COMMENTARY

From bouncy legs to poisoned arrows: elastic movements in invertebrates

S. N. Patek[1,*], D. M. Dudek[2] and M. V. Rosario[1]

[1]Department of Biology, University of Massachusetts Amherst, MA 01003, USA and [2]Department of Engineering Science and Mechanics, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

*Author for correspondence (patek@bio.umass.edu)

Summary

Elastic mechanisms in the invertebrates are fantastically diverse, yet much of this diversity can be captured by examining just a few fundamental physical principles. Our goals for this commentary are threefold. First, we aim to synthesize and simplify the fundamental principles underlying elastic mechanisms and show how different configurations of basic building blocks can be used for different functions. Second, we compare single rapid movements and rhythmic movements across six invertebrate examples – ranging from poisonous cnidarians to high-jumping froghoppers – and identify remarkable functional properties arising from their underlying elastic systems. Finally, we look to the future of this field and find two prime areas for exciting new discoveries – the evolutionary dynamics of elastic mechanisms and biomimicry of invertebrate elastic materials and mechanics.

Key words: biomechanics, elastic mechanisms, invertebrates, power amplification.

Introduction

Inserting a spring into a biological system offers a myriad of opportunities, ranging from powerful weaponry to efficient running. At one end of the spectrum, a spring can allow an animal to produce extremely fast movements – far faster than possible by muscle alone. These single rapid movements occur in systems ranging from jumping cicadas and box mites (Gorb, 2004; Wauthy et al., 1998) to fast-feeding termites and snapping shrimp (Gronenberg, 1996a; Seid et al., 2009; Versluis et al., 2000). At the other end of the spectrum, springs can provide outstanding efficiency and stability for continuous, long-term movements. These rhythmic movements include mechanisms ranging from flying fruit flies to singing katydids (Bennet-Clark, 1999; Dickinson and Lighton, 1995; Montealegre-Z et al., 2006).

The materials and mechanical properties of these elastic mechanisms are superbly diverse, yet they are united by shared physical principles and component parts (Claverie et al., 2011). Using a human-engineered example, an archer uses muscles to slowly flex a bow and store elastic energy. When ready to shoot the arrow, the archer releases the stored energy by letting go of the taut string. The arrow is shot far more rapidly than would have been possible if the archer had simply thrown the arrow. The basic building blocks of archery and any fast biological system are an engine (the archer's muscles), an amplifier (the springy bow and latch-like fingers) and tool (arrow). The unifying principle is called power amplification: the amplifier reduces the time to perform the engine's work.

These same components can be used quite differently to generate rhythmic movements. In rhythmic movements, the key is to improve energetic efficiency by storing and returning elastic strain energy in each cycle and to simplify control by restoring structures to their rest positions without involving muscles or reflexes. Thus, the rapid release associated with power amplification can be less important in rhythmic movements, whereas the use of the engine, amplifier and tool components to efficiently transduce power from muscle to tool is of paramount importance.

In this commentary, we will explore the mechanics and function of single rapid movements and rhythmic movements, each with examples from three invertebrate systems. We have chosen these examples so that each highlights different principles of materials and mechanics. We conclude by examining the directions for the field, looking at both the potential for biologically inspired systems and the integration of macro-evolutionary analyses with the fundamental physical principles of elastic biomechanics. Keeping to the style of a *Journal of Experimental Biology* commentary, our goal is to stimulate interest in the intriguing world of invertebrate elastic systems and identify organizing principles, rather than to provide an in-depth review. Toward that end, we have also provided a glossary at the end of the paper to define technical terms.

Single rapid movements
Balancing stiffness and elasticity in jumping froghoppers

In this first example of a single rapid movement, we highlight jumping froghoppers (Hemiptera: Cercopoidea) as a system yielding new insights into the balance between the stiffness necessary to store substantial elastic potential energy and the elasticity required to permit spring flexion without failure (Fig. 1). Unlike many long-legged insect jumpers (e.g. bush crickets) that make use of the mechanical advantage of their legs to achieve great heights, froghopper insects are short-legged hoppers that, nonetheless, manage to outperform all other jumping insects relative to body size (Burrows and Morris, 2003). Circumventing the limitations of their short legs, froghoppers use a potent power amplification system that exerts force against the ground equal to 414 times their body weight and can propel the insects to heights of 115 body lengths.

The key to these powerful jumps is a spring called the pleural arch, which extends between the thorax and femur (Burrows et al., 2008). In preparation for a jump, the pleural arch is compressed like an archer's bow while rotation of the coxa is prevented by latch-like protrusions between the coxa and femur (Burrows, 2003;

Burrows, 2006). When enough energy has been stored for a jump, a slight shift in the position of the coxa causes the latch to disengage. The pleural arch then extends and pushes the distal edge of the coxa resulting in a rotation of the leg segments forcefully toward the ground to produce a spring-loaded leap.

A close look at the material composition of the pleural arch yields important insights into the way arthropods balance the stiff properties of cuticle with the deformable properties of resilin, the arthropod elastic protein. The discovery of resilin in the 1960s, and the ease with which it can be detected with present-day methods, laid the foundation for the argument that resilin serves as the primary material for elastic energy storage and release in arthropods (Alexander, 1966; Andersen, 1963; Andersen, 1964; Andersen, 1966; Andersen and Weis-Fogh, 1964; Bennet-Clark, 2007; Sannasi, 1969). However, in froghoppers, Burrows et al. (Burrows et al., 2008) found that the pleural arches are composites made of approximately 80% chitinous material and 20% resilin and that resilin only deforms by ~9% – far less than had been assumed for other power-amplified systems. When the elastic potential energy is calculated separately for the resilin and chitinous materials under compression (the displacement applied to each is set equal to the total displacement observed during spring-loading in preparation for an actual jump), the cuticle in the froghopper is able to store most of the required energy whereas the resilin stores at most 2% of the required energy (Burrows et al., 2008); this finding is in surprising contrast to previous expectations that resilin is the primary site for elastic energy storage in arthropod jumps.

Consequently, the incorporation of chitinous material provides the stiffness necessary to store substantial elastic energy to power the froghopper's jump, whereas resilin probably functions to provide flexibility and restoration of the original shape of the pleural arch after each jump (Burrows et al., 2008). Indeed, the authors draw interesting comparisons to composite bows used by archers, which lose less energy to vibration, maintain higher performance over repeated use and retain their original shape better than single-material bows. The possibility that composite spring materials confer these same benefits in arthropods remains to be tested, but these observations raise important and interesting questions about the material requirements for achieving an appropriate balance of stiffness and elasticity in arthropod springs.

Exoskeletal integration of striking mantis shrimp

Although froghoppers are the fastest jumpers in air, mantis shrimp (Crustacea: Stomatopoda) are among the fastest strikers in water. Indeed, the extreme energetics of their raptorial strikes exceed the power of any known muscle, thus they must also use a potent spring to power their fast predatory strikes (Patek et al., 2004) (Fig. 1). In this example, we examine a spring that is tightly integrated with the exoskeleton of an appendage segment. One recurring theme in studies of elastic energy storage in invertebrates is that it is often difficult to find a spring and even more challenging to characterize its properties. The result is a substantial literature about the kinematics and energetics of single fast movements with remarkably little information about the underlying spring mechanics – this has certainly been the case for mantis shrimp, until recently.

The mantis shrimp's power amplification mechanism operates similarly to an archer's bow: a large, slowly contracting extensor muscle compresses a spring that is subsequently released by a latch controlled with flexor muscles (Burrows, 1969; Burrows and Hoyle, 1972; McNeill et al., 1972; Patek et al., 2004; Patek et al., 2007). Mantis shrimp raptorial appendages can reach speeds of

$23\,\mathrm{m\,s^{-1}}$ and peak accelerations up to $104\,\mathrm{km\,s^{-2}}$ in less than 3 ms (Patek et al., 2004). They wield appendages that range from hammers that crush hard-shelled prey (Patek and Caldwell, 2005) to spear-shaped appendages that capture elusive prey (Caldwell and Dingle, 1976). Some species also use their raptorial appendages to settle disputes with conspecifics by hammering each other's telson (tail plate) (Caldwell, 1979), which functions like an inelastic punching bag to provide mechanical information about the size of each individual (Taylor and Patek, 2010).

The search for the mantis shrimp's spring has spanned four decades, beginning with an initial hypothesis that elastic energy was stored in the extensor muscle and apodeme, followed by a hypothesis that a discrete structure in the merus (the saddle) provided the needed elastic energy, and finally culminating in a multi-faceted understanding that mineralized regions of the exoskeleton flex in synchronization with the saddle to store substantial elastic energy (Burrows, 1969; Patek et al., 2004; Zack et al., 2009). Unlike the discretely formed pleural arch in froghoppers, much of the merus segment of the mantis shrimp's raptorial appendage flexes to store elastic energy.

The exoskeletal integration of the mantis shrimp's spring has a number of interesting consequences both for elastic energy storage and transduction of the spring's potential energy into the fast rotation of the weapon-bearing distal segments. Strips of highly mineralized exoskeleton embedded in the merus, called the ventral bars, flex with mechanical behavior similar to a linear spring (Zack et al., 2009). The ventral bars are similar to human-engineered tape springs – long, thin beams with a hemispheric cross section – that can be flexed to store elastic energy (Seffen, 2001). Imagine a thin, elongate strip of metal fixed at one end and flexed at the other; when the flexed end is released, the strip of metal rapidly extends and returns to its original state. In the mantis shrimp's case, the rapid rotation of this springy strip of exoskeleton is part of a four-bar linkage system that forces the distal segments to rotate outward and strike the prey (Patek et al., 2007). The result is a potent spring mechanism that both stores elastic potential energy and transduces it through a linkage mechanism to yield rapid rotation.

When springs are tightly integrated into the exoskeleton, rather than formed as discrete structures like the froghopper's pleural arch, they pose challenges for correctly characterizing isolated spring behavior. However, exoskeleton-integrated springs offer considerable opportunities for mechanical integration and transduction – ideas that have rarely been explored in arthropod systems (although see the cicada example below). Much remains to be discovered about mantis shrimp springs, beginning with identifying the material composition of the spring and ultimately examining the variation in spring and linkage mechanics across the remarkable diversity of stomatopod weaponry.

Pressure and control in stinging jellyfish

Elastic structures at the cellular level use the same fundamental engine, amplifier and tool components and power amplification principles as we have seen in the froghopper, mantis shrimp and archer, but the underlying mechanisms are fundamentally different. One of the most remarkable examples of cellular power amplification is found in the nematocyst discharge system of stinging cnidarians (e.g. jellyfish) (Fig. 1). In this case, osmotic manipulations and microscopic elastic fibers serve as mechanisms for storing and releasing elastic energy.

The cnidae that characterize the phylum Cnidaria are capsules with tube-like invaginations that can be explosively everted for functions ranging from gluing prey to killing predators. Some
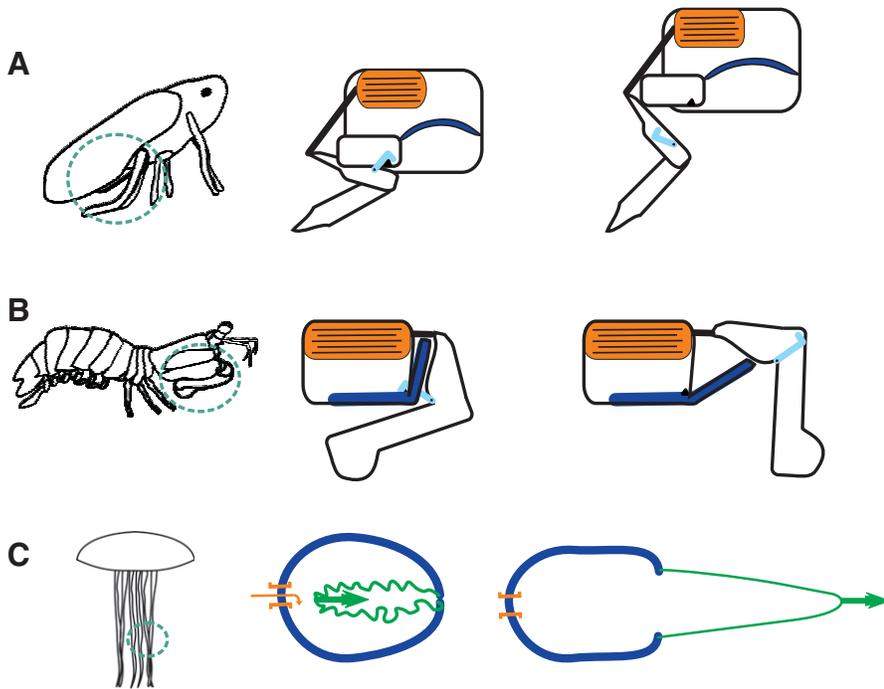
Fig. 1. Single rapid movements are driven by a diversity of elastic structures. Froghoppers (A) generate impressive jumps by pre-loading an elastic pleural arch located between the femur and body and then controlling the release through latch-like protrusions between the coxa and femur. Mantis shrimp (B) strike with raptorial appendages using an elastic ventral bar, analogous to a tape spring, which is released with a latch. Many cnidarians (C) sting with poisonous stylets (green) that are fired from a pressurized cellular capsule. The engine is most probably powered by membrane ion pumps that generate a high pressure within the capsule and stretch elastic elements in the walls of the nematocyte. The tool is the stylet. For all images, the engine is orange, the spring is dark blue, and the latch (if present) is light blue.

species use specialized cnidae, called nematocysts, which fire a microscopic poison spear (stylet). Each stylet is housed in its own exocytotic organelle (nematocyte) and is ejected within 700 ns with accelerations in the region of $5 \times 10^6\,\textbf{\textit{g}}$ (Holstein and Tardent, 1984; Nüchter et al., 2006). The combination of extreme acceleration and the tiny tips of the stylets (15 nm) yields pressure at the point of impact exceeding 7 GPa (similar to a bullet fired from a gun) (Nüchter et al., 2006). Simply visualizing this phenomenon has been a technical feat, and the underlying elastic mechanism has been equally challenging to discern.

The key to the elastic power of this system is a combination of osmotic pressure and membrane elasticity in the organelle that houses the stylet. This organelle works like a pressurized balloon with walls composed of flexible mini-collagen (collagen-like peptides) fiber layers oriented at angles to each other; as the balloon expands, these angled fiber layers evenly distribute the tension (Holstein et al., 1994). The fiber layers are stretched as osmotic pressure increases to 15 MPa within the cell (Holstein et al., 1994) and give the capsule's wall an elastic modulus of 1 GPa (Weber, 1989). In this system, the engine is found in the ion channels in the membrane that mediate the build-up of pressure in the cell. The amplifier is located in the elastic walls and the tool is the tiny, poison stylet that strikes with the pressure of a bullet.

One remaining mystery of this system is how the stylet release is actually triggered. Rapid, *in vitro* depolarization of the membrane somehow causes the stretched walls and high internal pressure to propel the stylet out of the organelle (Nüchter et al., 2006), and hair-like cnidocils respond to mechanical stimuli (Brinkmann et al., 1996). The puzzle of the controlled release of the stylet is of interest not just in cnidarians, but also in animals that 'steal' nematocysts. Some nudibranchs (gastropod sea slugs), ctenophores and flatworms consume cnidarians and steal their nematocysts in a mechanism called kleptocnidae (reviewed by Greenwood, 2009). Thus, along with basic questions about how these organelles function, the ability to both steal and wield the power of these organelles raises fascinating questions about their evolutionary origins and how the organisms that 'house' these organelles successfully control them.

Rhythmic movements
Efficient power transduction of singing cicadas

The constant, loud drone of cicadas (Hemiptera: Cicadidae) through hot summer days is one of the best examples of how an elastic mechanism can confer tremendously efficient power transduction during rhythmic movements (Fig. 2). In this case, we see a combination of the principles observed in the froghopper and mantis shrimp examples above – composite materials and mechanical integration – yet in a system that specializes in extremely efficient continuous movement, rather than discrete, rapid movements.

Cicadas (*Cyclochila australasiae*) produce continuous 4 kHz vibrations by coupling the contraction of a single muscle to a composite structure, called the tymbal, made of integrated strips of resilin and cuticle. Located on each side of the abdomen, the tymbal consists of a large, lightly sclerotized tymbal plate and multiple thin, sclerotized ribs coupled together with thin resilin strips (Fig. 2). A thick triangular pad of resilin connects the dorsal tips of the plate and ribs. Elastic energy is stored when the muscle attached to the tymbal plate contracts, thereby causing the plate to swing ventrally, distorting the thick resilin pad (Fig. 2). Loud clicks are produced when the ribs suddenly buckle inward, which both releases stored elastic energy from the resilin pad and sets up resonant oscillations in the tymbal plate (Bennet-Clark, 1997; Young and Bennet-Clark, 1995). Sound is emitted from resonating abdominal airsacs that connect the vibrating tymbal to thin, membranous tympana on the ventral surface of the abdomen.

This system is impressive for two reasons. First, the resilience of the entire tymbal mechanism is very high (78%) (Bennet-Clark, 1997) because of the fantastic efficiency of the thick resilin pad acting as an elastic antagonist to the tymbal muscle. Second, the tymbal mechanism functions simultaneously as a displacement, frequency and power amplifier as well as a power transducer. How are all of these functions achieved? The tymbal plate amplifies the

contraction distance of the tymbal muscle by acting as a lever; the short end of the lever attaches to the resilin pad and the long end of the lever extends the length of the tymbal plate (Young and Bennet-Clark, 1995). Then, the buckling ribs and tymbal plate vibrations amplify the underlying 120 Hz muscle contractions to emit 4 kHz sound (Young and Bennet-Clark, 1995). This amplification is achieved by resilin strips that tightly couple the ribs to one another at the dorsal and ventral ends, forcing them to buckle in rapid succession. The middle of each rib is left free to vibrate at ~4 kHz resonant frequency. Power amplification is also achieved through the buckling of the ribs, essentially acting as an unstable latch: energy is slowly (2–4 ms) stored in the resilin pad until the ribs buckle and release the energy in one-tenth the time (~200 μs) (Bennet-Clark, 1997). Finally, the tymbal is a power transducer, converting high pressure muscle power at the tymbal plate into low pressure sound power at the tympana (Young and Bennet-Clark, 1995), converting almost half of the mechanical energy of tymbal buckling into sound energy (Bennet-Clark and Daws, 1999).

The cicada tymbal mechanism exemplifies nearly all the primary concepts and components of elastic mechanisms in invertebrates. The mechanism tightly integrates the exoskeleton with resilin to achieve a dynamically flexible, oscillating structure to efficiently maintain rhythmic movement. It also uses a latch-like system in the buckling ribs to amplify the power output. It is difficult to imagine a better example of the utility of elastic mechanisms in arthropods than this complex system for sound production that is controlled and driven by a single muscle.

Simplification of control in running cockroaches

This second example of a rhythmic movement looks at elastic mechanisms from the vantage point of improving efficiency and circumventing neural response time in terrestrial runners. Like vertebrate runners, many arthropods of varying morphology, leg number and body mass run with the dynamics of a spring-loaded inverted pendulum (Blickhan et al., 1993). Although vertebrates such as kangaroos and humans have tendons that serve as effective springs to improve running efficiency (Alexander, 2003), only the fast and versatile hindlegs of running cockroaches (Neoptera: Blattaria) have been identified as being capable of storing and returning energy during running in invertebrates (Dudek and Full, 2006). In all likelihood, these springs only contribute marginally to improving energetic efficiency in cockroaches, but they play an important role in stabilizing locomotion and thus offer important insights into this classic biomechanical locomotor model (Fig. 2).

The principal engines for the loading of cockroach leg springs are the kinetic and gravitational potential energies of the body and the large lateral and opposing forces generated by the three legs in contact with the ground. As in the examples above, the spring is not localized to a single element (Dudek and Full, 2006). The springs are found in the resilin pads and cuticular deformation of the legs, which store elastic energy when the cockroach's center of mass falls from foot touchdown to mid-stance. The hindleg can store and return passively between 60 and 75% of the elastic strain energy from oscillations, which translates to as much as 40% of the total mechanical work required to lift and accelerate the center of mass during running (Dudek and Full, 2006). This is almost certainly an overestimate of energy storage and return in this system. As estimates of total work performed during running improve and Dudek and Full's simplifying assumptions are tested, the estimated contribution of the spring to energy conservation will undoubtedly decrease (Dudek and Full, 2006). The fact remains that the efficiency of running insects might be improved, however

slightly, by energy passively stored and returned in the legs. Any such benefit in cockroaches probably arises as a by-product of the role of the leg spring in passively stabilizing running.

Efficiency is centrally important in locomotion, but the ability to respond quickly to perturbations may be even more important (Koditschek et al., 2004). Response time is where we see another key facet of incorporating springs into the cockroach's legs. When subjected to large impulse perturbations, isolated cockroach legs can recover to their original position in less time than a single leg swing period (Dudek and Full, 2007). Recovery from similar perturbations to intact legs of running cockroaches requires as little as 7 ms, and averages only 16 ms, with no change in the activation pattern of an important stance-initiating muscle (Dudek et al., 2005). Given that the fastest neural reflexes observed in cockroaches are 16–17 ms, these spring-initiated response times may indeed allow cockroaches to rely on passive mechanical properties to maintain stability more quickly and simply than by invoking neural control. It is clear that in cockroaches, the passive mechanical properties of individual legs determine the system behavior and are well suited to both improving mechanical efficiency during stance and simplifying the control of locomotion during swing.

Environmental accommodation in swimming scallops

If terrestrial invertebrates suffer from a dearth of rhythmic spring mechanisms improving efficiency of locomotion, many flying and swimming invertebrates make use of such mechanisms, from flying insects (Dickinson and Lighton, 1995; Jensen and Weis-Fogh, 1962) to burrowing nematodes (Fang-Yen et al., 2010) and swimming leeches (Tian et al., 2007). In this example, we focus on the inherent costs of spring systems. Specifically, we take a close look at scallops (Bivalvia: Ostreoida: Pectinidae) – a simply dynamic invertebrate that can swim with only a single muscle. One cost experienced by scallops is the decrease in elasticity of rubber proteins in lower temperature environments, so we highlight a scallop (*Adamussium colbecki*) that can swim under extreme temperature conditions through subtle changes in spring mechanics (Fig. 2).

Scallop swimming is powered by jet propulsion, produced when water squirts from openings near the hinge as the shells are repeatedly and rhythmically closed by the adductor muscle to generate a pulsing, swimming movement. The valves reopen due to the recoil of the elastic protein, abductin, which is compressed at the hinge during each power stroke (Fig. 2). This pad of abductin, also known as the hinge ligament or resilium, is the sole antagonist to the adductor muscle. By measuring the decay in the amplitude of free oscillations of the valves in air, the resilience of abductin was found to average 91% (Alexander, 1966). Despite the impressive ability of this protein to store and return elastic strain energy, the momentum and energy required to maintain valve oscillations is only 1% of the total hydrodynamic work performed to produce the jet (Cheng et al., 1996). Therefore, even large changes to abductin resilience would not dramatically change the energetic efficiency of scallop swimming.

It is therefore very interesting that the sole adaptation found so far to allow Antarctic scallops to swim in cold, viscous water is abductin that is 3% more resilient than the abductin found in more temperate relatives (Denny and Miller, 2006). Scallops swimming in cold water are always near the brink of not being able to swim at all for several reasons. In addition to the increased viscosity of the water, the cold makes scallop swimming difficult by reducing the adductor muscle's power output. These difficulties could be offset by increasing both the stiffness of the resilium and the power-to-mass ratio of the adductor muscle, but both of these factors are
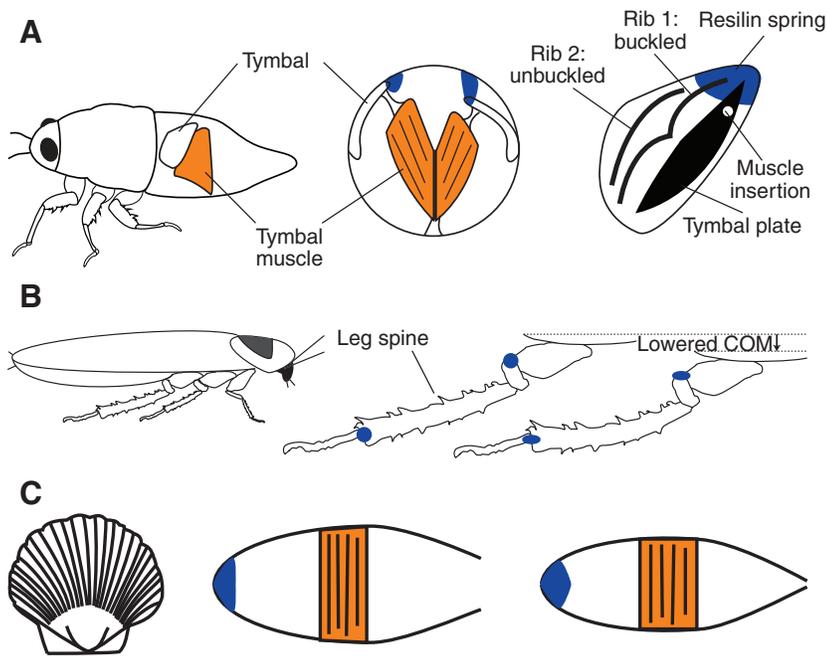
Fig. 2. Cockroaches, cicadas and scallops utilize multiple mechanisms to achieve efficient, rhythmic movements. (A) Cicada. (Left) Sounds are produced by the abdominal tymbal and powered by the tymbal muscle. (Middle) A transverse section of a cicada's abdomen shows the left tymbal muscle and plate in the resting position and the right tymbal muscle and plate in the contracted position. The contraction of the right-hand muscle causes the deflection and deformation of the tymbal plate and deformation of the resilin pad (blue). (Right) A magnified, dorsal view of the tymbal illustrates the location of the tymbal muscle insertion on the ventral side of the tymbal plate. The attachment and orientation of the tymbal muscle thus pulls the tymbal plate down and away from the ribs. The tymbal plate is connected to the ribs with resilin, and beyond a certain amount of deformation, the ribs rapidly and progressively buckle from posterior to anterior (only two ribs are shown). (B) Cockroaches run with the dynamics of a spring-loaded inverted pendulum. As the center of mass (COM) lowers from foot touchdown to mid-stance, elastic strain energy is stored in resilin pads (blue circles) and bending leg segments. As much as 75% of this energy may be returned when these structures rebound each step. (C) Scallops close the gap between the valves by contracting the adductor muscle. Valves reopen due to elastic recoil of the compressed pad of abductin (blue circle) in the hinge. For all images, the engine is orange and the spring is dark blue.

actually lower in Antarctic species than in warm water species (Denny and Miller, 2006). The energetic efficiency may also be improved slightly by swimming at the resonant frequency of the valve–abductin system, but all scallops appear to do this, so Antarctic scallops are not gaining a benefit that the more temperate species lack (Denny and Miller, 2006). It appears that as small an effect as increasing abductin resilience can have, it is sufficient to keep Antarctic scallops off the sea floor and away from predators.

As this example demonstrates, changes in temperature can have dramatic effects on both the mechanical properties of passive skeletal elements and the kinetics of muscle activation. It is therefore surprising how little emphasis has been placed on the effects of temperature on biomechanics in general, and elastic mechanisms in particular, for primarily poikilothermic invertebrates. Many interesting discoveries are no doubt waiting to be made on the link between environmental conditions and biomechanical performance.

The next steps

Even for just the six examples outlined above, many years of research are still necessary to disentangle all of their intriguing mysteries. Nonetheless, two new areas of research are presently emerging in this field. The first centers on the evolution of elastic mechanisms and how these systems originate and evolve. The second area is arising through collaborations between engineers and biologists who use invertebrate elastic systems as the basis for biomimetic design. In this final section of the paper, we examine the current work in these two areas and suggest new directions for the field.

Evolution of elastic mechanisms

With the intense focus on discovery and characterization of elastic mechanisms, hypotheses about their evolutionary history have remained largely untested. Surprisingly, we were unable to find any publications about phylogeny-based or macro-evolutionary studies of invertebrate elastic mechanisms. Elastic mechanisms are sometimes compared and contrasted between species, such as in

the cicadas and mantis shrimp described above (Bennet-Clark, 1999; Burrows, 1969). However, more robust conclusions can be drawn when analyses are performed in the context of a phylogeny and conducted using quantitative, statistical approaches (Autumn et al., 2002; Harvey and Pagel, 1991; Pagel, 1999). For example, one might test whether the shift in abductin behavior in Antarctic scallops was correlated with a historical invasion into colder waters or whether this elastic behavior was already present in a clade of scallops that existed (and perhaps still exist) in temperate climates and simply facilitated radiation into colder waters. Adopting approaches taken by biologists studying the evolutionary mechanics of fish feeding, one might also test whether particular features of the cicada's tymbal mechanism promoted an increased radiation rate of the clade or whether particular elastic features, such as resilience or resonance, exhibit variable modes of evolution (Alfaro et al., 2004; Collar et al., 2005; Wainwright, 2007).

The evolutionary origins of elastic mechanisms also stand to reveal key connections between mechanical principles and macro-evolutionary processes. An example of a single rapid movement that has independently evolved three to five times with remarkably convergent structures is found in the trap-jaw ants (Hymenoptera: Formicidae) (Moreau et al., 2006). Trap-jaw ants are polyphyletic – the group is defined by their power-amplified jaws, not shared ancestry. Not only do many of these ants use their fast mandibles for prey capture, with strikes speeds of over $48\,\mathrm{m\,s^{-1}}$ and accelerations of $10^5\,g$, some species also jump with their jaws (Patek et al., 2006; Spagna et al., 2008). The impact of the powerful mandibles results in a propulsive force that can launch the ants into the air, as well as punch intruders backward (Carlin and Gladstein, 1989; Patek et al., 2006; Spagna et al., 2008). All trap-jaw ants use large, slowly contracting muscles to load an as-yet undetermined spring that is later released with a trigger and latch system (Gronenberg, 1995; Gronenberg et al., 1993). However, because of their independent evolutionary origins, each ant group uses slightly different structures to achieve these rapid mandible movements (Gronenberg, 1996b; Gronenberg et al., 1998). Transitions from non-elastic to elastically driven movements (Paul, 2001) have the

potential to provide crucial information about the interplay between morphological variation, biomechanical principles and evolutionary diversification.

Arguably, the most comprehensive comparisons of elastic mechanisms have been undertaken for the four primary invertebrate elastic materials: resilin, abductin, mussel byssal threads and spider web capture lines (flagelliform silk). By looking at these materials at the molecular and structural levels, it is possible to reconstruct how elastic energy is stored and released differently, based on their molecular differences and how this molecular behavior relates to the contrasting functions of these materials (reviewed by Tatham and Shewry, 2002).

Resilin and abductin retain a high percentage of the energy (i.e. high resilience) to perform repeated, efficient movements or single rapid movements, whereas flagelliform silk and byssal threads exhibit molecular arrangements that are stretchy, but dissipate stored energy through heat loss and do not exhibit high resilience. How do these materials perform such different behaviors? When spider silk and byssal threads are stretched, the entropy of the elastomeric domains of the proteins is decreased, which causes a moderate restoring force coupled with dissipation of energy through heat in non-elastic portions of the protein. In contrast, resilin is thought to consist of unstructured domains and highly flexible poly-proline II structures moving in and out of a multi-conformational equilibrium that acts as an entropic spring. When resilin is stretched, the resulting decrease in conformational entropy generates the restoring force with minimal energy loss (Bochicchio et al., 2008). The elastic recoil of abductin is thought to be driven in part by a similar mechanism as in resilin (Bochicchio et al., 2008), but also with a hydrophobic mechanism such that stretching the material reveals hydrophobic protein regions and the resting state returns to a conformation where the hydrophobic regions are sequestered from the aqueous environment (Tatham and Shewry, 2002). Thus, all of these materials rely on entropic forces to return to their resting state, but the underlying molecular arrangements and the use of hydrophibicity to mediate interactions with the surrounding medium in some systems, produce an impressive array of elastic material behaviors.

Taking this comparative, molecular approach one step further, biologists can isolate recombinant biological proteins and compare them across species to identify the effects of amino acid sequence and composition on the properties and structure of elastomeric proteins without confounding structural influences. The key issue is isolating the protein; for example, if we were to try to figure out why scallop abductins differ between Antarctic and temperate scallops (Denny and Miller, 2006), there are a large number of confounding factors – different shapes, calcification levels or even genes. Recombinant abductins from multiple species are pure samples that are free of calcification and shape effects and can thus be used to determine the role, if any, of the subtle variations in amino acid sequences and compositions between scallop abductins (Denny and Miller, 2006) on material properties. Although fragments of abductin sequences from a single scallop species have been produced (Bochicchio et al., 2005), no full-length recombinant abductins have been generated to date. Nonetheless, this molecular-level approach is likely to reveal both the mechanisms for elastic behavior in biological proteins and also how biological systems have varied elastic behavior over evolutionary timescales.

Biologically inspired elastic systems

The remarkable abilities of the invertebrate elastic mechanisms featured thus far have repeatedly inspired engineers and biologists to think about the implications for human-designed devices. Here we briefly investigate biomimetic systems that emulate invertebrate elastic mechanisms from the perspectives of locomotor efficiency, minimization of computational processing during fast and irregular movements, and resilient, synthetic elastic proteins.

Small, efficient robots give humans access to otherwise inaccessible locations with minimal power requirements. However, the smaller the robot, the more likely it is to encounter terrain that is difficult to traverse (Armour et al., 2007; Kovac et al., 2008). Invertebrate jumping, one of the many locomotor solutions to overcoming large obstacles, has elicited attention in biomimetic robotics, not only to reduce the complexity of motor control (Buksh et al., 2010) compared with other forms of locomotion, but also because of the increased ratio of power output to mass (Kovac et al., 2008).

The influence of the elastic mechanisms underlying single, rapid movements in invertebrates is evident in the locomotor strategies and power amplification mechanisms in small jumping robots. For example, in order to minimize the mass of actuators and power supplies, a miniature 7g jumping robot was modeled after grasshoppers and locusts to slowly store energy in elastic elements before releasing the energy in a jump using a click mechanism (Kovac et al., 2008). The ability of the robot to slowly store energy in a spring in between jumps means that both a smaller actuator and smaller battery can be used, consequently reducing the mass of the robot and tending towards an increase in performance. A newly developed flea-inspired robot contains spring mechanisms modeled on the coxa and femur of a flea; the result is a small, efficient robot with a simple actuator (Buksh et al., 2010).

The invertebrate elastic approach to rhythmic movements inspired the design features of RHex, a hexapod robot. RHex is an example of an invertebrate-inspired robot capable of traversing difficult terrain using elastically driven, rhythmic locomotion (Altendorfer et al., 2001; Saranli et al., 2001). By controlling leg-timing and tuning leg stiffness relative to body mass similarly to many terrestrial runners, the robot employs the dynamics of a spring loaded inverted pendulum and is capable of rapidly and stably crossing obstacles and rough surfaces with only minimal sensing.

Emulation of hexapod runners gives RHex a number of excellent features, but early versions of the robot still lacked the ability to cross surfaces with large gaps. Turning again to biological inspiration, the engineers and biologists found a solution in spiders and cockroaches. When crossing surfaces with large holes, spiders and cockroaches run with elastic spines on their legs, rather than running on their feet (Fig. 2). When not in use, the leg spines maintain a constant, resting position with an internal spring. When a spine engages against a surface during forward locomotion and is pushed away from the leg, it is very stiff. However, when the leg slides along an object and the spine is pushed toward the leg, the joint of the spine is compliant. This makes the spines useful for pushing against the surface when engaged for forward locomotion while allowing them to easily collapse out of the way when being pulled out of debris. When springy spines, inspired by arthropods, were added to the legs of RHex, the robot could traverse previously impassable mesh surfaces without any change to its sensing or control strategy (Spagna et al., 2007).

In addition to robotic design, there is also a strong interest in synthesizing elastic proteins that have the remarkable resilience of resilin and abductin that we discussed above. Protein engineering can create novel materials with functions and properties that may not exist in nature. Such a strategy can be used as a bottom-up

approach to tune the macroscopic properties of a biomaterial by fine-tuning the properties of the individual molecular building blocks. For example, Lv et al. (Lv et al., 2010) combined a globular protein from *Streptococcus* sp. with resilin from a fruit fly to engineer a biomaterial that reproduces the unique combination of strength, extensibility and resilience of the muscle protein, titin. The stiffness and resilience of the material can be tuned by varying the proportion and arrangement of the globular and elastic domains, resulting in a material that acts as a resilient spring at low strains and a shock absorber at high strains.

The use of invertebrate elastic mechanisms as inspiration for engineered systems is showing great potential and it is likely that many more arthropod-like robots and synthetic proteins will be emerging from these collaborations between biologists and engineers.

Conclusions

Beginning with the essential building blocks of elastic mechanisms – the engine, amplifier and tool – and then configuring them for single rapid movements or rhythmic movements, we have traversed considerable taxonomic diversity and emergent elastic functions in the course of this brief commentary. The composite nature of froghopper springs, the tight integration of mantis shrimp springs, and the innumerable emergent transduction mechanisms of cicada tymbals all point to the fantastic versatility of arthropod cuticle and the remarkable arthropod elastic protein, resilin. The elastic engine of cockroach legs drives a system that is both efficient and easily controlled, to the point that it can even respond more quickly than a neural signal. Invertebrate elastic mechanisms outside the arthropods are woefully understudied, but the pressurized cellular balloon of nematocysts and the spring mechanics of cold *versus* temperate scallops point to great potential for discoveries in other branches of non-vertebrate Metazoa.

These inspiring invertebrate systems certainly deserve more study, both in terms of the basic biology and mechanics, and also with the new perspectives we have outlined here – quantitative evolutionary analyses and biomimetic approaches. That being said, our beginning messages of this essay, that all of these systems are governed by the same components and the same basic physical principles, apply to any other biological system. Certainly jumping vertebrates and running humans have captured the bulk of biologists' attention (Alexander, 2003), yet elastic mechanisms are pervasive in every branch of biology including ballistic plants and fungi (Edwards et al., 2005; Noblin et al., 2009; Pringle et al., 2005). Investigations of the interconnections between physics, biomechanics, evolution and biologically inspired engineering will continue to uncover new and important discoveries in the remarkable world of elastic mechanisms.

Glossary

Abductin
  Rubber-like protein found in molluscs.

Apodeme
  Arthropod tendon.

Efficiency
  The ratio between mechanical power output and metabolic power input. Typically, but not always, the efficiency of an activity increases as the material or structure being used becomes more resilient.

Elastic modulus (Young's modulus of elasticity)
  The resistance of a material or structure to deformation as determined from the slope of a stress *versus* strain plot (SI units: $N\,m^{-2}$).

Elastic potential energy
  Potential energy stored by a spring.

Failure
  The point at which a structure breaks or a system can no longer perform.

Mechanical advantage
  The factor by which either force or speed is amplified by a mechanism.

Power
  The rate at which work is performed [work ($N\,m$) divided by time (s); SI units: W].

Power amplification
  A system that decreases the time to perform work thereby increasing the power output.

Resilience
  The percentage of absorbed elastic energy that is recovered upon unloading.

Resilin
  Rubber-like protein found in arthropods.

Resilium
  The spring found adjacent to the hinge in scallops that opens the valves.

Stiffness
  The resistance of a material or structure to deformation. It is typically determined from the slope of a force *versus* extension plot (SI units: $N\,m^{-1}$).

Strain
  The amount of deformation of a structure relative to its resting length.

Stress
  The force applied to a material normalized by the cross-sectional area (SI units: $N\,m^{-2}$).

Work
  The distance over which a force is exerted (SI units: J).

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