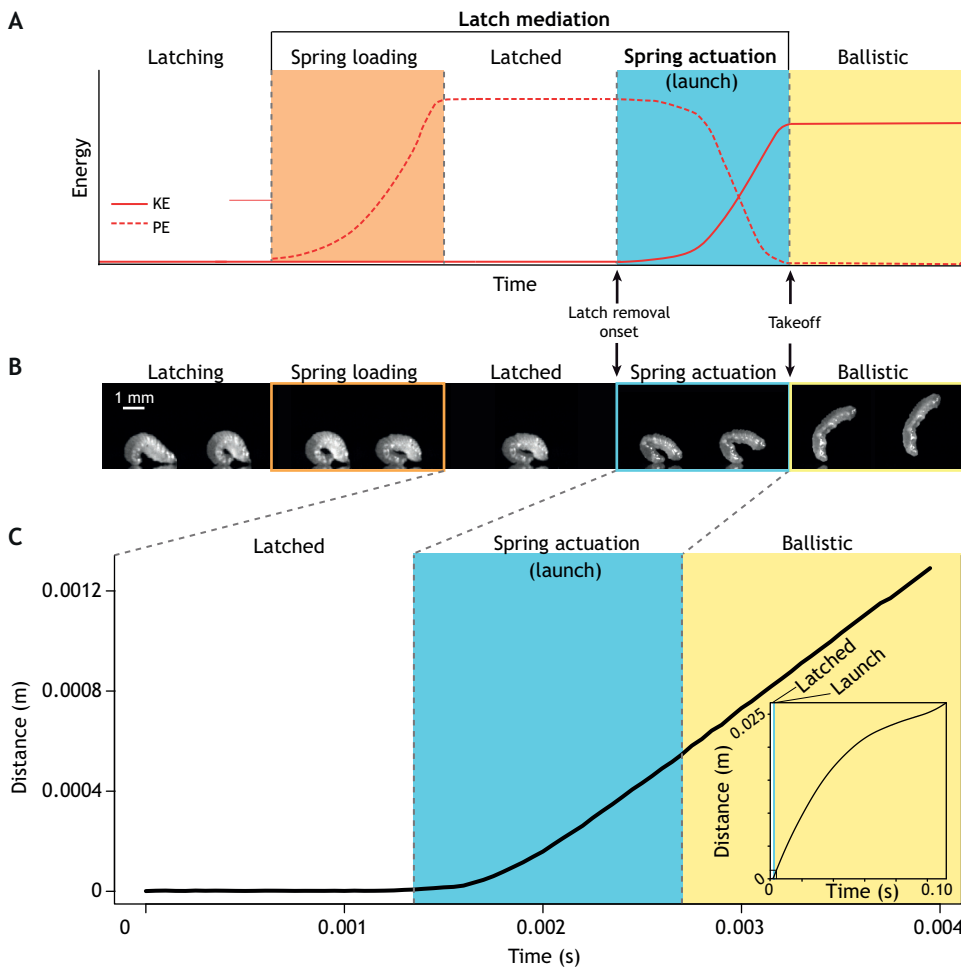


Fig. 1. Phases and energetics of latch-mediated spring actuation (LaMSA) in an idealized system compared with a biological example.

(A) The phases of a latch-mediated spring-actuated movement for a simple model of a projectile (modified from Ilton et al., 2018). After the system is latched, a motor loads energy into the spring, increasing the stored elastic potential energy (PE). During the launch phase (blue), the removal of the latch mediates the conversion of stored elastic potential energy to kinetic energy (KE), and thus the spring moves (actuates) the projectile mass, resulting in takeoff. The launch is the key time period for measurements of LaMSA. (B) Jumping gall midge larvae are exemplary biological latch-mediated spring-actuated projectiles. Frames from a high-speed video reveal how the larva forms an elastic loop with its body and engages an adhesive latch. During launch, the latch releases, and the larva pushes against the substrate until takeoff. (C) The launch phase (blue; used in calculations in Box 3) is very brief compared with the whole trajectory (inset). B and C were created from figures and data in Farley et al. (2019).

reversal, spring deformation and latch engagement are coupled into the same motion (Koh et al., 2013).

Once a latch has been identified, the next step is to determine the latch properties that mediate the flow of energy out of the spring and into motion. Depending on latch type, different properties affect energy release from the spring. With a contact latch, the shape and removal speed of the latch strongly influence system output (Ilton et al., 2018; Bolmin et al., 2019); however, tribological analyses of contact latches are still needed. Parameters such as droplet surface separation or rupture force are relevant for fluidic latches (Noblin et al., 2009; Liu et al., 2017), whereas linkage lengths and mechanical advantage are important for geometric latches (Koh et al., 2013; Longo et al., 2018; Olberding et al., 2019). It is as yet unknown which geometries, materials or dynamic features characterize effective latches and their roles across different situations.

Whole-system performance and trade-offs

Latches and springs operate in integrated systems in the context of particular environments. Loading mechanisms (e.g. motors, muscles), actuated masses, linkages, control mechanisms and environments all interact with the spring and latch to determine whole-system performance. With a better understanding of these interactions, the field can move towards robust comparative analyses, which will include testing scaling hypotheses and rigorously connecting biomechanics and performance.

In Box 3, we present challenges and best practices for researchers interested in the kinematics of LaMSA. Presently, kinematics are measured across inconsistent time periods and load masses, and typically without reporting uncertainty and error propagation. If the focus is on the dynamics and force–velocity relationships of spring actuation, measurements should be taken during the time period when the spring is actuating a relevant mass, which we define

as ‘launch’ (see Glossary; Fig. 1, Box 3). Researchers typically focus on video frame rate and video resolution when planning experiments, but substantial error and uncertainty (Appendix) are introduced by making highly precise but inaccurate measurements based on low-resolution calibration rulers visualized in high-resolution digital images. This problem is exacerbated for small, fast systems performing extremely rapid movements.

Provided that the measurements are consistent, comparable and accurate, the focus of investigations can shift towards the discovery of parameters that represent performance. Earlier, we noted that mechanical power output is not necessarily the key performance metric underlying the evolution of elastic recoil mechanisms. Currently, no single metric (e.g. power, velocity or duration) universally represents the performance advantage of latch-mediated spring-actuated systems (Patek, 2015; Ilton et al., 2018). Instead, temporal and spatial manipulations of energy flow conferred by latches and springs are key to the diverse uses and performance of LaMSA mechanisms. For biologists, the challenge is to discover the metrics that explain performance and, ultimately, fitness.

A brief look at the diversity of these systems points towards the many open questions of how their outputs relate to performance. For example, microscopic fungal ballistospores and stylets of jellyfish nematocysts are launched with high acceleration and low velocity using LaMSA; these mechanisms allow tiny structures in a viscous environment (low Reynolds number) to move a short distance (Nüchter et al., 2006; Liu et al., 2017; Roper and Seminara, 2019). Systems used for puncture (Anderson, 2018) are likely operating under different performance demands from those used for seed or pollen ejection (Sakes et al., 2016). Smashing mantis shrimp use springs and latches to drive hammer-like appendages to high accelerations, presumably to generate localized high pressure in order to fracture composite materials (Patek and Caldwell, 2005; Cox et al., 2014; McHenry et al., 2016).

Box 3. Analysis of LaMSA systems

To analyze the dynamics of LaMSA, the launch phase (Fig. 1) should be measured. Launch is the time period when the spring actuates movement. Launch is distinct from takeoff, which is the instant when the system transitions to ballistic (unpowered) motion. The table shows example data on LaMSA. Jumping gall midge larvae were analyzed during launch as defined here (Fig. 1; data from Farley et al., 2019). In contrast, mantis shrimp [data from Cox et al. (2014), Blanco and Patek (2014), and unpublished mass data (S.N.P.)] and trap-jaw ant (data from Patek et al., 2006) studies did not distinguish launch, takeoff and ballistic phases, so these values were calculated from reported speed and acceleration for this example.

The mass that is moved during launch should be carefully considered and reported. For instance, actuated mass varies between trap-jaw ant free strikes (no load on the mandibles) and jaw jumps (body mass is the load). Speed and acceleration in these two contexts differ by orders of magnitude even though they are both driven by the same trap-jaw mechanism.

Power density can be calculated relative to muscle mass (see Glossary; traditional approach) or relative to the spring that actually powers the movement (spring mass-specific power, see Glossary). Power density relative to muscle is typically far lower than when calculated relative to the spring (e.g. $4 \times 10^4 \text{ W kg}^{-1}$ versus $3.8 \times 10^6 \text{ W kg}^{-1}$ for mantis shrimp).

Determining the propagation of uncertainty and error (Appendix) is essential for fast movements in small systems that reach the limits of instrument resolution. Only the mantis shrimp dataset has sufficient ruler resolution and video frame rate to yield small uncertainties. The gall midge dataset has high uncertainty because of insufficient resolution of the scale bar, while uncertainty for the trap-jaw ant dataset is due to the short distance over which acceleration of the mass was calculated. Note that we assume, for the purposes of this example, that the pixel resolution of the image matches or is higher than that of the ruler.

Common name	Use	Accelerated mass (kg)	Launch duration (s)*	Launch distance (m)*	Launch speed (m s ⁻¹)*	Launch acceleration (m s ⁻²)*	Mass balance resolution (kg)	Ruler resolution (m)	Video image duration resolution (s)	% Uncertainty (speed/acceleration/muscle power density)
Trap-jaw ant	Strike	1.3×10^{-7}	6.4×10^{-5}	4.1×10^{-3}	64	1.0×10^6	1×10^{-10}	5×10^{-6}	2×10^{-5}	31/62/NA
	Jump	1.2×10^{-5}	3.4×10^{-5}	9.8×10^{-6}	0.29	8.6×10^3	1×10^{-7}	1×10^{-4}	3×10^{-4}	11/20/NA
Mantis shrimp	Strike	2.2×10^{-5}	7.2×10^{-4}	1.5×10^{-2}	20	7.8×10^4	1×10^{-7}	1×10^{-4}	3×10^{-5}	5/9/14
Gall midge larvae	Jump	1.3×10^{-6}	1.2×10^{-3}	6.2×10^{-4}	0.53	4.7×10^2	1×10^{-10}	2×10^{-5}	5×10^{-5}	10/12/21

*See Glossary.

For some organisms, the use of elastic structures allows them to maintain performance across a broad temperature range, thereby circumventing the thermal constraints on skeletal muscle (Anderson and Deban, 2010; Deban and Lappin, 2011; Deban and Scales, 2016).

Several studies have identified trade-offs within LaMSA systems. For instance, an organism's use of spring-driven movement can incur substantial costs, such as time required to load the system (Rosario et al., 2016) and the loss of real-time control when the system is released (Kagaya and Patek, 2016). The use of slowly contracting, force-modified muscles (e.g. muscles with long sarcomeres) to load stiff springs results in a long loading duration before any movement. In jumping insects and frogs, slowly loading stiff springs maximizes elastic energy, but this slow loading requires more time for the animal to prepare for rapid movement (Rosario et al., 2016). Exploring the complex interplay between loading time, spring stiffness and open-loop actuation is important for understanding variation and evolution of these diverse systems.

Finally, repeatability and damage resistance in LaMSA systems are so critical that trade-offs between damage resistance and performance in springs and latches may limit their utility. LaMSA mechanisms can enable controlled release of energy, such that internal damage is minimized, jerk is reduced and an otherwise explosive system can be used repeatedly (e.g. Bayley et al., 2012). In order to explore these aspects, one would need to demonstrate decreased performance with repeated use, and the proportion and context of failure or damage.

Spring and latch dynamics contribute to the remarkable outputs of LaMSA systems. However, many other components interact with springs and latches, including motors that act on the spring, actuated masses and the surrounding environment. Although we do not address these other integrated components here, they certainly deserve further attention in order to fully understand the dynamics and capabilities of LaMSA.

Conclusions

In this Commentary, we offer a principled foundation for the growing field of LaMSA, which is grounded in the shared features of these systems and extends beyond the classic power amplification framework. Moving beyond a focus on seemingly extreme power performance, we emphasize diverse capabilities within and across systems, including fracture, puncture, propulsion, energy conservation, dissipation and amplification (Roberts and Azizi, 2011; Richards and Sawicki, 2012; Ilton et al., 2018). LaMSA offers terminology that encompasses power-amplified mechanisms and unifies other biological and synthetic systems that are referred to as biological catapults, as well as shooting, snap-through and elastic recoil mechanisms.

Even though we have focused on springs and latches here, it is worth briefly revisiting the role of muscle. Naturally, muscles remain centrally important in LaMSA systems that use muscles to load springs, especially the integrated tuning of springs in series with muscles and within muscle itself (Roberts and Azizi, 2011). The field of muscle-tendon mechanics remains at the forefront of a cross-disciplinary understanding of how motors operate when in series with elastic elements. Integrating real dynamics of elastic actuators with latches as energy-flow mediators into these advanced models of motor-spring tuning will further propel the field.

At present, the major challenges to studying LaMSA are technological. The measurements we have described here draw on a long history of similar measurements in these and other systems, with the goal of obtaining rigorous, comparative data. However, to

move beyond these gross measures of system output, it is crucial to assess real-time energy flow and the dynamics of spring-actuated motion, including under varying loading regimes and within tuned systems. To do this, key technical advances and initiatives are needed, such as extremely high-rate and small-displacement dynamic materials testing of complex materials and geometries.

We conclude with a reference to Kuhn (1962) – a clarifying voice in the realm of scientific paradigms. He wrote that paradigms are ‘universally recognized scientific achievements that for a time model problems and solutions to a community of practitioners’, and that ‘...it is hard to make nature fit a paradigm. That is why the puzzles of normal science are so challenging and also why measurements undertaken without a paradigm so seldom lead to any conclusions at all’. While time will tell whether or not LaMSA becomes a paradigm, we hope that this Commentary, and its formalization of a name for this growing field, offers clarifying insights that will aid us in explaining nature and establishing a rigorous, cross-disciplinary framework.

APPENDIX

Uncertainty/error propagation calculations

In this Appendix, we summarize best practices for reporting uncertainty and error propagation in kinematic analyses. Uncertainty calculations are based on instrument resolution, and this determines the uncertainty in the final calculations (e.g. speed, power). Here, we consider three sources of uncertainty. (1) Mass resolution of the balance (B , kg). (2) Spatial resolution of the ruler used for calibrating high-speed images (L , m). We encourage researchers to use a stage micrometer to calibrate rulers used in high-speed images to improve distance uncertainty. The simple equations below assume that the pixel resolution of the image has greater precision than the ruler. If this is not the case, then an additional source of uncertainty is pixel resolution, which should be included in the propagation analysis. (3) Temporal resolution of high-speed imaging (H , s). This is calculated as the inverse of frame rate, $1/(\text{frames s}^{-1})$.

The following equations step through the calculations for the error/uncertainty propagation ratio which can then be multiplied by the system's outputs (e.g., mean acceleration) to yield the magnitude of uncertainty.

$$\text{Speed, } S = [(Ld^{-1})^2 + (Ht^{-1})^2]^{0.5}, \quad (\text{A1})$$

$$\text{Squared time} = (2Ht^{-1}), \quad (\text{A2})$$

$$\text{Cubed time} = (3Ht^{-1}), \quad (\text{A3})$$

$$\text{Acceleration} = [(Ld^{-1})^2 + (2Ht^{-1})^2]^{0.5}, \quad (\text{A4})$$

$$\text{Energy} = [(mB^{-1})^2 + (S)^2]^{0.5}, \quad (\text{A5})$$

$$\text{Power} = [(3Ht^{-1})^2 + (2Ld^{-1})^2 + (mB^{-1})^2]^{0.5}, \quad (\text{A6})$$

$$\text{Mass-specific power} = [(3Ht^{-1})^2 + (2Ld^{-1})^2]^{0.5}, \quad (\text{A7})$$

where d is launch distance, t is launch duration and m is mass of the accelerated object.

Acknowledgements

We are grateful to members of our MURI team and participants in the SICB 2019 workshop for discussion about ideas expressed in this Commentary. We thank the Patek lab for feedback and support, especially G. M. Farley, as well as the three reviewers and JEB Reviews Editor, Charlotte Rutledge.

Competing interests

The authors declare no competing or financial interests.

Funding

This material is based upon work supported by the U.S. Army Research Laboratory and the U.S. Army Research Office under contract/grant number W911NF-15-1-0358.

References

- Aerts, P. (1998). Vertical jumping in *Galago senegalensis*: the quest for an obligate mechanical power amplifier. *Philos. Trans. R. Soc. Lond. B* **353**, 1607–1620. doi:10.1098/rstb.1998.0313
- Aguilar, J., Lesov, A., Wiesenfeld, K. and Goldman, D. I. (2012). Lift-off dynamics in a simple jumping robot. *Phys. Rev. Lett.* **109**, 174301. doi:10.1103/PhysRevLett.109.174301
- Alexander, R. M. and Bennet-Clark, H. C. (1977). Storage of elastic strain energy in muscle and other tissues. *Nature* **265**, 114–117. doi:10.1038/265114a0
- Anderson, P. S. L. (2018). Making a point: shared mechanics underlying the diversity of biological puncture. *J. Exp. Biol.* **221**, jeb187294. doi:10.1242/jeb.187294
- Anderson, C. V. and Deban, S. M. (2010). Ballistic tongue projection in chameleons maintains high performance at low temperature. *Proc. Natl Acad. Sci. USA* **107**, 5495–5499. doi:10.1073/pnas.0910778107
- Askew, G. N. and Marsh, R. L. (2002). Muscle designed for maximum short-term power output: quail flight muscle. *J. Exp. Biol.* **205**, 2153–2160.
- Astley, H. C. and Roberts, T. J. (2012). Evidence for a vertebrate catapult: elastic energy storage in the plantaris tendon during frog jumping. *Biol. Lett.* **8**, 386–389. doi:10.1098/rsbl.2011.0982
- Astley, H. C. and Roberts, T. J. (2014). The mechanics of elastic loading and recoil in anuran jumping. *J. Exp. Biol.* **217**, 4372–4378. doi:10.1242/jeb.110296
- Barthelat, F., Yin, Z. and Buehler, M. J. (2016). Structure and mechanics of interfaces in biological materials. *Nat. Rev. Mater.* **1**, 16007. doi:10.1038/natrevmats.2016.7
- Bayley, T. G., Sutton, G. P. and Burrows, M. (2012). A buckling region in locust hindlegs contains resilin and absorbs energy when jumping or kicking goes wrong. *J. Exp. Biol.* **215**, 1151–1161. doi:10.1242/jeb.068080
- Bennet-Clark, H. C. (1975). The energetics of the jump of the locust *Schistocerca gregaria*. *J. Exp. Biol.* **63**, 53–83.
- Bennet-Clark, H. C. and Lucey, E. C. A. (1967). The jump of the flea: a study of the energetics and a model of the mechanism. *J. Exp. Biol.* **47**, 59–76.
- Blanco, M. M. and Patek, S. N. (2014). Muscle trade-offs in a power-amplified prey capture system. *Evolution* **68**, 1399–1414. doi:10.1111/evo.12365
- Bolmin, O., Wei, L., Hazel, A. M., Dunn, A. C., Wissa, A. and Alleyne, M. (2019). Latching of the click beetle (Coleoptera: Elateridae) thoracic hinge enabled by the morphology and mechanics of conformal structures. *J. Exp. Biol.* **222**, jeb196683. doi:10.1242/jeb.196683
- Burdick, J. and Fiorini, P. (2003). Minimalist jumping robots for celestial exploration. *Int. J. Robot. Res.* **22**, 653–674. doi:10.1177/02783649030227013
- Burrows, M. (1969). The mechanics and neural control of the prey capture strike in the mantid shrimps *Squilla* and *Hemisquilla*. *Z. vergl. Physiol.* **62**, 361–381. doi:10.1007/BF00299261
- Burrows, M. (2003). Frog hopper insects leap to new heights. *Nature* **424**, 509. doi:10.1038/424509a
- Burrows, M. and Dorosenko, M. (2015a). Jumping mechanisms and strategies in moths (Lepidoptera). *J. Exp. Biol.* **218**, 1655–1666. doi:10.1242/jeb.120741
- Burrows, M. and Dorosenko, M. (2015b). Jumping mechanisms in adult caddis flies (Insecta, Trichoptera). *J. Exp. Biol.* **218**, 2764–2774. doi:10.1242/jeb.123471
- Burrows, M. and Sutton, G. P. (2012). Locusts use a composite of resilin and hard cuticle as an energy store for jumping and kicking. *J. Exp. Biol.* **215**, 3501–3512. doi:10.1242/jeb.071993
- Burrows, M. and Sutton, G. P. (2013). Interacting gears synchronize propulsive leg movements in a jumping insect. *Science* **341**, 1254–1256. doi:10.1126/science.1240284
- Cox, S. M., Schmidt, D., Modarres-Sadeghi, Y. and Patek, S. N. (2014). A physical model of the extreme mantid shrimp strike: kinematics and cavitation of Ninjabot. *Bioinspir. Biomim.* **9**, 1–16. doi:10.1088/1748-3182/9/1/016014
- Deban, S. M. and Lappin, A. K. (2011). Thermal effects on the dynamics and motor control of ballistic prey capture in toads: maintaining high performance at low temperature. *J. Exp. Biol.* **214**, 1333–1346. doi:10.1242/jeb.048405
- Deban, S. M. and Scales, J. A. (2016). Dynamics and thermal sensitivity of ballistic and non-ballistic feeding in salamanders. *J. Exp. Biol.* **219**, 431–444. doi:10.1242/jeb.127407
- Deban, S. M., O'Reilly, J. C., Dicke, U. and van Leeuwen, J. L. (2007). Extremely high-power tongue projection in plethodontid salamanders. *J. Exp. Biol.* **210**, 655–667. doi:10.1242/jeb.02664
- Deegan, R. D. (2012). Finessing the fracture energy barrier in ballistic seed dispersal. *Proc. Natl. Acad. Sci. USA* **109**, 5166–5169. doi:10.1073/pnas.1119737109
- Dudte, L. H., Vouga, E., Tachi, T. and Mahadevan, L. (2016). Programming curvature using origami tessellations. *Nat. Mater.* **15**, 583. doi:10.1038/nmat4540
- Edwards, J., Whitaker, D., Klionsky, S. and Laskowski, M. J. (2005). A record-breaking pollen catapult. *Nature* **435**, 164. doi:10.1038/435164a
- Evans, M. E. G. (1972). The jump of the click beetle (Coleoptera, Elateridae)-a preliminary study. *J. Zool. Soc. Lond.* **167**, 319–336. doi:10.1111/j.1469-7998.1972.tb03115.x
- Evans, M. E. G. (1973). The jump of the click beetle (Coleoptera: Elateridae)-energetics and mechanics. *J. Zool. Soc. Lond.* **169**, 181–194. doi:10.1111/j.1469-7998.1973.tb04553.x
- Evans, A. A., Silverberg, J. L. and Santangelo, C. D. (2015). Lattice mechanics of origami tessellations. *Phys. Rev. E* **92**, 013205. doi:10.1103/PhysRevE.92.013205
- Farley, G. M., Wise, M. J., Harrison, J. S., Sutton, G. P., Kuo, C. and Patek, S. N. (2019). Adhesive latching and legless leaping in small, worm-like insect larvae. *J. Exp. Biol.* **222**. doi:10.1242/jeb.201129
- Forterre, Y., Skotheim, J. M., Dumais, J. and Mahadevan, L. (2005). How the Venus flytrap snaps. *Nature* **433**, 421–425. doi:10.1038/nature03185
- Galantis, A. and Woledge, R. C. (2003). The theoretical limits to the power output of a muscle-tendon complex with inertial and gravitational loads. *Proc. R. Soc. B* **270**, 1493–1498. doi:10.1098/rspb.2003.2403
- Gerratt, A. P. and Bergbreiter, S. (2012). Incorporating compliant elastomers for jumping locomotion in microrobots. *Smart Mater. Struct.* **22**, 014010. doi:10.1088/0964-1726/22/1/014010
- Gladman, A. S., Matsumoto, E. A., Nuzzo, R. G., Mahadevan, L. and Lewis, J. A. (2016). Biomimetic 4D printing. *Nat. Mater.* **15**, 413. doi:10.1038/nmat4544
- Gronenberg, W. (1996a). Fast actions in small animals: springs and click mechanisms. *J. Comp. Physiol. A* **178**, 727–734. doi:10.1007/BF00225821
- Gronenberg, W. (1996b). The trap-jaw mechanism in the dacetine ants *Dacetone armigerum* and *Strumigenys* sp. *J. Exp. Biol.* **199**, 2021–2033.
- Gronenberg, W. and Ehmer, B. (1996). The mandible mechanism of the ant genus *Anochetus* (Hymenoptera, Formicidae) and the possible evolution of trap-jaws. *Zoology* **99**, 153–162.
- Haldane, D. W., Plecnik, M. M., Yim, J. K. and Fearing, R. S. (2016). Robotic vertical jumping agility via series-elastic power modulation. *Sci. Robot.* **1**, eaag2048. doi:10.1126/scirobotics.aag2048
- Heitler, W. J. (1974). The locust jump. *J. Comp. Physiol.* **89**, 93–104. doi:10.1007/BF00696166
- Hill, A. V. (1938). The heat of shortening and the dynamic constants of muscle. *Proc. R. Soc. B* **126**, 136–195. doi:10.1098/rspb.1938.0050
- Huxley, A. F. (1957). Muscle structure and theories of contraction. *Prog. Biophys. Biophys. Chem.* **7**, 255–318. doi:10.1016/S0096-4174(18)30128-8
- Ilton, M., Bhamla, M. S., Ma, X., Cox, S. M., Fitchett, L. L., Kim, Y., Koh, J.-S., Krishnamurthy, D., Kuo, C.-Y., Temel, F. Z. et al. (2018). The principles of cascading power limits in small, fast biological and engineered systems. *Science* **360**, eaao1082. doi:10.1126/science.aao1082
- Kagaya, K., Patek, S. N. (2016). Feed-forward motor control of ultrafast, ballistic movements. *J. Exp. Biol.* **219**, 319–333. doi:10.1242/jeb.130518
- Kaji, T., Anker, A., Wirkner, C. S. and Palmer, A. R. (2018). Parallel saltatorial evolution of ultrafast movements in snapping shrimp claws. *Curr. Biol.* **28**, 106–113.e4. doi:10.1016/j.cub.2017.11.044
- Koh, J. S., Jung, S. P., Wood, R. J. and Cho, K. J. (2013). A jumping robotic insect based on a torque reversal catapult mechanism. In 2013 IEEE/RSJ International Conference on Intelligent Robots and Systems (IROS), pp. 3796–3801. Tokyo, Japan.
- Kovac, M., Fuchs, M., Guignard, A., Zufferey, J. C. and Floreano, D. (2008). A miniature 7g jumping robot. In 2008 IEEE International Conference on Robotics and Automation, Vol. 1–9, pp. 373–378. New York: USA.
- Kuhn, T. S. (1962). *The Structure of Scientific Revolutions*. Chicago: University of Chicago Press.
- Larabee, F. J., Gronenberg, W. and Suarez, A. V. (2017). Performance, morphology and control of power-amplified mandibles in the trap-jaw ant *Myrmoterus* (Hymenoptera: Formicidae). *J. Exp. Biol.* **220**, 3062–3071. doi:10.1242/jeb.156513
- Larabee, F. J., Smith, A. A. and Suarez, A. V. (2018). Snap-jaw morphology is specialized for high-speed power amplification in the Dracula ant, *Myrmica camillae*. *R. Soc. Open Sci.* **5**, 181447. doi:10.1098/rsos.181447
- Lee, H., Xia, C. and Fang, N. X. (2010). First jump of microgel; actuation speed enhancement by elastic instability. *Soft Mat.* **6**, 4342–4345. doi:10.1039/c0sm00092b
- Levin, A., Michaels, T. C. T., Adler-Abramovich, L., Mason, T. O., Müller, T., Zhang, B., Mahadevan, L., Gazit, E. and Knowles, T. P. J. (2016). Elastic instability-mediated actuation by a supra-molecular polymer. *Nat. Phys.* **12**, 926. doi:10.1038/nphys3808
- Liu, F., Chavez, R. L., Patek, S. N., Pringle, A., Feng, J. J. and Chen, C.-H. (2017). Asymmetric drop coalescence launches fungal ballistospores with directionality. *J. R. Soc. Interface* **14**, 184502. doi:10.1098/rsif.2017.0083
- Longo, S. J., Goodearly, T. and Wainwright, P. C. (2018). Extremely fast feeding strikes are powered by elastic recoil in a seahorse relative, the snipefish, *Macroramphosus scolopax*. *Proc. R. Soc. B* **285**, 20181078. doi:10.1098/rspb.2018.1078

- Marmottant, P., Ponomarenko, A. and Bienaimé, D. (2013). The walk and jump of *Equisetum* spores. *Proc. R. Soc. B* **280**, 20131465. doi:10.1098/rspb.2013.1465
- Marsh, R. L. and John-Alder, H. B. (1994). Jumping performance of hylid frogs measured with high-speed cine film. *J. Exp. Biol.* **188**, 131-141.
- McHenry, M. J., Claverie, T., Rosario, M. V. and Patek, S. N. (2012). Gearing for speed slows the predatory strike of a mantis shrimp. *J. Exp. Biol.* **215**, 1231-1245. doi:10.1242/jeb.061465
- McHenry, M. J., Anderson, P. S. L., Van Wassenbergh, S., Matthews, D. G., Summers, A. P. and Patek, S. N. (2016). The comparative hydrodynamics of rapid rotation by predatory appendages. *J. Exp. Biol.* **219**, 3399-3411. doi:10.1242/jeb.140590
- Noblin, X., Yang, S. and Dumais, J. (2009). Surface tension propulsion of fungal spores. *J. Exp. Biol.* **212**, 2835-2843. doi:10.1242/jeb.029975
- Nüchter, T., Benoit, M., Engel, U., Özbek, S. and Holstein, T. W. (2006). Nanosecond-scale kinetics of nematocyst discharge. *Curr. Biol.* **16**, R316-R318. doi:10.1016/j.cub.2006.03.089
- Olberding, J. P., Deban, S. M., Rosario, M. V. and Azizi, M. (2019). Modeling the determinants of mechanical advantage during jumping: consequences for spring- and muscle-driven movement. *Integr. Comp. Biol.* (in press).
- Olson, J. M. and Marsh, R. L. (1998). Activation patterns and length changes in hindlimb muscles of the bullfrog *Rana catesbeiana* during jumping. *J. Exp. Biol.* **201**, 2763-2777.
- Patek, S. N. (2015). The most powerful movements in biology. *Am. Sci.* **103**, 330-337. doi:10.1511/2015.116.330
- Patek, S. N. and Caldwell, R. L. (2005). Extreme impact and cavitation forces of a biological hammer: strike forces of the peacock mantis shrimp (*Odontodactylus scyllarus*). *J. Exp. Biol.* **208**, 3655-3664. doi:10.1242/jeb.01831
- Patek, S. N., Korff, W. L. and Caldwell, R. L. (2004). Deadly strike mechanism of a mantis shrimp. *Nature* **428**, 819-820. doi:10.1038/428819a
- Patek, S. N., Baio, J. E., Fisher, B. L. and Suarez, A. V. (2006). Multifunctionality and mechanical origins: ballistic jaw propulsion in trap-jaw ants. *Proc. Natl Acad. Sci. USA* **103**, 12787-12792. doi:10.1073/pnas.0604290103
- Patek, S. N., Nowroozi, B. N., Baio, J. E., Caldwell, R. L. and Summers, A. P. (2007). Linkage mechanics and power amplification of the mantis shrimp's strike. *J. Exp. Biol.* **210**, 3677-3688. doi:10.1242/jeb.006486
- Patek, S. N., Dudek, D. M. and Rosario, M. V. (2011). From bouncy legs to poisoned arrows: elastic movements in invertebrates. *J. Exp. Biol.* **214**, 1973-1980. doi:10.1242/jeb.038596
- Patek, S. N., Rosario, M. V. and Taylor, J. R. A. (2013). Comparative spring mechanics in mantis shrimp. *J. Exp. Biol.* **216**, 1317-1329. doi:10.1242/jeb.078998
- Peplowski, M. M. and Marsh, R. L. (1997). Work and power output in the hindlimb muscles of Cuban tree frogs *Osteopilus septentrionalis* during jumping. *J. Exp. Biol.* **200**, 2861-2870.
- Poppinga, S., Daber, L. E., Westermeier, A. S., Kruppert, S., Horstmann, M., Tollrian, R. and Speck, T. (2017). Biomechanical analysis of prey capture in the carnivorous Southern bladderwort (*Utricularia australis*). *Sci. Rep.* **7**, 1776. doi:10.1038/s41598-017-01954-3
- Reynaga, C. M., Eaton, C. E., Strong, G. A. and Azizi, E. (2019). Compliant substrates disrupt elastic energy storage in jumping tree frogs. *Integr. Comp. Biol.* doi: 10.1093/icb/icz069
- Richards, C. T. and Sawicki, G. S. (2012). Elastic recoil can either amplify or attenuate muscle-tendon power, depending on inertial vs. fluid dynamic loading. *J. Theor. Biol.* **313**, 68-78. doi: 10.1016/j.jtbi.2012.07.033
- Ritzmann, R. (1973). Snapping behavior of the shrimp *Alpheus californiensis*. *Science* **181**, 459-460. doi:10.1126/science.181.4098.459
- Roberts, T. J. and Azizi, E. (2011). Flexible mechanisms: the diverse roles of biological springs in vertebrate movement. *J. Exp. Biol.* **214**, 353-361. doi:10.1242/jeb.038588
- Roberts, T. J. and Marsh, R. L. (2003). Probing the limits to muscle-powered accelerations: lessons from jumping bullfrogs. *J. Exp. Biol.* **206**, 2567-2580. doi:10.1242/jeb.00452
- Rome, L. C. and Lindstedt, S. L. (1998). The quest for speed: muscles built for high-frequency contractions. *News Physiol. Sci.* **13**, 261-268. doi:10.1152/physiologyonline.1998.13.6.261
- Roper, M. and Seminara, A. (2019). Mycofluidics: the fluid mechanics of fungal adaptation. *Annu. Rev. Fluid Mech.* **51**, 511-538. doi:10.1146/annurev-fluid-122316-045308
- Rosario, M. V. and Patek, S. N. (2015). Multi-level analysis of elastic morphology: the mantis shrimp's spring. *J. Morphol.* **276**, 1123-1135. doi:10.1002/jmor.20398
- Rosario, M. V., Sutton, G. P., Patek, S. N. and Sawicki, G. S. (2016). Muscle-spring dynamics in time-limited, elastic movements. *Proc. R. Soc. B* **283**, 20161561. doi:10.1098/rspb.2016.1561
- Sakes, A., van der Wiel, M., Henselmans, P. W. J., van Leeuwen, J. L., Dodou, D. and Breedveld, P. (2016). Shooting mechanisms in nature: a systematic review. *PLoS ONE* **11**, e0158277. doi:10.1371/journal.pone.0158277
- Singh, A. K., Prabhakar, S. and Sane, S. P. (2011). The biomechanics of fast prey capture in aquatic bladderworts. *Biol. Lett.* **7**, 547-550. doi:10.1098/rsbl.2011.0057
- Siwanowicz, I. and Burrows, M. (2017). Three dimensional reconstruction of energy stores for jumping in planthoppers and froghoppers from confocal laser scanning microscopy. *eLife* **6**, e23824. doi:10.7554/eLife.23824
- Sutton, G. P., Mendoza, E., Azizi, E., Longo, S. J., Ilton, M. and Patek, S. N. (2019). Why don't large animals exclusively use springs to jump? Because they can jump higher without them. *J. Integr. Comp. Biol.* (in press).
- Tadayon, M., Amini, S., Masic, A. and Miserez, A. (2015). The mantis shrimp saddle: a biological spring combining stiffness and flexibility. *Adv. Funct. Mater.* **25**, 6437-6447. doi:10.1002/adfm.201502987
- Tadayon, M., Amini, S., Wang, Z. and Miserez, A. (2018). Biomechanical design of the mantis shrimp saddle: a biomineralized spring used for rapid raptorial strikes. *iScience* **8**, 271-282. doi:10.1016/j.isci.2018.08.022
- Van Wassenbergh, S., Strother, J. A., Flammang, B. E., Ferry-Graham, L. A. and Aerts, P. (2008). Extremely fast prey capture in pipefish is powered by elastic recoil. *J. R. Soc. Interface* **5**, 285-296. doi:10.1098/rsif.2007.1124
- Vincent, O., Weisskopf, C., Poppinga, S., Masselter, T., Speck, T., Joyeux, M., Quilliet, C. and Marmottant, P. (2011). Ultra-fast underwater suction traps. *Proc. R. Soc. B* **278**, 2909-2914. doi:10.1098/rspb.2010.2292
- Wegst, U. G. K. and Ashby, M. F. (2004). The mechanical efficiency of natural materials. *Philos. Mag.* **84**, 2167-2186. doi:10.1080/14786430410001680935
- Zack, T. I., Claverie, T. and Patek, S. N. (2009). Elastic energy storage in the mantis shrimp's fast predatory strike. *J. Exp. Biol.* **212**, 4002-4009. doi:10.1242/jeb.034801
- Zaitsev, V., Gvirsman, O., Ben Hanan, U., Weiss, A., Ayali, A. and Kosa, G. (2015). A locust-inspired miniature jumping robot. *Bioinspir. Biomim.* **10**, 066012. doi:10.1088/1748-3190/10/6/066012
- Zhao, J., Xu, J., Gao, B., Xi, N., Cintron, F. J., Mutka, M. W. and Xiao, L. (2013). MSU jumper: A single-motor-actuated miniature steerable jumping robot. *IEEE Trans. Robot.* **29**, 602-614. doi:10.1109/TRO.2013.2249371