Latch-mediated spring actuation (LaMSA): the power of integrated biomechanical systems

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Summary statement: Small organisms use spring propulsion and latch mediation to control cascading processes of energy release, ultimately transforming small amounts of energy into energy dense events.

Abstract

Across the tree of life – from fungi to frogs – organisms wield small amounts of energy to generate fast and potent movements. These movements are propelled with elastic structures and their loading and release are mediated by latch-like opposing forces. They comprise a class of elastic mechanisms termed latch-mediated spring actuation (LaMSA). Energy flow through LaMSA begins when an energy source loads elastic element(s) in the form of elastic potential energy. Opposing forces, often termed latches, prevent movement during loading of elastic potential energy. As the opposing forces are shifted, reduced or removed, elastic potential energy is transformed into kinetic energy of the spring and propelled mass. Removal of the opposing forces can occur instantaneously or throughout the movement, resulting in dramatically different outcomes for consistency and control of the movement. Structures used for storing elastic potential energy are often distinct from mechanisms that propel the mass: elastic potential energy is often distributed across surfaces and then transformed into localized mechanisms for propulsion. Organisms have evolved cascading springs and opposing forces not only to serially reduce the duration of energy release, but often to localize the most energy dense events outside of the body to sustain use without self-destruction. Principles of energy flow and control in LaMSA biomechanical systems are emerging at a rapid pace. New discoveries are catalyzing remarkable growth of the historic field of elastic mechanisms through experimental biomechanics, synthesis of novel materials and structures, and high-performance robotics systems.

Introduction

Manipulation of energy flow through integrated materials, structures, and the environment is key to spectacular movements in organisms (Dickinson et al., 2000). In particular, the ability to manipulate potential energy and kinetic energy is exemplified in elastic mechanisms (Alexander, 1988; Alexander & Bennet-Clark, 1977; Biewener & Patek, 2018; Vogel, 2009). In the past century, hundreds of *Journal of Experimental Biology* articles have revealed diverse movements that use elastic mechanisms, including cyclic, efficient locomotion in hopping wallabies, running dogs, and flying insects (Biewener & Baudinette, 1995; Ellington, 1985; Gregersen et al., 1998), power-enhanced locomotion in jumping frogs, humans, and insects (Bennet-Clark & Lucey, 1967; Farley et al., 2019; Farris et al., 2016; Mendoza & Azizi, 2021), reduction of damage in landing animals and colliding insect wings (Dick et al., 2021; Mountcastle & Combes, 2014), and sound production and reception in buzzing cicadas, singing bark beetles, rasping spiny lobsters, and listening salamanders (Lindeman & Yack, 2019; Patek, 2002; Pringle, 1954; Smith, 1968).

Amidst this engaging history of research has emerged a rapidly developing and interdisciplinary field that focuses on the integrated biomechanics of elastic mechanisms in ultrafast, small, spring-propelled systems (Fig. 1). These organisms use a class of elastic mechanisms recently termed Latch Mediated Spring Actuation (LaMSA) (Fig. 2) (Longo et al., 2019), referred to historically by various terms including catapults, click mechanisms, and power amplification (Box 1) (Biewener & Patek, 2018; Gronenberg, 1996; Patek et al., 2011; Vogel, 2009). LaMSA encompasses the realm of the fastest jumpers, strikers, and shooters which are primarily propelled using elastic potential energy. They include irresistibly fascinating organisms – from rapidly-striking chameleon tongues (the subject of one of the first elastic mechanisms paper published in JEB's history) (Zood, 1933) to recent studies including trap-jaw spider mandibles (Wood, 2020), snapping seahorse heads (Avidan & Holzman, 2021), larval mantis shrimp strikes (Harrison et al., 2021), cavitation-shooting snapping shrimp (Longo et al., 2023), and trap-jaw ant strikes (Larabee et al., 2017; Sutton et al., 2022).

Unlike cyclic movements which have been the focus of most elastic mechanisms research, such as flying, trotting, running, hopping, vibrating, and sensing, many LaMSA systems are aperiodic, not cyclic, and not energetically efficient (Ilton et al., 2018; Ilton et al., 2019; Kagaya & Patek, 2016; Marsh, 2022; Patek et al., 2011; Roberts & Azizi, 2011; Sutton et al., 2019). LaMSA systems often take orders of magnitude longer duration to load compared to the duration of spring propulsion (the time period when the spring propels or launches a mass). They use opposing forces (more colloquially termed latches) to enable the prolonged process of elastic energy storage (Galantis & Woledge, 2003; Ilton et al., 2018). Latches are rapidly or gradually removed such that they mediate the transformation from elastic potential energy to kinetic energy of the spring and propelled mass (Fig. 2) (Divi et al., 2020). This process generates brief, intense, spring-propelled movements that can result in jumping, spearing, puncturing, fracturing, cavitation, and high acceleration projectile launching (Ilton et al., 2018).

Even though the popular appeal of LaMSA systems often revolves around extraordinary accelerations and the amplification of mechanical power output enabled by this aperiodic process (Fig. 1; Box 1) (Patek, 2015, 2016), perhaps even more remarkable is the evolution of dynamically integrated LaMSA components that enable small organisms to perform potent movements with small (µJ-mJ) amounts of energy, over short durations (µs-ms) and displacements (µm-mm) (Vogel, 2005a; Vogel, 2005b). From the earliest studies to the latest research, these systems exemplify how organisms use integrated mechanisms to manipulate energy and perform movements still unmatched by human engineering. As will be addressed in this review, LaMSA research constitutes an interdisciplinary field with insights into tiny energy-controlling structures, manipulation of fluids, environment-system tuning and robustness, control of energy flow, and mechanisms for wielding highly energetic events without self-destruction. Following the generative process of examining energetics *via* structures, systems, and environments (Dickinson et al., 2000) and grounded in the integrated components that comprise the LaMSA framework (Fig. 2) (Ilton et al., 2018; Longo et al., 2019), the review begins with the principles of energy sources and ends with the remarkable consequences of integrated and cascading spring-propelled and latch-mediated systems.

Energy source

In LaMSA systems, energy sources serve the function of loading energy into an elastic structure, such as a spring (Fig. 2). Seemingly a simple task, this process is achieved through diverse mechanisms. Numerous animals use muscles as the energy source: a muscle contracts to generate force and displacement in an elastic structure (Fig. 3) (Alexander & Bennet-Clark, 1977). The mechanical work of the muscle is thereby transformed into elastic potential energy.

Countless organisms, including plants, animals, and fungi, manipulate liquids to load elastic mechanisms: by moving fluids, organisms induce deformation and thereby perform work on surrounding elastic structures (Bauer et al., 2021; Edwards et al., 2019; Farley et al., 2019; Sakes et al., 2016; Skotheim & Mahadevan, 2005).

Given that work is defined as the product of force and displacement, energy sources can maximize mechanical work through various combinations of force and displacement (Fig. 3). However, in systems at the mm-scale or smaller - such as a flea's leg or a trap-jaw ant's head - displacement is inherently limited. Therefore, small mechanisms can prioritize force over displacement to generate sufficient work to load an elastic mechanism. Upper limits to the mechanical power of any motor-like system causes tradeoffs between force and velocity (Galantis & Woledge, 2003; Ilton et al., 2018; Peplowski & Marsh, 1997). Therefore, high force, low displacement energy sources perform work more slowly than low force, high displacement energy sources (Bennet-Clark, 1975; Roberts, 2016; Rosario et al., 2016). Consequently, LaMSA energy sources typically perform work on elastic mechanisms by slowly generating high forces over small displacements, which can result in orders of magnitude differences between the duration over which the energy source is active and the duration of the final movement. For example, loading durations of legless jumping gall midge larvae (*Contarinia* sp.) and body-snapping click beetles (*Campsosternus auratus)* are orders of magnitude longer than takeoff (Bolmin et al., 2021; Farley et al., 2019).

It is an intriguing puzzle as to whether LaMSA energy sources are the cause of the high force, long durations required for spring loading or whether small, rapidly propelled masses demand these properties of the energy sources (Bobbert, 2013; Galantis & Woledge, 2003; Gronenberg, 1996; Ilton et al., 2018; Sutton et al., 2019). Evolutionary and comparative analyses offer insights through comparisons of spring and muscle evolution across closely related clades with and without LaMSA. Ants have independently evolved LaMSA numerous times (e.g., trap-jaw, Dracula, or snap-jaw ants) (Booher et al., 2021; Gibson et al., 2018; Larabee et al., 2016; Larabee et al., 2017; Larabee et al., 2018; Patek et al., 2006). In ant clades with LaMSA, spring-loading mandible muscles exhibit more force-modified morphology, including longer sarcomeres and more pennate arrangements, than closely related species without LaMSA (Booher et al., 2021; Gronenberg et al., 1997; Spagna et al., 2008). Across mantis shrimp (Stomatopoda), increased force capacity of spring loading muscles is correlated with increased elastic potential energy (Blanco & Patek, 2014; Patek et al., 2013). Spring-loading muscle properties are correlated with jump performance in frogs (Fig. 3) (Mendoza & Azizi, 2021; Mendoza et al., 2020), but spring-loading muscles do not appreciably vary across performance in tongue-shooting salamanders (Deban et al., 2020; Olberding et al., 2018) possibly due to the restricted range of sarcomere lengths in vertebrates (Biewener & Patek, 2018).

Force-displacement dynamics of energy sources influence how organisms use LaMSA. Jumping animals requiring a rapid response and fast spring-loading muscle contraction must load the elastic mechanism within a shorter duration and with less force than animals that can take more time to load a stiffer elastic mechanism prior to jumping. Indeed, animals preparing quickly for a jump are able to load maximal energy by using less stiff springs (i.e., springs loaded more quickly and with less force), whereas animals with longer spring-loading durations prior to a jump achieve maximal elastic potential energy by using more stiff springs (Roberts, 2016; Rosario et al., 2016). Mantis shrimp species requiring fast responses to capture evasive prey ("spearers") have faster-contracting, shorter sarcomere length muscles than mantis shrimp species that slowly load springs as they prepare to smash a snail ("smashers") (Blanco & Patek, 2014). Mantis shrimp (*Gonodactylaceus bredini*) increase the duration of spring-loading muscle contractions to increase strike forces (Kagaya & Patek, 2016). Similarly, Cuban tree frogs (*Osteopilus septentrionalis*) increase the duration of spring-loading muscle contractions to increase the work performed by the muscle on the elastic mechanism and enhance jump power (Marsh, 2022). Locusts (*Schistocerca gregaria*) also vary leg velocity through changes in spring-loading muscle contractions (Burrows & Morris, 2001).

The energy source can be part of the propelled mass or located separately from the part of the body that is being propelled. The mass of the energy source is consequential for both total energy requirements and the pathways through which energy is loaded into the elastic mechanism (Fig. 1) (Cox et al., 2014; Galantis & Woledge, 2003; Sawicki et al., 2015). Insect and frog jumps propel the entire body mass including the energy source (i.e., the leg muscles that load the elastic mechanism). In contrast, other LaMSA systems only propel one part of the body – such as the prey-capturing tongue of salamanders and toads which does not carry the mass of the spring-loading muscles that propel the tongue (Deban et al., 2007; Lappin et al., 2006). Animals can also do both with the same mechanism: some trap-jaw ant species use their mandibles to capture prey, which does not require propelling the energy source, and they also use their ultrafast mandible snaps to propel their body in a jump, which does require propulsion of the energy source (Larabee & Suarez, 2015; Patek et al., 2006; Spagna et al., 2009). Likewise, a locust can propel its whole body in a jump or perform a high speed kick with one leg (Burrows & Morris, 2001). Therefore, systems that do not (always) require whole body propulsion can locate the mass of the energy source outside of the propelled body part, thereby decreasing the mass of the propelled system. This arrangement both reduces energy requirements for propulsion and removes size constraints of the energy source.

Storage of elastic potential energy

Storage of elastic potential energy requires integration of an energy source, elastic mechanism, and an opposing force that holds the system in place while it is loaded (Figs. 2, 3). In other words, storage of elastic potential energy requires two mechanisms: a mechanism to perform work on an elastic element and an opposing force to hold the elastic element in place while it is loaded. Elastic mechanisms encompass systems and structures that deform when forces are applied and recoil when released. In LaMSA mechanisms, the recoil of the elastic mechanism actuates (propels) movement of the propelled mass. Latch mechanisms encompass any opposing force that holds the system in place during deformation of the elastic mechanism. Detailed consideration of the terminology surrounding elastic mechanisms and latches is addressed elsewhere, including the similar use of the term catch mechanism (Divi et al., 2020; Ilton et al., 2018; Longo et al., 2019). Given that deformable structures and mechanisms that generate forces to oppose or facilitate deformation of structures are omnipresent in organisms, myriad latches and elastic mechanisms have evolved anywhere from inside cells to outside of the body.

Storage of elastic potential energy is a dynamic interaction between an energy source and an elastic structure (Fig. 3). Therefore, the force-displacement properties of both mechanisms together define the energy that can be stored. This interplay between muscles and elastic mechanisms is particularly compelling when illustrated through overlaid graphs of work produced by both the energy source and elastic mechanism (Fig. 3) (Cox et al., 2021). This approach yields insights into the tradeoffs experienced by organisms with limited time to load elastic potential energy (requiring faster loading at lower forces) (Rosario et al., 2016) and scaling rules imposed by the upper limits of elastic energy storage (Mendoza & Azizi, 2021;

Sutton et al., 2019). Some organisms, such as mantis shrimp, adjust the loading of elastic energy storage depending on the particular context in which they are using the movement, such as feeding or fighting (Green et al., 2019; Kagaya & Patek, 2016). Spring loading in locusts (*Schistocerca gregaria*) is correlated both with leg speed and the behavioral context of the leg movement (Burrows & Morris, 2001). Across development, locusts vary their elastic mechanism depending on the need for faster, but less energetically efficient jumps in the solitary morph or slower, more energetically efficient jumps in the gregarious morph; solitary jumpers produce greater jump performance by developing larger spring-loading muscles and less-stiff springs than the gregarious jumpers (Rogers et al., 2016).

Although they have been an important focus of research (Alexander, 1988), tendons (termed apodemes when in arthropods) can be a limited pathway for energy storage in small LaMSA systems. Like elastic bands, tendons are deformed primarily along their long axis with length changes of up to 10%, such that a longer tendon can store proportionally more elastic energy than a small tendon (with the same material stiffness) due to its absolutely longer displacement (Alexander & Bennet-Clark, 1977; Roberts, 2016; Zajac, 1989). Consequently, when located in a small space with limited room for a long, stretchy tendon, a tendon would potentially need to be prohibitively stiff to store sufficient elastic energy via a small displacement (Sutton et al., 2019).

Deformable, shell-like structures are key to achieving sufficient elastic energy storage in small LaMSA systems (Fig. 4). These structures generate rapid snapping movements through geometric instabilities (Forterre et al., 2005; Holmes & Crosby, 2007; Skotheim & Mahadevan, 2005) and exemplify strong yet flexible geometries built of robust, thin-walled curvatures (Heitler, 1977; Mensch et al., 2021; Patek et al., 2004; Tadayon et al., 2015; Tadayon et al., 2018). At the subcellular scale, nematocysts (cells containing propulsive organelles characteristic of cnidarians) integrate stretchy elastomeric proteins (Cnidoins) and stiffer micro-collagen fibers into spectacular shapes that surround and sequentially propel microscopic spears and adhesive devices (Beckmann et al., 2015; Karabulut et al., 2022). Mantis shrimp load elastic energy into the exoskeleton of the merus segment of their raptorial appendage: the exoskeleton deforms as a complex, monolithic structure comprised of varying material density integrated across complex shapes (Patek et al., 2007; Rosario & Patek, 2015; Tadayon et al., 2015; Tadayon et al., 2018). Jumping insects use springs with complex shapes built of rubber-like resilin integrated with stiff cuticle (Burrows et al., 2008; Burrows & Sutton, 2012; Heitler, 1977; Katz & Gosline, 1994). Trap-jaw ants deform their shell-like head exoskeleton to store elastic energy (Fig. 4) (Larabee et al., 2017; Sutton et al., 2022). Even spiders build LaMSA mechanisms out of integrated materials and shapes such that they can reel in the web to load it and then release it to propel their body and the web toward prey (Alexander & Bhamla, 2020; Han et al., 2019).

Complex geometries characteristic of arthropod exoskeletons and plants can make use of displacements that do not require large forces and can be distributed across a larger area than a strap-like tendon (Katz & Gosline, 1994). For example, trap-jaw ants combine deformation of their head exoskeleton and apodeme deformation to power ultrafast mandible strikes (Fig. 4) (Sutton et al., 2022). There is not enough space in the head to permit sufficient length change of the apodeme to power the mandible strike. Instead, by combining head deformation with apodeme stretching, they can store sufficient energy to propel the mandibles with exceptional mechanical power density. This potency of additive displacements of elastic structures may explain why LaMSA is disproportionately found in arthropods (animals with thin-walled, shell-like exoskeletons) and plants (built primarily using tube-like structures) which inherently have structures that can evolve to distribute elastic potential energy via small displacements across their surfaces (Fig. 4) (Sakes et al., 2016). These geometries can enhance a structure's energy density (elastic potential energy divided by the mass of the deforming structure).

Organisms produce latch-like opposing forces with mechanisms ranging from antagonistic muscle contractions to adhesive microscopic hairs. Antagonistic muscle arrangements are well suited to provide opposing forces to loading elastic mechanisms, such that one muscle performs work on the elastic mechanism while its antagonist holds the system in place (Abbott et al., 2019; Bennet-Clark, 1975; Bennet-Clark & Lucey, 1967; Heitler & Burrows, 1977). The leverage of antagonist muscles can be enhanced with additional latch structures: embedded in the flexor muscle apodemes of mantis shrimp, flea beetles, and other insects are hard structures (sclerites) that further enhance mechanical advantage of the flexor muscle contraction (Burrows, 1969; Kagaya & Patek, 2016; Nadein & Betz, 2016; Patek et al., 2007; Ruan et al., 2020). Other latches range from adhesive hairs or fluids that hold the curled up body of insect larvae and nematodes in place while the animal loads elastic potential energy prior to a jump (Campbell & Kaya, 1999; Farley et al., 2019) to combinations of mechanical advantage and shifting moment arms that enable insect and frog legs to dynamically oppose the forces loading elastic energy into tendons (Astley & Roberts, 2014; Burrows & Morris, 2003). Even within a clade, latches evolve with varying capacities and mechanisms: some snapping shrimp species rely on a large adhesive disc to oppose spring loading forces whereas other species have minimal to no adhesive discs and instead use shifting geometries and antagonistic muscles to hold the system in place prior to snapping (Kaji et al., 2018; Longo et al., 2023; Ritzmann, 1974).

Transformation from elastic potential energy to kinetic energy

The energetic transformation from elastic potential energy to kinetic energy begins with and is guided by the dynamic removal of the latch-like opposing forces that enables the storage of elastic potential energy (Figs. 2, 5). Kinetic energy includes a spring's energetics as it propels itself and any attached mass, such as the propelled body of a jumping insect. We will address the mechanisms of transformation of spring potential energy to the kinetic energy of the propelled mass in the next section. In this section, we primarily focus on the role of latch removal on this energetic transformation.

The removal of latch-like opposing forces is central to the transformation of elastic potential to kinetic energy. Latch removal can occur across time ranges from a brief event at the onset of spring actuation to an event that spans the duration of spring actuation (Figs. 2,5) (Divi et al., 2020; Ilton et al., 2018; Olberding et al., 2019). If a latch is removed at the start of spring actuation, then the dynamic interaction between spring forces and internal forces of the driven mass will largely guide propulsion. If a latch is removed over a larger proportion of the duration of spring actuation, then the latch and spring dynamics together determine dynamics of spring actuation (Fig. 5) (Divi et al., 2020; Hyun et al., 2023). These latch removal dynamics impact whether an organism can control the dynamics of spring actuation and whether substantial energetic losses are incurred due to the mechanism and scaling of latch removal.

Organisms can use latch removal to produce consistent spring-propelled movement regardless of variability during loading of elastic potential energy. A snapping shrimp species (*Alpheus heterochaelis*) uses a torque reversal latch mechanism to mediate the transformation from elastic potential to kinetic energy and reduce the effects of variable spring loading to yield consistent snap kinematics (Longo et al., 2023). Intriguing from an evolutionary perspective, mathematical modeling demonstrates that the torque reversal mechanism in *A. heterochaelis* could instead yield variable snaps simply through subtle modifications of their joint morphology and geometry (Longo et al., 2023). It is not yet known whether other snapping shrimp species vary geometry-based latch removal dynamics. In trap-jaw ants, latch removal reduces variation in spring loading such that mandible strikes remain consistent regardless of the fatigue level of the spring-loading muscle (Larabee et al., 2022).

A mechanism incorporating variation in latch removal duration can allow organisms to produce either consistent or variable kinematics. Dracula ants (*Mystrium camillae*) press their mandibles together, deform the mandibles to store elastic potential energy, and use friction between the mandibles as the latch (Fig. 5) (Larabee et al., 2018). Depending on the size and speed of the interacting surfaces during release of elastic potential energy, the latch removal process produces consistent or variable mandible kinematics (Divi et al., 2020). Comparative studies of click beetles, which use a combination of bending beams, snap-through transitions, and frictional opposing forces, reveal the integrated evolution of latch removal dynamics, spring propulsion energetics, and body size (Bolmin et al., 2022; Bolmin et al., 2021; Bolmin et al., 2019). Even the snapping of human fingers leverages the dynamics (and lossiness) of frictional latching mechanisms to enable tunable outputs (Acharya et al., 2021).

Latch removal based solely on relaxing antagonist muscles allows some adjustments to energetic outputs. However, relaxing muscles offer limited power enhancement without additional integrated latches to reduce the duration of energy release (Abbott et al., 2019; Burrows & Hoyle, 1972; Galantis & Woledge, 2003; McNeill et al., 1972; Sawicki et al., 2015). Even so, subtle changes in the duration of relaxation influences the power outputs of spring-propelled movements, including possibly through eccentric muscle contraction dynamics (Abbott et al., 2019; Sawicki et al., 2015). Compared to systems solely relying on the relaxation of muscle antagonists, the integration of mechanical advantage, geometric over-centering, and integrated contact latches facilitates greater energy storage as well as controllability of the rate of energy release (Galantis & Woledge, 2003; Steinhardt et al., 2021).

Dynamics of latch removal can be tuned to the physical environment, such that removal occurs only under specific environmental conditions (Kim et al., 2021). In some predatory plants, external conditions for stimulating latch removal are driven by the movement of prey or other hydrodynamic cues (Bauer et al., 2021). Materials of the latch itself can be changed based on ambient conditions. In pines, resin holds the scales of the cones closed until the right conditions for seed release. When a particular combination of temperature and humidity is reached, the physical properties of resin change such that the resin releases its holding force on the scales, at which point the scales pop open to allow later release of the pine seeds (Horstmann et al., 2022). These discoveries encourage further investigations into the tuning of latch dynamics, especially in systems requiring deployment during specific environmental conditions (Kim et al., 2021).

LaMSA springs are effective for propulsion of small masses, but that effectiveness is not synonymous with efficiency: the transformation from potential to kinetic elastic energy can incur significant energetic losses (Hyun et al., 2023; Ilton et al., 2019; Liang & Crosby, 2020a, 2020b). LaMSA springs deliver energy during recoil, and then oscillations afterward may reduce damage by dissipating energy but do not further propel the system (Burrows & Morris, 2003; Sutton et al., 2022); this process is fundamentally different from the oscillatory elastic mechanisms in flying insects and larger jumpers, such as kangaroos, which efficiently cycle energy (Roberts & Azizi, 2011). Most studies treat springs as Hookean (ideal, massless). However, in tiny spring-propelled systems, the spring's mass can be consequential, especially when the mass of the spring exceeds that of the propelled mass (Ilton et al., 2018). Physical models, theory, and mathematical modeling point toward upper limits to recoil velocity given a spring's inertia, yet studies in biology are currently lacking (Ilton et al., 2018; Ilton et al., 2019; Longo et al., 2019). Energetic losses of propulsive springs at small scales make LaMSA systems not as efficient as oscillatory locomotor systems, but those energetic losses offer pathways for control of energy transformations just as we observed in latch mechanisms (Hyun et al., 2023; Kim et al., 2021; Liang & Crosby, 2020a, 2020b). These losses allow regulation of the timing of energy release – such as for tuning with environments – and for coordination with the release of the latch mechanism (Hyun et al., 2023).

Given our focus on energy flow, we have not comprehensively reviewed the stunning diversity of biological latches and the principles underlying whether or not the latches can be used, re-used, or reset. Several studies have collated this information (Ilton et al., 2019; Longo et al., 2019; Sakes et al., 2016); however, even with advances in high speed imaging, few studies have successfully measured the short timeline and tiny displacements of real-time latch removal in organisms.

Dynamics of spring-propelled masses

Now that we have examined elastic energy storage and release, we can probe the energetics of spring-propelled masses. The transformation from spring potential energy to kinetic energy of a propelled mass - simultaneously (Fig. 2) or sequentially - requires a mechanism to deliver energy from an elastic structure to the propelled mass. In other words, the elastic structure must perform work (i.e., deliver force and displacement) on the propelled mass. How the energy source performs work on the elastic mechanism to load elastic potential energy is often distinct from how elastic structures perform work on a propelled mass (Fig. 4). Furthermore, as a spring propels a mass, resistive forces (such as drag) on the propelled mass also exert force back on the elastic mechanism. These resistive forces can include substantial and dynamically changing environmental forces on the mass as it is propelled. We focus here on the integration of the propulsive elastic structure and the propelled mass, regardless of whether the mass ultimately stays attached to the organism (e.g., an insect's leg) or if it is propelled into the environment (e.g., a cone snail's harpoon) (Schulz et al., 2019). The intriguing distinctions among single-use, re-useable, re-settable LaMSA mechanisms are considered elsewhere (Ilton et al., 2018; Longo et al., 2019; Sakes et al., 2016).

Organisms have evolved remarkable pathways to transform distributed energy storage across surfaces to localized mechanisms for propulsion (Fig. 4). In many cases, multiple springs act at multiple locations to develop rapid rotation, such as in the mouthparts of dragonfly larvae, snapping heads of feeding seahorses and snipefish, snapping mouthparts of spiders, recoiling pleural arches powering planthopper and flea jumps, and the rapid strikes of both mantis shrimp and snapping shrimp (Büsse et al., 2021; Longo et al., 2018; Longo et al., 2023; Rothschild & Schlein, 1975; Siwanowicz & Burrows, 2017; Steinhardt et al., 2021; Van Wassenbergh et al., 2008; Wood, 2020). The transformation of distributed deformations of shapes into directed motion is also the norm in plants and fungi. Fungal ballistospores are fired with the surface tension energy of a droplet, yet the gradual formation of distributed and stored energy via the surface tension of a droplet is distinct from the directed energy delivery to the spores: the delivery of energy to the spore utilizes directional micro-fluidics to launch the spore in a particular direction (Liu et al., 2017). Bunchberry plants (*Cornus canadensis*) transform distributed elastic potential energy into a directional catapult to launch pollen into the air (Whitaker et al., 2007). Pilobolus fungi and sphagnum moss transform displacements distributed across a shape into remarkably controlled and directional projectile release (Edwards et al., 2019; Page, 1964; Whitaker & Edwards, 2010). Bladderworts suck water into their traps with the elastic recoil of their bladder walls (Fig. 4) (Singh et al., 2011; Vincent et al., 2011).

In arthropods, integration of apodeme recoil with exoskeletal deformation confers three additional capabilities: development of torque, reduction of joint constraints, and use of the mechanism with or without activating the LaMSA mechanism (Fig. 4). While these capabilities are widespread in arthropods (Bennet-Clark & Lucey, 1967; Büsse et al., 2021), an intensively studied example is found in *Odontomachus* trap-jaw ants. Trap-jaw ants use the combined outward recoil of the head capsule and shortening recoil of an apodeme to rapidly torque a tiny mandible closed at high rotation rates (Fig. 4) (Sutton et al., 2022). Exoskeletal and apodeme recoil also provides the spring-driven torque of jumping insect legs (Bennet-Clark, 1975; Burrows & Morris, 2001). This mechanism, termed a dual spring force couple by Sutton et al (2022), transforms the energy stored across the entire trap-jaw ant's head capsule into work delivered at one location and solely along the plane of a tiny mandible's rotation (Sutton et al., 2022). The combination of the push by the recoiling head capsule and the pull by the recoiling muscle-apodeme unit also reduces the need for joint constraints on the mandible, which would otherwise cause such high friction at these tiny scales that the movement could not occur at the observed rotation rates. Even with the evolution of this intriguing mechanism, trap-jaw ants have retained the ability to move their mandibles directly with muscle and with multiple degrees of freedom. They can simply contract the mandible closer muscle to move the mandible; alternatively, they can engage the latches and then contract the mandible closer muscle which loads elastic energy into the head and closer muscle apodeme (Fig. 4). This multifunctionality – the ability to switch in and out of using the LaMSA mechanism - is also observed in mantis shrimp and insect jumpers (Burrows & Morris, 2001; Steinhardt et al., 2021).

Loading imposed by the environment on the propelled mass, such as drag forces, is dependent on rate and length scales, especially in the fluid regimes at which LaMSA often is used (Fig. 1) (Vogel, 2005a). Larval mantis shrimp, nematocysts, and ballistospores use spring propulsion to transition the propelled mass from viscous to inertial fluid regimes (Hamlet et al., 2020; Harrison et al., 2021; Liu et al., 2017). Adult mantis shrimp experience considerable tradeoffs among the inertial forces, fluid forces, out lever length, and strike kinematics given the costly fluid dynamic forces during their ultrafast rotations (Anderson et al., 2014; McHenry et al., 2016). Animals that jump from flexible substrates – such as leaves and branches – sometimes can recapture substrate energy to enhance propulsion and in other cases experience energetic losses or disruption to the elastic mechanism (Astley et al., 2015; Reynaga et al., 2019). Spinning seeds often manipulate fluid dynamics for stabilization, efficiency, and directionality (Cooper et al., 2018; Vogel, 2005a; Vogel, 2005b, 2009).

Tuning of the magnitude of the projectile mass to the spring and latch dynamics determines the characteristics of the movement - regardless of whether spring propulsion ultimately enhances mechanical power output (Burrows & Morris, 2001; Cook et al., 2022; Ilton et al., 2018). Therefore, organisms can switch into or out of using LaMSA depending on the size of the accelerated mass and the degree of tuning between LaMSA components and the accelerated mass (Cook et al., 2022; Ilton et al., 2018). This interplay between projectile mass, kinematics, and LaMSA components is a fascinating area for experimental manipulations of projectile mass and for analyses of developmental and size-based evolutionary transitions to and from the use of LaMSA systems (Harrison & Patek, 2023; Harrison et al., 2021).

Principles of cascading time compression to achieve extreme mechanical power density

The spectacular movements produced by LaMSA mechanisms are achieved not by using large amounts of energy, but instead by reducing the time over which energy is released. LaMSA mechanisms are low energy systems, in the sense that they are small and use minimal energy to move – often on the order of μJ (e.g., Kuan et al., 2020; Sakes et al., 2016; Sutton et al., 2022). The key to their potency is the enhancement of mechanical power through reduction of duration at each stage of energy flow. In many LaMSA systems, this is achieved not by sequentially operating one of each of the components we have discussed thus far, but instead through dynamic interactions between (sometimes multiple) springs, latches, and energy sources to reduce durations, enhance the rate of energy release, and move potent energetic events outside of the organism to avoid failure and damage. This review began by considering the historical focus on mechanical power (work divided by time) of a whole body compared to its spring-loading muscles (Box 1). In contrast, dynamic interactions among LaMSA components are the foundation of the latest emerging discoveries exploring the control of power enhancement at each step from energy source to the use of the movements in daily life (Fig. 6).

The cascading reduction of the duration of energy release is evident in extreme temporal asymmetries – in some cases spanning nine orders of magnitude (Fig. 6). Locusts (*Schistocerca gregaria*) load springs in their jumping legs for up to 800 ms, spring propulsion occurs in less than 5 ms, and legs can be fully propelled within 3 ms (Burrows & Morris, 2001). In snapping shrimp (*Alpheus heterochaelis*), spring-loading durations of 390 ms are transformed to strike durations averaging 0.7 ms which ultimately yield cavitation bubble collapse lasting nanoseconds - a cascade spanning eight orders of magnitude (Brennen, 1995; Lohse, 2005; Lohse et al., 2001; Longo et al., 2023; Versluis et al., 2000). In snapping fern sporangia, spring loading durations of 60 s are transformed to 0.7 µs launches – a transformation over seven orders of magnitude (Noblin et al., 2012). Smashing mantis shrimp transform a 300 ms spring-loading duration to a 49 µs impact accompanied by a nanosecond scale cavitation bubble collapse –an eight order of magnitude reduction of duration (Fig. 6) (Patek, 2019; Patek & Caldwell, 2005; Patek et al., 2004).

Underlying these extreme LaMSA examples is the use of multiple integrated LaMSA components, such as multiple latches, springs, and even the outcomes of the movements. At the subcellular scale, nematocysts exemplify a cascade of integrated, sequential, and repeated elastic and latch mechanisms to sling-shot their microscopic weaponry. They utilize multiple elastic mechanisms operating sequentially at the organelle level as well as at the level of tube eversion, and their latch mechanisms include touch-sensitive processes, osmotic pressure release, and recoiling Cnidoin proteins (Beckmann et al., 2015; Hamlet et al., 2020; Karabulut et al., 2022; Nüchter et al., 2006). Mantis shrimp (Stomatopoda) sequentially use three different latches to control energy release: two contact latches (hard structures embedded in their apodemes) and a hypothesized geometric over-centering (torque reversal) latch (Fig. 6) (Burrows, 1969; Kagaya & Patek, 2016; Patek et al., 2007; Steinhardt et al., 2021). They use a four-bar linkage mechanism embedded in their elastic mechanism to transform spring propulsion into rotation (McHenry et al., 2016; McHenry et al., 2012; Patek et al., 2007; Steinhardt et al., 2021). The relative dimensions of the four bar linkage vary across species, influencing the rate of energy release and correlating with the behavioral use of the appendages (Anderson et al., 2014; Claverie & Patek, 2013). Each of these integrated and sequential mechanical systems allow mantis shrimp to reduce the duration of energy release. Similarly, snapping shrimp have evolved a diverse array and varying degrees of integration between adhesive latches and geometric latches, and even varying degrees of shooting water jets with or without cavitation bubbles (Kaji et al., 2018; Longo et al., 2023; Patek & Longo, 2018; Ritzmann, 1973; Ritzmann, 1974).

LaMSA mechanisms not only confer remarkable control of the rate of energy release, but they also enable organisms to circumvent their small size to achieve large-animal performance and use potentially damaging energetic events outside of their body. For example, the peak impact forces of snail-smashing mantis shrimp rival the bite forces of alligators and hyenas (Patek, 2019; Patek & Caldwell, 2005), ultimately enabling small mantis shrimp to externally consume and process snails that cannot fit between their mandibles (Crane et al., 2018). The nematocysts of cnidarians and harpoons of cone snails enable external poisoning and capture of large prey (Hamlet et al., 2020; Nüchter et al., 2006; Schulz et al., 2019; Schulz et al., 2004).

Cavitation is one of the most notable examples of cascading energy release to yield external energetic events. Cavitation is arguably most brief and energetically potent event in biology; multiple organisms using LaMSA wield cavitation as the ultimate use of their rapid movements (Brennen, 1995; Caupin & Herbert, 2006; Cox et al., 2014; Koukouvinis et al., 2017; Lohse, 2005; Lohse et al., 2001; Patek & Caldwell, 2005; Versluis et al., 2000). Smashing mantis shrimp cavitate during snail shell impact, thereby doubling the number of impacts used to fracture shells (Cox et al., 2014; Crane et al., 2018; Patek & Caldwell, 2005; Patek et al., 2004). Similarly, snapping shrimp shoot water jets that cavitate at a distance from their body, effectively knocking out prey and deterring competitors with no damage to themselves (Dinh & Patek, 2022; Kingston et al., 2022).

These uses of LaMSA mechanisms are fundamentally distinct from other types of elastic mechanisms, noted in the Introduction, that serve to cycle energy efficiently or strategically within a body, particularly for locomotor and acoustic systems (Patek et al., 2011; Roberts & Azizi, 2011). In other words, in many LaMSA mechanisms, the pathway of energy flow does not necessarily end with the propelled mass; instead, it often concludes with the propelled mass interacting with the environment to generate energetically concentrated events, such as puncture (Anderson, 2018). Furthermore, by moving the final, brief and intense release of energy outside of the body, organisms can avoid self-destruction and repeatedly use the mechanism.

Conclusions and Future Directions

Discoveries emerging from the integrated dynamics of LaMSA components exemplify why these systems have generated enduring interest to researchers for over a century. Until recently, high speed imaging of LaMSA systems primarily focused on whole body dynamics which typically requires on the order of 10^2-10^3 frames per second (Sakes et al., 2016), yet the flow of energy through ultrafast, integrated LaMSA components has been largely or entirely invisible to high speed imaging and materials testing in the fastest systems which typically require 10^4-10^6 frames per second imaging (Longo et al., 2019). To measure energy flow through integrated LaMSA components, it is essential to study the components and how they dynamically interact *in vivo*. Visualization must navigate ultra-high speed imaging to capture brief movements of latches and high resolution imaging to resolve tiny displacements of propulsive springs (e.g., Longo et al., 2021; Nüchter et al., 2006; Pringle et al., 2005). Likewise, when measuring flow from energy source to environment, such as through puncture, impact and cavitation, the requisite sample rates for sensors are high (10^5-10^6 samples per second) (Jorge et al., 2021; Patek & Caldwell, 2005). Substantial technical improvements in extreme high speed imaging, dynamic sensing, and unrestrictive analog to digital data acquisition sample rates (McHenry & Hedrick, 2023) have allowed researchers to increasingly focus on *in vivo* experiments with real-time spring and latch dynamics, resulting in an exciting uptick in the pace of discovery.

Experimental biomechanics research addressing energy flow through LaMSA components is revealing remarkable pathways and principles in multiple fields. LaMSA research is engaging thermal physiology and climate change research, given the lower sensitivity to temperature of springs than the underlying muscles - meaning that LaMSA systems can be robust to thermal extremes (Anderson & Deban, 2010; Anderson & Deban, 2012; Deban & Lappin, 2011; Olberding & Deban, 2021; Scales et al., 2017). Behavioral research is focusing on the intersection of biomechanical systems and the evolved behavior of animals to resolve potentially lethal conflicts (Dinh & Patek, 2022; Franklin et al., 2019; Green et al., 2019; Green & Patek, 2018; Taylor & Patek, 2010). Evolutionary research is incorporating the mechanical sensitivity of these integrated components into core principles of rates and patterns of evolutionary change (Anderson, 2022; Claverie & Patek, 2013; Muñoz et al., 2017; Muñoz et al., 2018). The evolutionary history of LaMSA mechanisms is emerging as insightful for addressing fundamental questions about the connections among evolutionary biomechanics, ecology, geography, and climatic shifts (Friedman & Muñoz, 2022; Mendoza et al., 2020; Moen et al., 2022; Moen et al., 2013). These discoveries in biology are catalyzing a burgeoning field of exploration and inventions of synthetic systems that rely on many of the principles addressed in this review – including metamaterials, latching, jumping, fluid dynamics, and cascading energy control (Divi et al., 2020; Duduta et al., 2019; Haldane et al., 2016; Hawkes et al., 2022; Ilton et al., 2019; Kim et al., 2021; Koh et al., 2015; Liang & Crosby, 2020a, 2020b; Ma et al.; Steinhardt et al., 2021; Wang et al., 2023; Zhang et al., 2020).

Perusing JEB's century of comparative biomechanics research, and the thousands of papers examining elastic mechanisms, it is exciting and inspiring to witness broadly insightful growth of the field of latch-mediated spring actuated systems from a strong foundation in the historical fields of insect and vertebrate jumping and such classic paradigms as power amplification (Vogel, 2005a; Vogel, 2005b, 2009). The ability of these systems to inspire discovery, catalyze new pathways for cross-cutting discoveries in the field of biology, and to open new pathways for novel design in materials and robotics is as much a testament to the extraordinary organisms populating our planet as it is a testament to the tenacity of researchers working for the past century to explore the often-invisible and technically challenging realm of integrated biomechanical systems.

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Boxes

Box 1: The term "power amplification" was first mentioned in the *Journal of Experimental Biology* in a classic study of locust jumping energetics (Bennet-Clark, 1975). Subsequently addressed in numerous JEB review articles (James et al., 2007; Longo et al., 2019; Patek et al., 2011; Roberts, 2016; Roberts & Azizi, 2011), power amplification (units: W kg^{-1}) expresses the mechanical power output of a movement (Watts) relative to the mass of the muscle (kg) used to produce that movement. If the mechanical power output relative to muscle mass of the focal movement exceeds the maximum mass specific power output of the muscle, then it is inferred that something other than muscle must be responsible for the enhanced power output (i.e., a spring). Power amplification is essentially a "mechanism-free" metric that allows characterization of a system as spring-propelled without knowledge of the integrated components that generate this power amplification. Power amplification can be effective when applied to spring-propelled animal movements which use clearly-delineated muscle(s) with known maximum power output to load springs. However, it is less useful for the myriad systems across the tree of life that do not use muscle or for which key information about spring-loading muscles is not known or available (Longo et al., 2019). Indeed, some animals with muscles, such as cnidarians, use non-muscle mechanisms to load springs inside organelles (Beckmann et al., 2015; Karabulut et al., 2022). While the strengths, limitations, and best practices for using the power amplification metric are detailed elsewhere (Longo et al., 2019), suffice it to say that this historic metric was not intended to address the energetics of integrated LaMSA systems (the focus of this review) – comprised of energy sources, latches, springs, propelled mass, and interactions between the moving mass and surrounding environment.

Figures

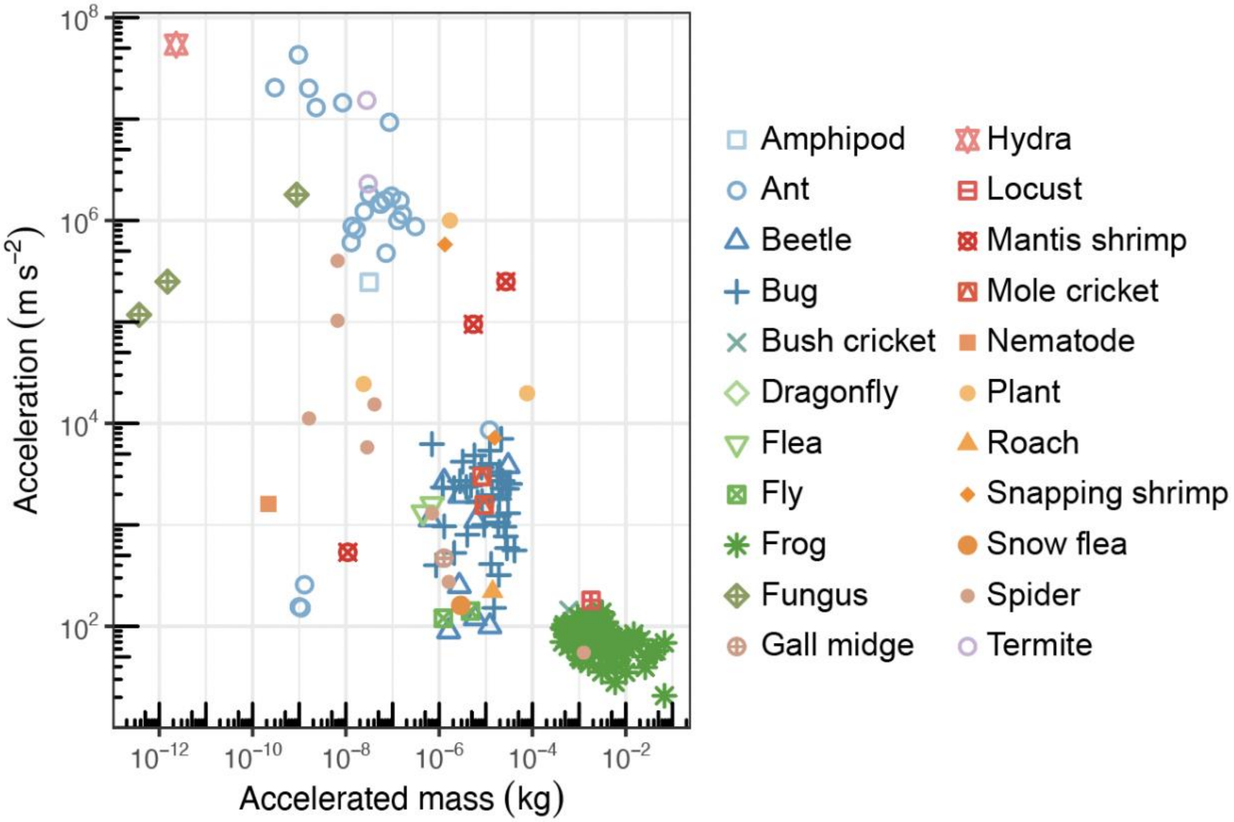

Figure 1. Small organisms use springs and latches to achieve extraordinary accelerations. Accelerated mass is defined as the mass propelled by the elastic mechanism, such that a jumping insect's propelled mass is comprised of the entire body mass whereas a termite's accelerated mass only includes one striking mandible. Data are compiled and replotted from sources detailed in (Cooper et al., 2018; Harrison & Patek, 2023; Harrison et al., 2021; Ilton et al., 2018; Patek, 2019; Poppinga et al., 2019; Sakes et al., 2016; Whitaker et al., 2007).

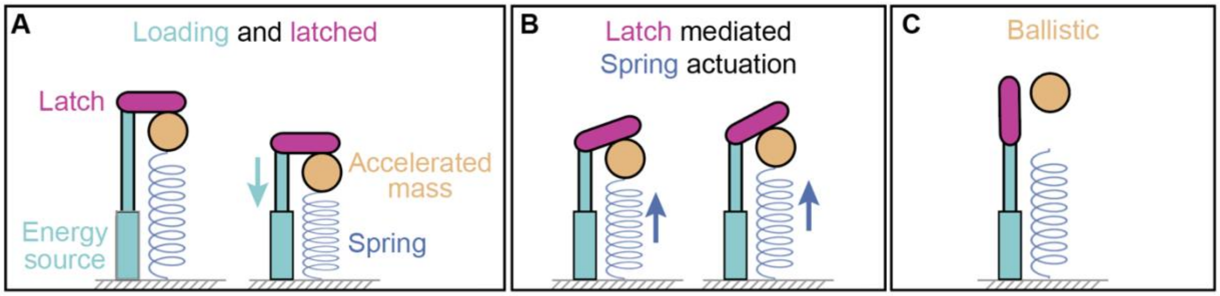

Figure 2: Latch-mediated spring actuation (LaMSA) exemplifies the power of integrated biomechanical systems to control and manipulate energy flow. (**A**) LaMSA begins with an energy source (turquoise), such as a muscle, loading energy into an elastic structure, such as a spring (blue). An opposing force (termed a latch, pink) holds the system in place while energy is loaded. (**B**) Latch removal can happen nearly instantaneously at the onset of spring actuation or it can occur throughout spring actuation, thereby mediating spring actuation as shown here. Elastic potential energy is transformed into kinetic energy as the latch is removed. In the depicted mechanism, kinetic energy of the spring and accelerated mass (orange) are inextricably coupled until the mass separates from the spring. In tiny systems, spring mass can be large compared to the propelled mass, such that idealized, massless Hookean spring assumptions are not applicable; both the propelled mass and spring mass can be important to the dynamics of these systems (Hyun et al., 2023; Ilton et al., 2018). (**C**) Once the mass is ballistic (i.e., no longer powered by spring actuation), the spring dissipates any residual energy through oscillations. This schematic depicts a mass that separates from the spring and is propelled into the environment; however, the propelled mass often remains attached to the organism, such that the mass can be spring-actuated throughout its motion or it can transition to ballistic movement (i.e., no longer powered by spring actuation) even while still attached to the organism. Energetic losses occur throughout this process such that the final energy of the propelled mass is less than the initial elastic potential energy.

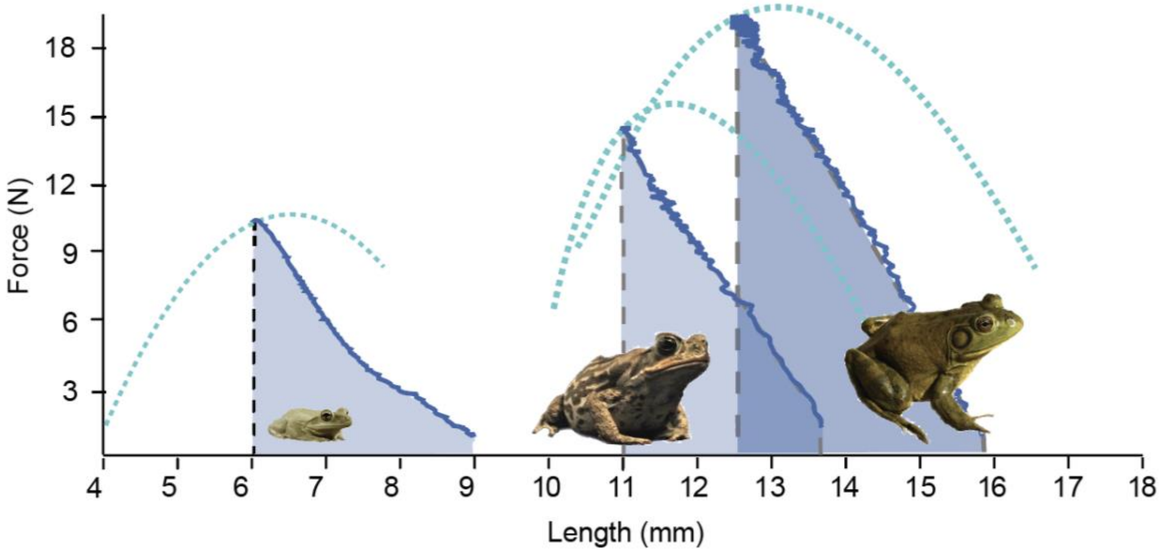

Figure 3: Force-length properties of the energy source are tuned with work of elastic structures through their intersecting force and length relationships. Cuban tree frogs (left; *Osteopilus septentrionalis*) can store considerably more elastic potential energy (16 mJ; blue shaded region) relative to body mass (28 g), and thereby produce more potent jumps, than the much larger cane toad (middle: *Rhinella marina*; 20 mJ, 90 g) and bull frog (right: *Rana catesbeiana*; 47 mJ, 99 g). Evolutionary tuning between motor and elastic structure is exemplified by this experimental study of muscle force-length relations (turquoise dashed lines) and spring force-length relations (solid blue lines) across species. Modified and adapted from Mendoza and Azizi (2021). Photos reproduced with permission from Mendoza and Azizi; images not to scale.

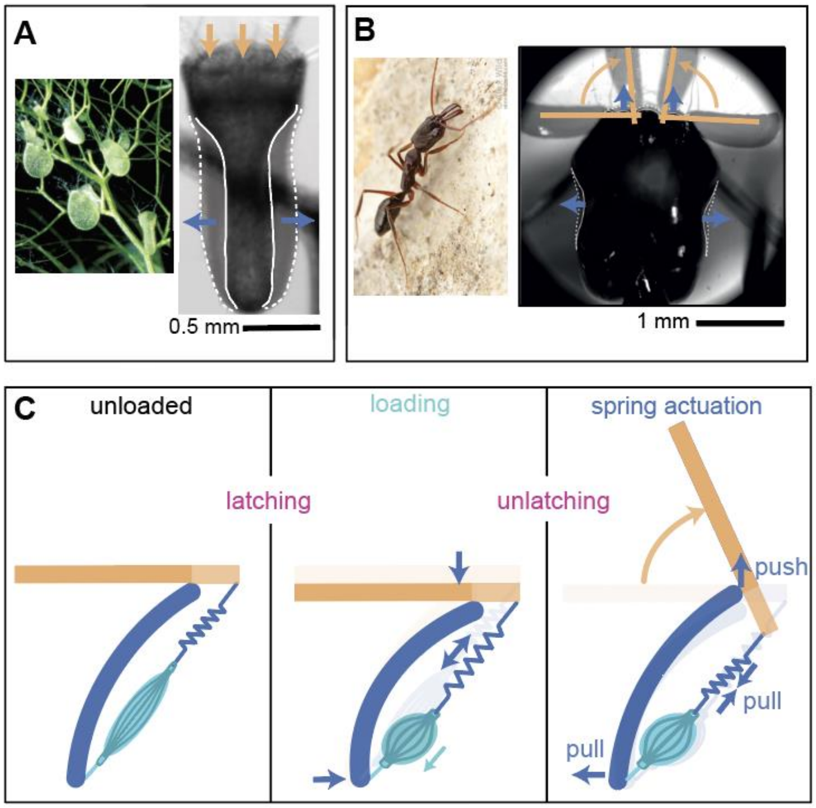

Figure 4. Diverse organisms leverage distributed displacements across the surfaces of shapes to store elastic potential energy, yet these storage mechanisms are often distinct from the spring actuation mechanisms used for propelling a mass. (A) Aquatic bladderwort plants (*Utricularia inflata*) grow prey-trapping bladders. Right image: These bladders store elastic potential energy by pumping water out of their bladder (solid white line) so that, when latch removal occurs, their bladder walls recoil outward (dashed white lines; blue arrows) to suction water and prey inwards (orange arrows). Modified from (Vincent et al., 2011) with permission from Royal Society Publishing. Photo by Barry Rice © 2023, used with permission. (B) Similarly, trap-jaw ants *(Odontomachus brunneus*) capture prey with their mandibles. They store elastic potential energy by deforming their head exoskeleton (right image; ventral view) indicated as anterior and medial flexion (solid white lines). When the latches are removed, the head recoils anteriorly and laterally (dashed white lines; blue arrows). Head exoskeleton recoil and internal apodeme recoil together generate mandible rotation (orange arrows). (C) Many arthropods combine shape deformation (push and pull) and apodeme recoil (pull) to operate dual spring force couples which develop rapid torque using minimal joint constraints. These images illustrate the dual spring force couple in trap-jaw ants (depicting one half of the ant's head). The "unloaded" phase is also the state trap-jaw ants use when directly moving the mandible with muscle (i.e., when they have not activated their LaMSA mechanism). B and C adapted from (Sutton et al., 2022). *O. brunneus* photo © Alex Wild, used by permission.

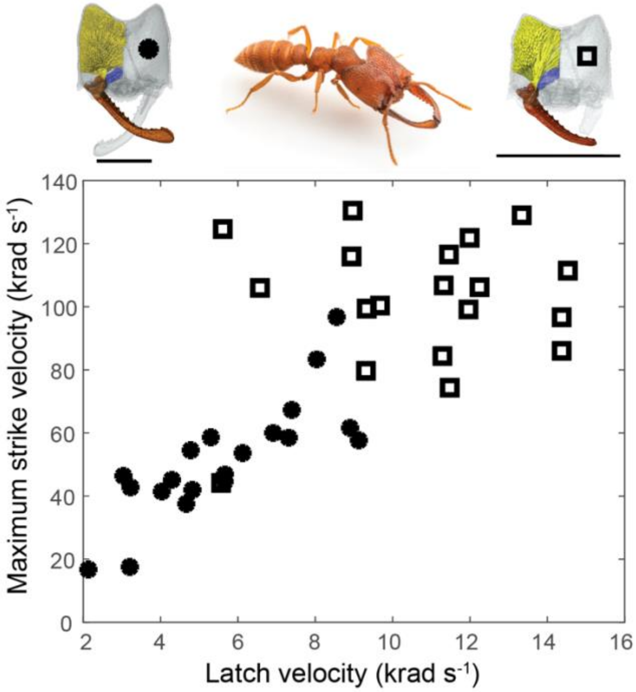

Figure 5: Latch mediation can strongly or minimally influence the kinematics of the propelled mass. Dracula ants (*Mystrium camellae*) store elastic potential energy by bending their mandibles and use friction between the mandible tips as their latch mechanism (Larabee et al., 2018). Two types of Dracula ant workers use this mechanism, the larger major ant workers (filled circles) and the smaller minor ant workers (squares). Scale bars 0.1 mm. As latch velocity is varied in the major ants, their strike velocity is also varied. By contrast, regardless of latch velocity in the minor ants, strike velocity remains in the same range. Reconstructed microCT images from (Larabee et al., 2018); data from (Divi et al., 2020); *M. camellae* photo © Alex Wild, used by permission.

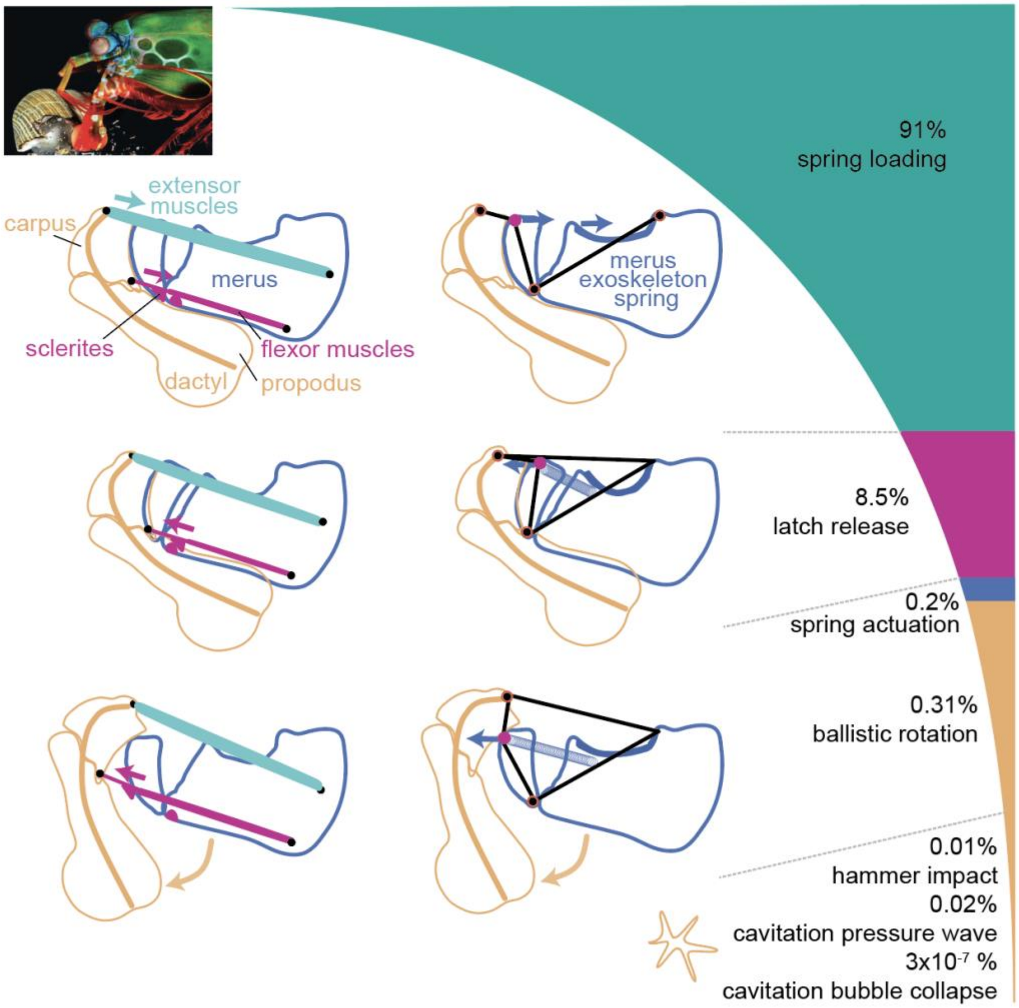
91%
spring loading
extensor
muscles
carpus
merus
sclerites
flexor muscles
dactyl
propodus
merus
exoskeleton
spring
8.5%
latch release
0.2%
spring actuation
0.31%
ballistic rotation
0.01%
hammer impact
0.02%
cavitation pressure wave
3x10⁻⁷ %
cavitation bubble collapse

Figure 6: The cascading reduction of time achieved through integrated components of LaMSA is exemplified in the snail-smashing raptorial appendages of mantis shrimp (Stomatopoda). Smashing mantis shrimp use raptorial appendages to strike hard shelled prey with high peak forces and cavitation bubbles (photo inset). Raptorial appendage schematics (lateral view, distal to left) contrast the actions and geometry of muscles and sclerites (left column) with springs and linkages (right column). The merus segment's extensor muscles (turquoise) load elastic potential energy via distributed displacements across the merus exoskeleton (blue) (Burrows, 1969; Burrows & Hoyle, 1972; McNeill et al., 1972; Patek et al., 2004; Patek et al., 2007; Patek et al., 2013; Rosario & Patek, 2015; Zack et al., 2009). Antagonist flexor muscles (pink) and embedded sclerites (pink) prevent movement during spring loading (Burrows, 1969; Patek et al., 2007). Latch release occurs sequentially, beginning with relaxation of flexor muscles, then release of the sclerites (Burrows, 1969; Burrows & Hoyle, 1972; Kagaya & Patek, 2016; McNeill et al., 1972) and concluding with a hypothesized torque reversal of the four bar linkage system (Steinhardt et al., 2021). Recoiling elastic exoskeleton (blue) pushes the distal segments which comprise the accelerated mass (orange) (McHenry et al., 2012; Patek et al., 2004; Patek et al., 2007). Spring actuation ends as the appendage rotates ballistically to its target, causing an impact followed by cavitation bubble implosion (Crane et al., 2018; Patek & Caldwell, 2005; Patek et al., 2004; Patek et al., 2007). Colored areas indicate the percent of total duration (~368 ms total duration): spring loading (turquoise), latch release (pink), spring actuation (blue) and strike, impact and cavitation bubble collapse (orange). Adapted from (Patek, 2019). Photo courtesy of Roy Caldwell.

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