

## Ritualized fighting and biological armor: the impact mechanics of the mantis shrimp's telson

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### SUMMARY

**Resisting impact and avoiding injury are central to survival in situations ranging from the abiotic forces of crashing waves to biotic collisions with aggressive conspecifics. Although impacts and collisions in biology are ubiquitous, most studies focus on the material properties of biological structures under static loading. Here, we examine the mechanical impact properties of the mantis shrimp's telson, a piece of abdominal armor that withstands repeated, intense impacts from the potent hammer-like appendages used by conspecifics during ritualized fighting. We measured the coefficient of restitution, an index of elasticity, of the telson and compared it with that of an adjacent abdominal segment that is not impacted. We found that the telson behaves more like an inelastic punching bag than an elastic trampoline, dissipating 69% of the impact energy. Furthermore, although the abdominal segment provides no mechanical correlates with size, the telson's coefficient of restitution, displacement and impact duration all correlate with body size. The telson's mineralization patterns were determined through micro-CT (Computed Tomography) and correspond to the mechanical behavior of the telson during impact. The mineralized central region of the telson 'punched' inward during an impact whereas the surrounding areas provided elasticity owing to their reduced mineralization. Thus, the telson effectively dissipates impact energy while potentially providing the size-related information crucial to its role in conspecific assessment. This study reveals the mechanical infrastructure of impact resistance in biological armor and opens a new window to the biomechanical underpinnings of animal behavior and assessment.**

Key words: stomatopod, mantis shrimp, impact, coefficient of restitution.

### INTRODUCTION

Lethal weapons pose a challenge for many animal systems. How can disputes be settled without mutual destruction? One widespread tactic is for animals to assess each other's resource holding potential (i.e. body size, weapon size, strength, and energy reserves) before fully escalating the dispute (Maynard Smith, 1974; Maynard Smith, 1976; Maynard Smith and Parker, 1967; Maynard Smith and Price, 1973; Parker, 1974; Arnott and Elwood, 2008; Arnott and Elwood, 2009; Sneddon et al., 1997). This has led to the evolution of dramatic ritualized displays in animal systems. Many mantis shrimp (Stomatopoda) wield extremely high peak impact forces with their raptorial appendages and can kill conspecifics with a single blow. However, some mantis shrimp perform ritualized assessment strikes in which one individual strikes the telson (tail plate) of the other contestant (Fig. 1) (Caldwell and Dingle, 1976). Although the impact forces of these raptorial strikes are sufficient to fracture mollusk shells and crab carapaces, their conspecifics' telsons effectively resist these extreme impacts.

Although collisions are prolific in nature, few studies have characterized the mechanics and energy exchange of biological impacts, perhaps because of the challenges inherent in measuring transient impacts and in characterizing the response of structures over extremely small spatial and temporal scales. Impacts in biological systems that have been studied from a behavioral perspective include birds pecking snails, ungulates ramming each other with elongate horns, and trap-jaw ants firing their mandibles to eject intruders (Butler and Kirbyson, 1979; Carlin and Gladstein, 1989; Kitchener, 1987; Kitchener, 1991; Patek et al., 2006; Snyder

and Snyder, 1969). These studies primarily focused on the behavior and mechanics of the biological hammer, with the exception of Kitchener (Kitchener, 1987), who examined the fracture behavior of horn material. Biological impacts that have been studied from an energetic perspective include sea urchins and barnacles that are struck by wave-propelled debris (Barnes et al., 1970; Pentcheff, 1991; Shanks and Wright, 1986; Strathmann, 1981), but these studies only focused on the amount of energy necessary to cause damage.

Mantis shrimp fighting represents an extreme example of biological impacts. During disputes over burrows, two mantis shrimp, from either sex, take turns striking each other on the telson. The strikes of some mantis shrimp species can reach speeds of up to 23 m s<sup>-1</sup> and peak forces of up to 1500 N (Patek et al., 2007; Patek and Caldwell, 2005; Patek et al., 2004). The telson experiences multiple, forceful impacts within a single agonistic encounter, and individuals might face many agonistic situations between molts. Interestingly, telsons appear to be more heavily armored in species that participate in ritualized fighting, and it has been suggested that telson armor co-evolved with this behavior (Caldwell and Dingle, 1976). However, the response of the telson to impact forces and the characteristics that confer the ability to withstand repeated, forceful impacts are unknown.

A specialized morphology is required to resist powerful impacts. This is because impact forces occur over very short time periods and can have different effects than forces applied over longer time scales (Biewener, 2003; Imre et al., 2008; Tabor, 1948). For example, baseball bats become highly flexible on the time scale of a collision with a baseball (1 ms) (Adair, 1995). Owing to the

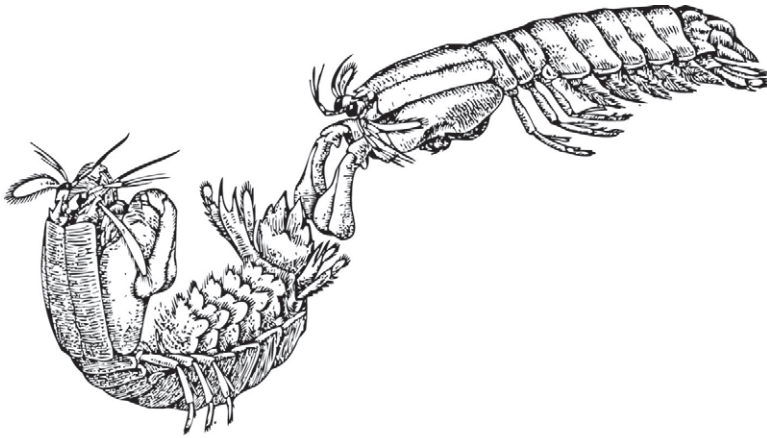


Fig. 1. Ritualized fighting in mantis shrimp. The animal on the left is in a coiled position, presenting its telson to the opponent. The animal on the right is striking the telson of the opponent with both raptorial appendages. Adapted from Caldwell and Dingle (Caldwell and Dingle, 1976).

frequent, harmful impact loads experienced by humans (e.g. automobile crashes, explosions, gun shots), an extensive amount of research has been conducted on the design of impact-resistant armor (Cheeseman and Bogetti, 2003; Qiao et al., 2008; Tabiei and Nilakantan, 2008). To effectively resist impact, a material must be able to absorb the energy of the impact and resist penetration of an object. Compliant materials are generally effective at absorbing and distributing impact energy, whereas hard materials effectively resist penetration. Compliance and hardness are both inherent properties of materials and structural design.

The characterization of impact resistant materials has received intense focus in engineered systems, but rarely in biological systems. For example, engineers and materials scientists use several impact-testing techniques, including, for example, Charpy, Izod, and Hopkinson bar tests (Cantwell and Morton, 1991; Ruiz and Mines, 1985). These instruments are designed to test materials of precise geometry, and are therefore insufficient for determining how complex animal structures respond to impact. Thus, biologists have typically used impacts of known force to characterize the fracture and damage patterns in biological systems. For example, by dropping weights onto sea urchins, Strathmann (Strathmann, 1981) determined that spines protect the underlying test by absorbing and dispersing the impact energy. Dropping weights on barnacles led Shanks and Wright (Shanks and Wright, 1986) to demonstrate that breaking strength and shell fracture patterns were species specific, and that aggregations of barnacles were more resistant to impact than solitary animals. This same method allowed other authors to determine that barnacle species living in areas exposed to wave-borne debris are less prone to damage from impacts than species living in protected areas (Barnes et al., 1970; Pentcheff, 1991). In addition to these few invertebrate examples, bone impact mechanics have been studied extensively (e.g. Burgin and Aspden, 2008; Currey, 1979; Jaslow and Biewener, 1995; Reilly and Currey, 2000).

Here, we examine the impact response of a mantis shrimp telson by employing a technique used extensively in engineering, sports science, and food science to analyze impacts: the coefficient of restitution. For a collision, the coefficient of restitution,  $e$ , is the ratio of the relative velocity after impact to the relative velocity before impact; it is essentially a measure of the energy dynamics of a collision. The coefficient of restitution is most notably used to characterize and regulate a variety of objects that experience collisions, including automobiles, body armor, sports equipment, and even fruits and vegetables (e.g. Dikshit and Sundararajan, 1992; Haake et al., 2003; Jindal and Mohsenin, 1978; McHenry and McHenry, 1997; Nathan, 2003; Pang et al., 1992; Shenoy et al.,

2001). The coefficient of restitution has the advantage of providing a quantifiable characteristic of impact to compare among structures of diverse shapes and sizes. Using the mantis shrimp *Neogonodactylus wennerae* (Crustacea: Stomatopoda), we probe whether the telson acts as a ‘punching bag’ (inelastic) or a ‘trampoline’ (elastic) when impacted, and examine if there are particular mineralization patterns of the telson that confer mechanical stability.

## MATERIALS AND METHODS

### Animal acquisition and maintenance

*Neogonodactylus wennerae* (Crustacea: Stomatopoda: Gonodactylidae) specimens were purchased from a commercial supplier (Tampa Bay Saltwater, Tampa Bay, FL, USA) and maintained in the laboratory in 21 and 350 ml plastic cups filled with artificial sea water [salinity: 35 p.p.t. (parts per thousand); 22°C]. Animals were fed fresh grass shrimp and water was changed twice weekly. A total of 17 individuals were used for this study, encompassing male and female animals from 0.47 to 4.60 g body mass. Immediately prior to each test, animals were placed in a freezer until dead, but not frozen. Body mass and sex were determined for each animal prior to testing. The molt stage for each animal was determined by removing and examining a pleopod under the microscope (Reaka, 1975). All animals used in this study were in the intermolt phase.

### Mineralization patterns

Telson and abdomen mineralization was characterized using calibrated micro-CT scans (model HMXST225, X-Tek, Nikon Metrology NV, Leuven, Belgium) and 3-D reconstruction software (VGStudio Max v. 2.0.5, Volume Graphics GmbH, Heidelberg, Germany). A freshly frozen *N. wennerae* was scanned with 0.0261 mm × 0.0261 mm × 0.0261 mm Voxel size. Density was calibrated using a known volume of water and pixel values were converted to Hounsfield units; lighter pixel color indicates greater material density. The isosurface rendering algorithm generated images showing surface configuration and the sum along ray algorithm produced images showing relative density.

### Coefficient of restitution tests

In order to characterize the response of the telson to impact, we employed a method conventional to various engineering and sports sciences to calculate the coefficient of restitution. The basic principle of the method is that the amount of elastic energy absorbed by an object can be measured by the loss of momentum of a colliding

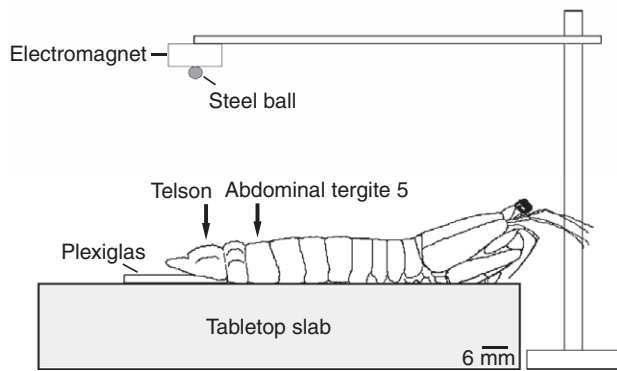


Fig. 2. Experimental set-up. The mantis shrimp is secured to the tabletop slab and the Plexiglas strip with glue. A small steel ball is released from an electromagnet and dropped onto the telson and abdominal tergite 5, as indicated by the thick, black arrows.

object, such as a steel ball. Thus, we dropped steel balls from a known height and measured the velocity before and after impact with a horizontally mounted telson. Although it would have been simpler to measure the ratio between the drop and the rebound heights of the steel ball (another way to calculate the coefficient of restitution), we wanted enough video resolution to visualize details of the impact, which placed the bounce distances of the steel ball beyond the field of view of the camera. Specifically, a small 440C stainless steel ball (6.33 mm diameter; 1.022 g; Rockwell C: 58–65; Small Parts, Miramar, FL, USA) was dropped through the air from an electromagnet (model E-66-100-34, Magnetic Sensor Systems, Van Nuys, CA, USA) that was attached to a ring stand approximately 100 mm above the target (Fig. 2). This gave an impact velocity of  $1.67 \text{ ms}^{-1}$ . No spin of the ball was detected.

A 440C stainless steel ball was chosen because of its high hardness value, which approximates the hardness of the striking surface of the raptorial appendage (i.e. the dactyl heel) (Currey et al., 1982). Furthermore, steel balls are nearly perfectly elastic (Cross, 1999). Thus, the coefficient of restitution value will represent the object colliding with the steel ball, assuming that the object is not as hard (Cross, 1999; Tirupataiah et al., 1990). The dactyl heel is significantly harder than the telson (B. Swanson, personal communication).

Intact animals were secured on top of an approximately 2.5 cm thick steel counter top slab beneath the electromagnet (Fig. 2). To prevent dislodgement of the animal at impact, a small drop of glue (5-star Super Glue, Surehold, Chicago, IL, USA) was placed on the tip and base of each uropod, and at the base of both sides of the fourth abdominal tergite. Animals were positioned horizontally with the telson resting on a small, 3.0 mm thick Plexiglas strip to position it so that a direct, collinear impact could be achieved (Fig. 2). Thus, the telson was mounted on a Plexiglas strip glued to a steel slab, whereas the rest of the animal was mounted directly onto the steel slab. Because the steel slab and the Plexiglas strip might differ in stiffness, and the stiffness of the mounting surface might influence the collision mechanics, we compared the coefficient of restitution of these two mounting surfaces. We found that the coefficient of restitution was identical for the table slab ( $0.89 \pm 0.00$ ) and the Plexiglas strip on the table slab ( $0.89 \pm 0.00$ ). We therefore assumed that the use of these two mounting surfaces would not result in differences between the impact response of the telson and abdomen.

For each animal, the ball was dropped 10 times onto each of two targets: the center carina (ridge) of the telson and the center of the fifth abdominal tergite (Fig. 2). To control for test order effects, the telson was tested first in 10 of the animals, whereas the abdomen was tested first in six animals, all chosen randomly. Dehydration was prevented by placing a saltwater-soaked paper towel over the animal between ball drops (Hepburn et al., 1975; Joffe et al., 1975). To test the elasticity of the ball and the mounting surfaces, the ball was dropped 10 times onto the table slab and the Plexiglas strip. Furthermore, because repeated impacts might result in changes in the impact behavior of the telson, because of plastic deformation and residual stresses (Seifried et al., 2005), one of the 16 animals was impacted 100 times on each target to identify any changes in the coefficient of restitution.

All ball drop tests were recorded with a high-speed digital video camera (AF micro Nikkor 105 mm lens, Nikon, Melville, NY, USA; APX-RS high speed video camera, Photron, San Diego, CA, USA) at  $15,000 \text{ frames s}^{-1}$ , 0.067 ms shutter duration, and  $256 \times 512$  pixel resolution. A small  $10 \text{ mm} \times 10 \text{ mm}$  grid was placed in the camera's field of view to be used for calibration in addition to the ball.

#### Coefficient of restitution analysis

The coefficient of restitution was calculated by measuring the velocity before and after ball impact. First, we determined the first and last video frames in which the ball was in contact with the specimen (IrfanView v. 4.20, Irfan Skiljan, Austria). Then, we measured the displacement of the ball over the 10 frames preceding contact and the 10 frames following separation (SigmaScan Pro 5.00, SPSS, Chicago, IL, USA). From these distances and changes in time, the impact and separation velocities were determined and used to calculate the coefficient of restitution,  $e$ :

$$e = \frac{v_f}{v_i}, \quad (1)$$

where  $v_f$  is the velocity at separation and  $v_i$  is the velocity at impact (Goldsmith, 1960; Stronge, 2000). The amount of energy lost during impact can be calculated as:

$$1 - e^2, \quad (2)$$

where  $e$  is the coefficient of restitution (Cross, 2000; Nathan, 2000).

Additionally, the duration of impact, defined as the time between first contact and separation, was recorded. Impulse was calculated using the change in momentum:

$$I = m\Delta v, \quad (3)$$

where  $I$  is the impulse,  $m$  is the mass of the ball, and  $\Delta v$  is the change in ball velocity (i.e.  $v_i + v_f$ ). Finally, the deformation of the telson and abdomen during impact was estimated as the displacement of the ball during the compression phase of impact, i.e. the distance between the frame of first contact and the frame in which the downward velocity of the ball reached zero with no further compression.

The coefficient of restitution, impact duration, impulse and displacement (i.e. the distance the ball travels after contact with the exoskeleton) were calculated for each drop test and then averaged for each animal ( $N=16$ ). These average values were then compared across sexes using  $t$ -tests. Because no significant differences were observed between sexes, data from male and female animals were combined. The average values of the impact parameters were then compared between the telson and the abdomen using paired  $t$ -tests, and with body mass using least

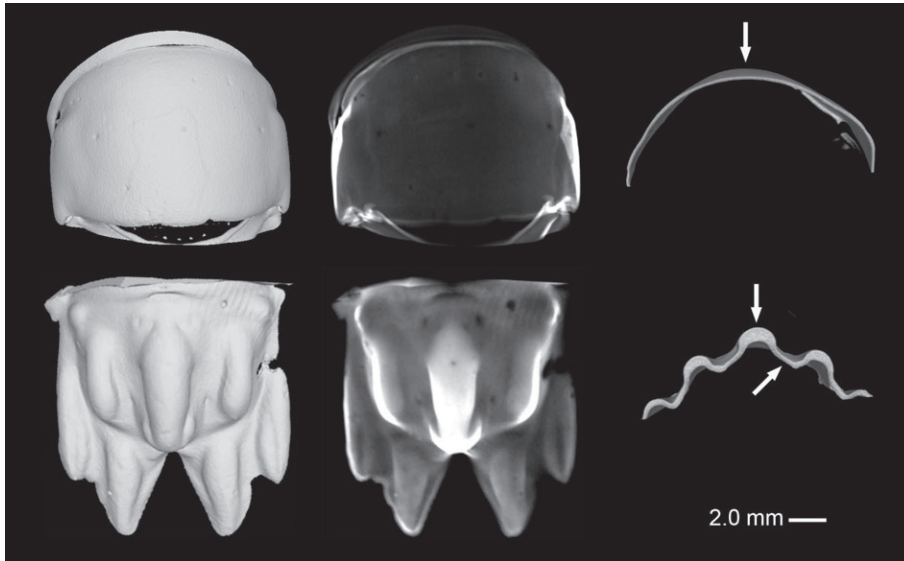


Fig. 3. Micro-CT images of the fifth abdominal tergite (top row) and the telson (bottom row). The surface conformation is visible in the left images. The center images show relative mineralization with the brighter white indicating greater mineralization. The right-hand images are transverse sections showing cuticle thickness at the midpoint of the structure. Arrows indicate the locations where cuticle thickness was measured. The dorsal arrows also indicate the location of ball impact.

squares linear regression. Finally, to further understand the results in the context of scale, measurements of cuticle thickness at locations of impact were made on frozen animals following experimentation. Thickness was measured with digital calipers at the dorsal center of the fifth abdominal tergite (e.g. impact location), the dorsal center of the central carina (e.g. impact location), and the center of the area between the central and the lateral carina (Fig. 3). These measurements were then compared with body mass using least squares linear regression. Statistics were performed with JMP 7 (SAS Institute, Cary, NC, USA). Results are represented as mean  $\pm$  s.d.

#### Spring impact analysis

The impact between rigid objects is often modeled as a spring system, in which a small stiff spring separates the contact areas of the two colliding objects (Stronge, 2000). As stiffness increases, the contact area becomes small, so that the impact duration decreases and there is less time for significant deformation to occur. The stiffness of the colliding objects is an important factor determining impact behavior. Thus, impact can also be modeled as a collision between two springs (Bayman, 1976; Cross, 1999; Cross, 2000). We calculated the spring stiffness,  $k$ , of the telson and abdomen using two different equations:

$$k = \frac{mv^2}{x^2}, \quad (4)$$

where  $m$  is the mass of ball,  $v$  is the velocity of ball at impact and  $x$  is the displacement distance, and:

$$k = m \frac{\pi^2}{t^2}, \quad (5)$$

where  $m$  is the mass of ball and  $t$  is the duration of impact (Haake et al., 2003).

## RESULTS

### Mineralization patterns

There were clear differences in the amounts and patterns of mineralization between the telson and the abdomen (Fig. 3). The telson has considerable mineralization concentrated in the carinae, whereas the abdomen has only slight mineralization along the lateral edges.

### Impact parameters

The average coefficient of restitution for the telson,  $0.56 \pm 0.083$ , was significantly lower than that of the abdomen,  $0.67 \pm 0.046$  (paired  $t$ -test,  $N=16$ , d.f.=15,  $t=4.7$ ,  $P=0.0003$ ; Fig. 4A). The telson therefore dissipates 69% of the energy during impact, whereas the abdomen loses 55%. The duration of the impact was significantly lower for the telson than for the abdomen (telson,  $0.54 \pm 0.16$  ms; abdomen,  $0.65 \pm 0.11$  ms; paired  $t$ -test,  $N=16$ , d.f.=15,  $t=2.3$ ,  $P=0.035$ ; Fig. 4B). Also, the impulse on the telson,  $2.5 \pm 0.14$  mNs, was significantly lower than that on the abdomen,  $2.7 \pm 0.084$  mNs (paired  $t$ -test,  $N=16$ , d.f.=15,  $t=5.1$ ,  $P=0.0001$ ; Fig. 4C). Displacement during impact was  $0.17 \pm 0.03$  mm for the telson, which was significantly less than that of the abdomen,  $0.26 \pm 0.05$  mm (paired  $t$ -test,  $N=16$ , d.f.=15,  $t=8.8$ ,  $P<0.001$ ; Fig. 4D). For the smallest individual (0.47 g), there was damage to the abdomen during the second ball drop test, therefore only the first abdomen ball drop test on this animal was used in the analyses.

There were no sexual differences in the telson and the abdominal coefficient of restitution, impulse, impact duration, and displacement during impact ( $t$ -tests: all  $P$ -values were greater than 0.14).

Neither the telson nor the abdomen showed a significant change in the coefficient of restitution across 100 impacts (Fig. 5).

### Scaling of impact parameters

The telson and the abdomen differed in their scaling relationships with the measured impact parameters. The telson coefficient of restitution was negatively correlated with body mass [least-square regression (LSR): slope= $-0.052$ , d.f.=15,  $R^2=0.54$ ,  $F=17$ ,  $P=0.0011$ ] (Fig. 6A). The abdomen coefficient of restitution, however, was not correlated with body mass (LSR: slope= $-0.0045$ , d.f.=15,  $R^2=0.013$ ,  $F=0.18$ ,  $P=0.68$ ). Telson impulse was also negatively correlated with body mass (LSR: slope= $-8.6 \times 10^{-5}$ , d.f.=15,  $R^2=0.51$ ,  $F=15$ ,  $P=0.0019$ ), whereas abdomen impulse showed no correlation (LSR: slope= $-1.6 \times 10^{-5}$ , d.f.=15,  $R^2=0.047$ ,  $F=0.69$ ,  $P=0.42$ ) (Fig. 6B). Impact duration was positively correlated with body mass for the telson (LSR: slope= $9.6 \times 10^{-5}$ , d.f.=15,  $R^2=0.50$ ,  $F=14$ ,  $P=0.0023$ ), but not for the abdomen (LSR: slope= $-1.6 \times 10^{-5}$ , d.f.=15,  $R^2=0.028$ ,  $F=0.41$ ,  $P=0.53$ ) (Fig. 6C). Neither telson nor abdomen displacement during impact was correlated with body mass (LSR telson: slope= $0.0064$ , d.f.=15,



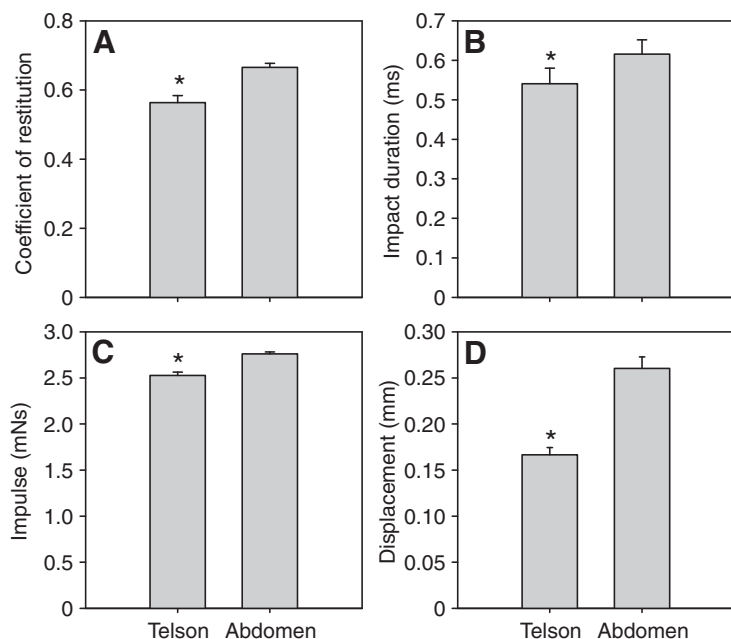


Fig. 4. Comparison of telson and abdomen impact parameters. The telson has a significantly lower coefficient of restitution (A), impact duration (B), impulse (C) and displacement (D) than the abdomen. Error bars represent s.e.m. \* $P < 0.05$ .

$R^2=0.056$ ,  $F=0.83$ ,  $P=0.38$ ; LSR abdomen: slope= $-0.0036$ , d.f.=15,  $R^2=0.0073$ ,  $F=0.10$ ,  $P=0.75$ ) (Fig. 6D).

#### Cuticle thickness measurements

The average cuticle thickness was  $0.15 \pm 0.05$  mm in the abdomen,  $0.22 \pm 0.08$  mm in the telson between the carinae, and  $0.43 \pm 0.09$  mm in the telson central carina. All were significantly different from each other (paired  $t$ -tests,  $N=13$ , d.f.=12,  $P$ -values all less than 0.004; Fig. 7A).

Cuticle thickness of the abdomen and the central carina were both positively correlated with body mass (LSR abdomen: slope= $0.025$ , d.f.=12,  $R^2=0.33$ ,  $P=0.039$ ; LSR central carina: slope= $0.061$ , d.f.=12,  $R^2=0.49$ ,  $P=0.008$ ), but not with the cuticle between the carina (LSR: slope= $0.019$ , d.f.=12,  $R^2=0.075$ ,  $P=0.37$ ) (Fig. 7B).

#### Spring properties

The spring constant was larger for the telson than for the abdomen, whether it was calculated using equation 4 (telson,  $7.1 \times 10^4$  kg s $^{-2}$ ; abdomen,  $2.4 \times 10^4$  kg s $^{-2}$ ; paired  $t$ -test, d.f.=15,  $t=4.6$ ,  $P < 0.001$ ) or

equation 5 (telson,  $5.3 \times 10^4$  kg s $^{-2}$ ; abdomen,  $2.7 \times 10^4$  kg s $^{-2}$ ; paired  $t$ -test, d.f.=15,  $t=2.1$ ,  $P < 0.05$ ).

#### DISCUSSION

Whether the telson responds like a trampoline (elastic) or a punching bag (inelastic) has implications both for its behavioral role in conspecific assessment and for the mechanical properties of the structure. Our coefficient of restitution measurements, in the context of our experimental design, showed that the telson of *N. wennerae* operates inelastically, and thus responds more like a punching bag than a trampoline to impacts. Indeed, the coefficient of restitution value is similar to that of a baseball striking an ash wall (i.e. a large plate composed of wood used to make baseball bats) (Hendee et al., 1998). Furthermore, although the abdominal segment's mechanical properties reveal little information about the size of the individual, the telson's coefficient of restitution, impulse and impact duration all scale with body size, suggesting that the telson might indeed convey size-based information during ritualized assessments. Thus, the combination of an energy-absorptive punching bag and the correlation between size and key mechanical variables reveal a biomechanically and behaviourally informative structure at the center of this classic example of a ritualized assessment strategy.

#### Limitations of the experimental design

Based on the coefficient of restitution, the telson is as elastic as a major league baseball. However, it is important to note that the coefficient of restitution is a characteristic of a collision; it is not a material property. The coefficient of restitution depends on the size, shape, structural and material properties, and relative velocities of the two impacting objects (Cross, 2000; Goldsmith, 1960; Stronge, 2000). Under certain conditions, such as one of the colliding objects being significantly more rigid than the other, the coefficient of restitution can be referred to as a property of the less rigid object (Cross, 2000). This method has been used extensively in the sporting goods industry to regulate equipment, but the test methods used are highly variable among the different sports, making a broad interpretation of the coefficient of restitution difficult. For example, a baseball shot at an ash wall at  $26.8$  m s $^{-1}$  has a coefficient of

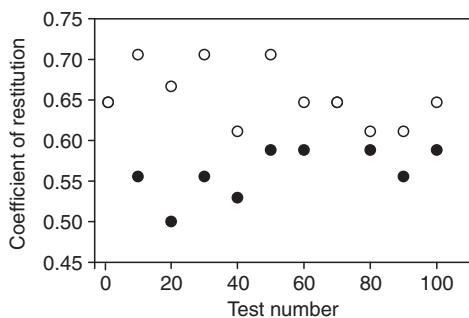


Fig. 5. Coefficient of restitution for repeated impacts. The telson and abdomen of one individual were each impacted 100 times. Each circle represents a single impact test; only every tenth impact is included in the graph. The telson (black circles) and abdomen (white circles) showed no pattern of change in the coefficient of restitution across 100 impact tests.

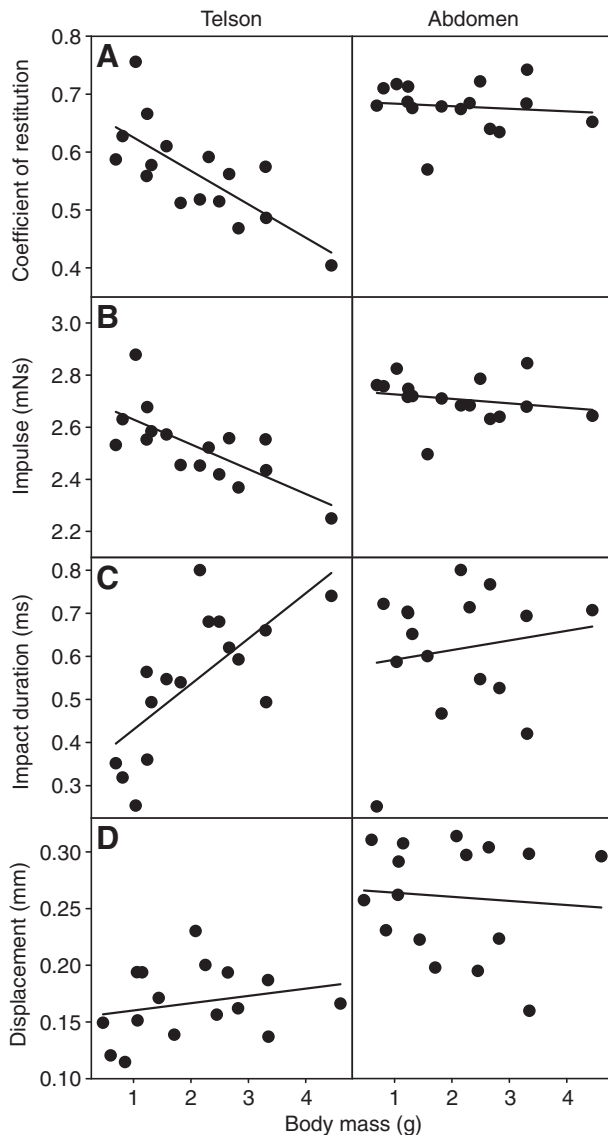


Fig. 6. Scaling of impact parameters relative to body mass. The coefficient of restitution (A) and the impulse (B) are negatively correlated with body mass for the telson. Impact duration (C) is positively correlated with body mass for the telson, whereas displacement is not correlated (D). None of the impact parameters scaled with body mass for the abdomen (A–D).

restitution of 0.55 (Hendee et al., 1998), a golf ball hitting steel at  $62 \text{ m s}^{-1}$  has a coefficient of restitution of 0.77 (Arakawa et al., 2009), a tennis ball hitting a racket at  $8.3 \text{ m s}^{-1}$  has a coefficient of restitution of 0.89 (Brody, 1979), and a ping pong ball hitting a lab bench at  $2.4 \text{ m s}^{-1}$  has a coefficient of restitution of 0.94 (Nagurka, 2003). If the test conditions are held constant, then a steel ball has a coefficient of restitution very similar to those of a golf ball and a tennis ball at low impact velocities (Cross, 1999). This variability presents a potential difficulty because the test conditions must be held constant to be able to draw comparisons, yet such conditions might not reflect the natural collision parameters of the objects involved.

The dynamic behavior of sports balls might be different under actual playing conditions, just like the telson might behave differently during actual ritualized fighting. For instance, mantis shrimp can strike with speeds of up to  $23 \text{ m s}^{-1}$  (Patek et al., 2004), which results in significantly more energy at impact than the velocity

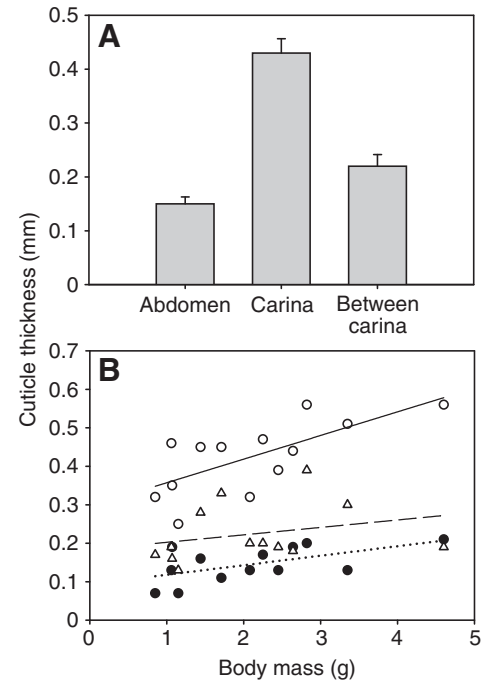


Fig. 7. Average cuticle thickness and scaling. (A) Cuticle thickness is significantly different across the three measured locations; the center carina is thickest and the abdominal tergite is thinnest. Error bars represent s.e.m. (B) Thickness of the cuticle in the central carina (white circles, solid line) and the abdominal tergite (black circles, dotted line) are positively correlated with body mass, but the cuticle between the carinae (white triangles, dashed line) is not.

we used in this study, which was  $1.67 \text{ m s}^{-1}$ . However, kinetic energy is dependent on both mass and velocity:

$$\frac{1}{2} mv^2. \quad (6)$$

We therefore accounted for the slower impact velocity of our tests by using a steel ball that was larger in mass than the appendage of an average size *N. wennerae*. The impact energy in our tests was approximately the same as that estimated for an average size animal striking at  $15 \text{ m s}^{-1}$ .

The mounting of mantis shrimp in our study also presents challenges with interpretation of the results, because not only could the rigidity of the mounting surface influence the observed impact response, but any type of mounting system diverges from the natural conditions in which mantis shrimp fight. During ritualized fighting, the animal receiving the strike is typically in a coiled position (Fig. 1), in which its freedom of movement and flexible posture might help absorb and dissipate more of the impact energy. Thus, we might expect an even lower coefficient of restitution during actual fighting. The differences might not be too great, though, given that the impact response of large armor plates was the same whether they were rigidly clamped or hanging and free to move (Dikshit and Sundararajan, 1992).

Furthermore, mantis shrimp are aquatic, and the water medium might influence the energy dynamics of impact. Just as a loose animal posture might dissipate more energy, movement in a dense medium might incur more energy loss. In fact, the coefficient of restitution is strongly correlated with the Stokes number, which is the ratio of particle inertia to viscous drag (Gondret et al., 2002;

Joseph et al., 2001; Turmel and Locat, 2007). For impacts at a constant velocity, the coefficient of restitution decreases as viscosity increases (Ruiz-Angulo and Hunt, 2010). Thus, we might expect a slight decrease in the coefficient of restitution if our tests were conducted in water. But for Stokes numbers greater than 1000, the hydrodynamic effects become negligible (Ruiz-Angulo and Hunt, 2010). Therefore we might not observe any difference in the coefficient of restitution if our experiment was performed in water, where the Stokes number would be approximately 8400. It would be ideal, although quite challenging, to measure the coefficient of restitution from live, interacting animals to accurately assess the contribution of body posture and the water medium to the transfer of energy during impact.

#### Interpretation of the coefficient of restitution

With a coefficient of restitution of 0.56, the telson is significantly less elastic than the abdomen (0.66), and very similar to a major league baseball (0.55 for a ball against an ash wall, 0.45–0.50 for a ball colliding with a bat during play) (Hendee et al., 1998). Like a baseball, the telson is not an efficient spring; it loses a significant amount of energy when it is compressed during impact (69%). Although we could not determine the mechanism(s) of energy dissipation in this study, during a collision, energy can be lost to light, heat, sound, vibration, internal friction and plastic deformation, depending on the shape and material properties of the structure (Goldsmith, 1960; Stronge, 2000). The amount of energy lost to light, heat and sound is generally small (Goldsmith, 1960). Regardless of how energy is lost, the fact that most of it is dissipated during impact implies that the telson functions more like a punching bag than a trampoline, which would return most of the impact energy.

Like a stiffer spring, the telson compresses less and has a significantly shorter impact duration than does the abdomen. However, the spring constants for both the telson and the abdomen were significantly different between the two calculation methods, which is likely to reflect the fact that one equation is based on time and the other on displacement. In our tests, the spatial resolution was less than the temporal resolution, so equation 5 might be more accurate.

Analyzing impact in terms of the coefficient of restitution provides a significant advancement over methods previously used by biologists, which were limited to determining the amount of impact energy necessary to break a structure (Barnes et al., 1970; Pentcheff, 1991; Shanks and Wright, 1986; Strathmann, 1981). Breaking strength is not necessarily the most relevant material property, particularly given that many animals operate with significant safety factors (Biewener, 2003; Hahn and LaBarbera, 1993). The coefficient of restitution has the benefit of providing measures of the energy dynamics and structural response of organisms to biologically relevant collision parameters. This technique is especially useful for understanding the evolution of morphologies that endure repeated impacts.

#### Morphology and mineralization

The difference in the impact response of the telson compared with that of the abdomen reflects the remarkable morphology and mineralization patterns of the telson. Whereas the abdominal tergite is a curved sheet of thin cuticle that is fairly compliant, the shape of the telson is more complex, with three longitudinally oriented carinae arising from the domed dorsal surface (Fig. 3). When animals strike the telson, the dactyl heel of the raptorial appendage typically makes contact with the carina; for animals of similar size, the dactyl heel is too large to fit between the carinae (J.R.A.T.,

personal observation). The cuticle that forms the carinae is approximately twice the thickness of other regions of the telson.

During impact, the carina shows no observable deformation; however, the entire domed surface compresses. When impacts of sufficient energy are incurred, fractures occur along the bases of the carina and the dome. It appears that the carinae provide stiffness, while the cuticle surrounding them provides compliance. The interplay between these two parts of the telson, along with the composite nature of the cuticle, provides an interesting balance between stiffness and compliance that might facilitate greater effectiveness at resisting powerful ballistic impacts. Indeed, combining materials with different properties, such as energy absorbing fiber composites and penetration-resistant ceramics, is a common strategy used by engineers in the design of armor (Lee et al., 2001; Qiao et al., 2008).

#### Role of the telson in ritualized fighting

The elasticity of the telson and the mechanism of energy dissipation might be crucial factors in assessment during fighting for both participants. If the telson had a trampoline effect, like a tennis racket or hollow metal bat, the impacting object (e.g. the raptorial appendage) would bounce back with a greater velocity (Brody, 1979; Cross, 2000; Nathan et al., 2004). We found, however, that the telson functions more like a punching bag: it absorbs and dissipates most of the impact energy so that less is transferred back to the appendage of the striking individual. Determining how this energy exchange is interpreted and acted upon will be important for understanding the role that telson morphology plays in the evolution of ritualized fighting.

It is especially interesting to consider how the energy exchange during impact might change throughout the molt cycle and thus might influence ritualized fighting. Like all other crustaceans, stomatopods periodically shed their exoskeleton and secrete a new one (i.e. molting) (Reaka, 1975). During molting, the cuticle that comprises the exoskeleton undergoes such dramatic changes in structure and mechanical properties, becoming as flimsy as plastic wrap before hardening, that animals must rely on hydrostatic skeletal support (Taylor et al., 2007; Taylor and Kier, 2003; Taylor and Kier, 2006). Newly molted animals cannot strike with their soft raptorial appendages and therefore tend to bluff or flee their cavities when threatened by intruders (Steger and Caldwell, 1983). If an intruder were to strike the telson of a newly molted animal, much of the impact energy may be lost as the telson deforms significantly or even tears. This mechanical response might signal to the intruder the defenseless condition of the occupant and result in immediate removal or fatal injury. The telson mechanical properties would be an honest signal of the animal's ability to fight and therefore might be one reason why newly molted animals tend to flee their cavities before contests escalate beyond threat displays.

#### Scaling

Our study revealed that most of the telson impact parameters, but not those of the abdomen, scale with body size. For instance, larger animals have a lower telson coefficient of restitution but the same abdomen coefficient of restitution as smaller animals. This is interesting because the coefficient of restitution is influenced by the sizes and masses of the colliding objects (Goldsmith, 1952), so we might expect that the abdominal coefficient of restitution would scale as well. However, other factors that influence the coefficient of restitution, such as object shape and stiffness (Goldsmith, 1952), might be more significant.

We do not know how material and structural stiffness scales for the telson or the abdomen; there is minimal literature on the scaling of exoskeleton material properties (Borrell, 2004; Katz and Gosline, 1992; Katz and Gosline, 1993; Katz and Gosline, 1994; Zack et al., 2009). But stiffness is often correlated with cuticle thickness (Currey, 1967; Wainwright et al., 1982; Wainwright et al., 1976), and the cuticle thickness of both the carinae and the abdomen increases with body size. Conversely, the increase in impact duration with body size would suggest a decrease in stiffness (Cross, 2000; Rajalingham and Rakheja, 2000).

The decrease in telson coefficient of restitution with body size indicates that larger animals are dissipating more energy during impact. At the same time, the increase in impact duration and decrease in impulse with size imply that larger animals can withstand greater impact forces. Together, these results suggest that as animals grow, their telsons are capable of withstanding the larger strike forces typically generated by larger animals. Furthermore, the impact dynamics might indicate the mechanical potency of the individuals during the fight, further enhancing the effectiveness of this structure during ritualized behavior.

### Conclusion

Mantis shrimp are one of many groups of animals that experience repeated, violent impacts. Our knowledge about how animals withstand such collisions has thus far been primarily limited to determining their breaking strength. By applying a concept commonly used in physics and engineering, the coefficient of restitution, we were able to conduct an informative impact analysis of the mantis shrimp telson armor. Our study shows that the telson is relatively inelastic and functions like a punching bag, dissipating most of the impact energy. Furthermore, the impact response of the telson, together with the morphology and mineralization patterns, indicate that the telson is composed of stiff and compliant regions, a characteristic that is effective in the design of impact-resistant armor. The integration of biomechanical analyses with behavioral research holds great potential for understanding the evolution of impact resistance, biological armor and ritualized fighting across diverse biological systems.

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