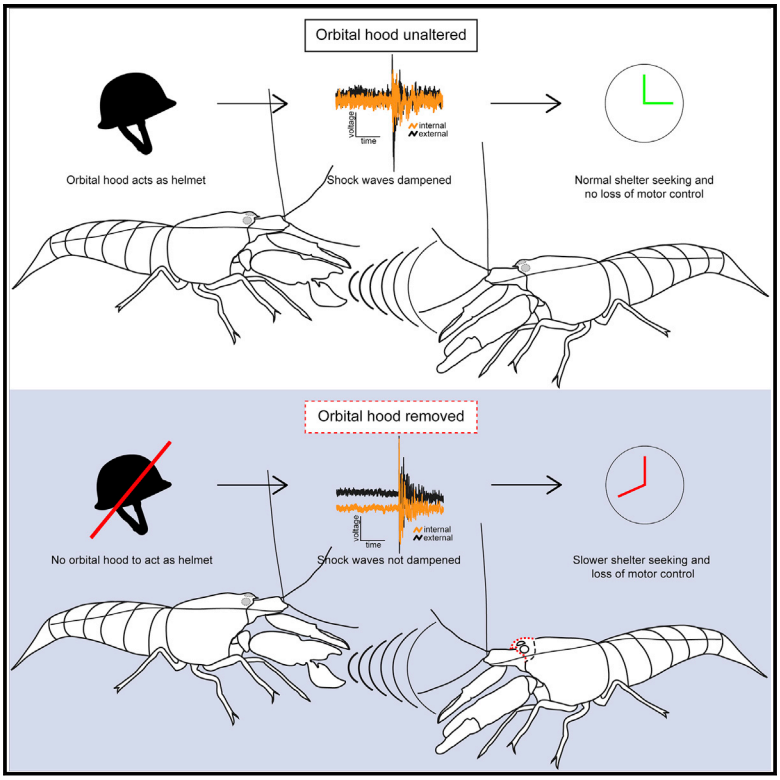
Report

Current Biology

Snapping shrimp have helmets that protect their brains by dampening shock waves

Graphical abstract



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In brief

Kingston et al. find snapping shrimp have helmet-like orbital hoods that protect their brains from the shock waves they produce with their snapping claws. Shock wave exposure slows shelter-seeking and causes loss of motor control in animals without orbital hoods. Orbital hoods protect shrimp from blast-induced neurotrauma by dampening shock waves.

Highlights

- Helmet-like orbital hoods mitigate blast-induced neurotrauma in snapping shrimp
- Snapping shrimp without orbital hoods lose motor control after shock wave exposure
- Orbital hoods protect neural tissue in snapping shrimp by dampening shock waves
- Orbital hoods dampen shock waves by trapping and expelling water

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Snapping shrimp have helmets that protect their brains by dampening shock waves

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SUMMARY

Shock waves are supersonic high-amplitude pressure waves that cause barotrauma when they transfer kinetic energy to the tissues of animals.[1–4] Snapping shrimp (Alpheidae) produce shock waves and are exposed to them frequently, so we asked if these animals have evolved mechanisms of physical protection against them. Snapping shrimp generate shock waves by closing their snapping claws rapidly enough to form cavitation bubbles that release energy as an audible "snap" and a shock wave when they collapse.[5–8] We tested if snapping shrimp are protected from shock waves by a helmet-like extension of their exoskeleton termed the orbital hood. Using behavioral trials, we found shock wave exposure slowed shelter-seeking and caused a loss of motor control in *Alpheus heterochaelis* from which we had removed orbital hoods but did not significantly affect behavior in shrimp with unaltered orbital hoods. Shock waves thus have the potential to harm snapping shrimp but may not do so under natural conditions because of protection provided to shrimp by their orbital hoods. Using pressure recordings, we discovered the orbital hoods of *A. heterochaelis* dampen shock waves. Sealing the anterior openings of orbital hoods diminished how much they altered the magnitudes of shock waves, which suggests these helmet-like structures dampen shock waves by trapping and expelling water so that kinetic energy is redirected and released away from the heads of shrimp. Our results indicate orbital hoods mitigate blast-induced neurotrauma in snapping shrimp by dampening shock waves, making them the first biological armor system known to have such a function.

RESULTS AND DISCUSSION

Orbital hoods protect snapping shrimp from short-term behavioral effects of shock wave exposure

Shock waves are produced by explosions and other sudden, violent changes in pressure. They include a pressure rise in which the surrounding medium is compressed (overpressure) followed by a pressure drop in which the medium expands (underpressure).[9] When shock waves pass through the bodies of animals, they cause barotrauma by transferring some of their kinetic energy to tissues as higher-frequency stress waves and lower-frequency shear waves.[4,10] Shock waves cause short- and long-term damage to many different tissue types, including neural structures such as eyes and brains. Blast-induced neurotrauma may be identified through changes in behavior, such as disorientation, loss of motor coordination, and deficits in spatial memory.[1,4,11–13] In some cases, these changes in behavior are associated with identifiable types of physical trauma such as diffuse axonal injury, reductions in cortical thickness, hemorrhagic lesions, vasospasm, and neural degeneration.[1,13–17]

Blast-induced neurotrauma may be a persistent natural threat to snapping shrimp (Figure 1A) because these decapods produce shock waves with their snapping claws[5,6] (Figure 1B). Evidence that these shock waves are powerful enough to cause harm include observations of snapping shrimp using them to stun or kill other crustaceans and fish.[18–20] Snapping shrimp, such as *Alpheus heterochaelis*, tend to be highly territorial,[21] and they risk blast-induced neurotrauma during frequent face-to-face agonistic encounters with conspecifics in which they produce shock waves within 1 cm of the heads of their rivals.[18,22–25] Snapping shrimp may also experience shock waves from their own snaps.[26] If so, blast-induced neurotrauma may be a near-constant threat to these animals: acoustic recordings indicate species of *Alpheus* and *Synalpheus* snap often throughout the day and night.[27–30] How do snapping shrimp survive frequent, close-range encounters with shock waves? We hypothesize that snapping shrimp, like other animals, are vulnerable to blast-induced neurotrauma, but have mechanisms of protection against shock waves that have yet to be identified. We predict the orbital hoods of snapping shrimp (Figure 1C) contribute to this protection. These helmet-like extensions of the exoskeleton cover the eyes and brains of animals, and they are present in many species of snapping shrimp but are absent in other crustaceans.[26]

We used behavioral trials to ask if shock wave exposure is harmful to *A. heterochaelis* and if orbital hoods help protect

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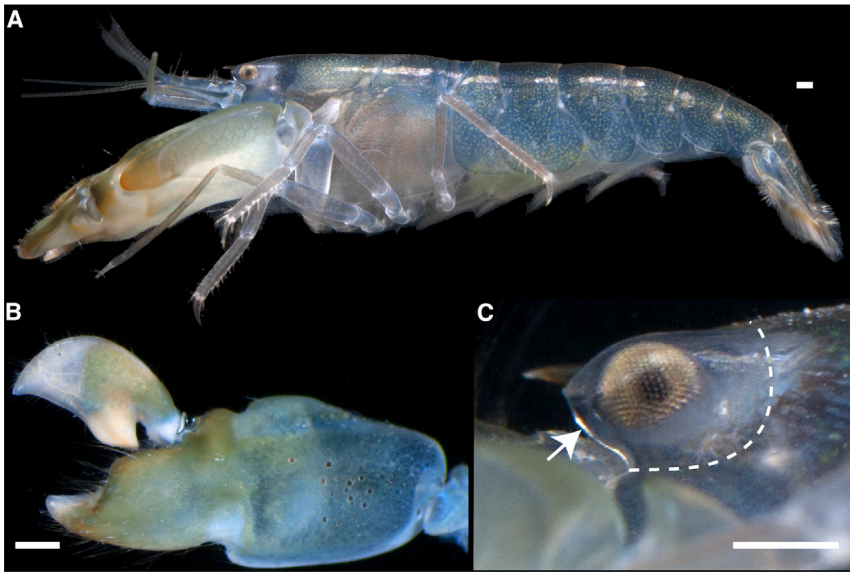

Figure 1. The bigclaw snapping shrimp, *Alpheus heterochaelis*

(A) Snapping shrimp can close their snapping claws (B) quickly enough to produce cavitation bubbles that release shock waves when they collapse. Snapping shrimp, such as *A. heterochaelis*, have orbital hoods (C) that cover their eyes (dashed line) while remaining open to the environment at the anterior end (arrow). Scale bars, 1 mm.

these shrimp from short-term effects of blast-induced neurotrauma such as disorientation and loss of motor control. We assessed blast-induced neurotrauma in snapping shrimp using behavioral tests because physical damage associated with blast-induced neurotrauma can be difficult to identify, even in animals with well-characterized nervous systems.[14] In these trials, we employed the reliable shelter-seeking behaviors of *A. heterochaelis*. Like many other snapping shrimp,[31] *A. heterochaelis* live in burrows and quickly seek natural or artificial burrows when they are threatened or in unfamiliar surroundings (Videos S1, S2, and S3). We predicted that after being exposed to shock waves and then placed in an unfamiliar setting, shrimp from which we had removed orbital hoods would take longer to reach their burrows than shrimp with unaltered orbital hoods.

To test our hypothesis, we compared how long it took shrimp from four treatment groups to successfully contact artificial burrows they had adopted as homes. These treatment groups included unarmored experimental (UE), shrimp without orbital hoods that we exposed to shock waves; armored experimental (AE), shrimp with unaltered orbital hoods that we exposed to shock waves; unarmored control (UC), shrimp without orbital hoods that we did not expose to shock waves; and armored control (AC), shrimp with unaltered orbital hoods that we did not expose to shock waves. To begin each shelter-seeking trial, we exposed test subjects in the experimental treatment groups (UE and AE) to three snaps from a conspecific; likewise, we exposed test subjects in the control treatment groups (UC and AC) to a conspecific but did not induce it to snap. After exposing a test subject to a conspecific, we released it at one end of a behavioral arena and timed how long it took to contact its burrow positioned at the opposite end of the arena.

Shrimp from the four treatment groups (n = 30 animals per treatment) differed significantly in how long they took to contact their artificial burrows (Kruskal-Wallis test, $H(3) = 23.01$, $p < 0.001$; Figure 2A; Data S1A). Pairwise comparisons using Dunn's test with Bonferroni correction revealed animals without orbital hoods that were exposed to shock waves took longer to contact their burrows than animals from the other three treatment groups. Shrimp from the UE treatment took 110 ± 123 s (mean ± SD) to contact their artificial burrows, making them significantly slower than shrimp from the AE (16 ± 27 s; $Z = 4.24$, $p < 0.001$), UC (29 ± 61 s; $Z = 3.83$, $p < 0.001$), or AC (19 ± 32 s; $Z = 3.59$, $p < 0.001$) treatments. Shock wave exposure did not slow shelter-seeking in animals with unaltered orbital hoods: shrimp from the AE treatment contacted their burrows just as quickly as shrimp from the AC treatment ($Z = 0.65$, $p = 0.515$). Surgery to remove orbital hoods did not slow shelter-seeking: shrimp from the UC (Figure 2C) and AC (Figure 2D) treatments took similar amounts of time to contact their artificial burrows ($Z = 0.23$, $p = 0.815$).

Slower shelter-seeking by animals from the UE treatment could indicate disorientation, loss of motor control, or both. Indeed, some individuals displayed behaviors consistent with disorientation (e.g., they walked or swam normally but had trouble locating their artificial burrow; Video S4), others lost motor control (e.g., they could not coordinate the movements of their appendages; Video S5), and some showed both disorientation and loss of motor control (Video S6). To compare loss of motor control between our treatment groups, we measured how long it took individuals to achieve a normal upright walking or swimming posture following their release into the behavioral arena.

Shrimp from the four treatment groups differed significantly in how long they took to achieve an upright posture (Figure 2B; Data S1B). Using Mood's median test, we found animals from the UE treatment took longer to achieve an upright posture than animals from the other three treatment groups ($\chi^2 = 15.41$, $p < 0.002$). Shrimp from the UE treatment took 32.5 ± 89.4 s to achieve an upright posture, a significantly longer time than shrimp from the AE (0.7 ± 0.7 s; $\chi^2 = 5.45$, $p < 0.02$), UC (0.7 ± 0.9 s; $\chi^2 = 5.45$, $p < 0.02$), or AC (0.6 ± 1.0 s; $\chi^2 = 11.88$, $p < 0.001$) treatments. Shock wave exposure did not impact motor control in animals with unaltered orbital hoods: shrimp from the AE treatment achieved an upright posture just as quickly as shrimp from the AC treatment ($\chi^2 = 1.96$, $p = 0.161$). Surgery to remove orbital hoods did not impact motor control: shrimp from the UC (Figure 2C) and AC (Figure 2D) treatments took similar amounts of time to achieve upright postures ($\chi^2 = 0.07$, $p = 0.796$). We conclude that shock waves produced by conspecifics can cause short-term behavioral effects in *A. heterochaelis* consistent with blast-induced neurotrauma, including loss of motor control. However, shock wave exposure did not cause short-term behavioral effects in animals with intact orbital hoods,

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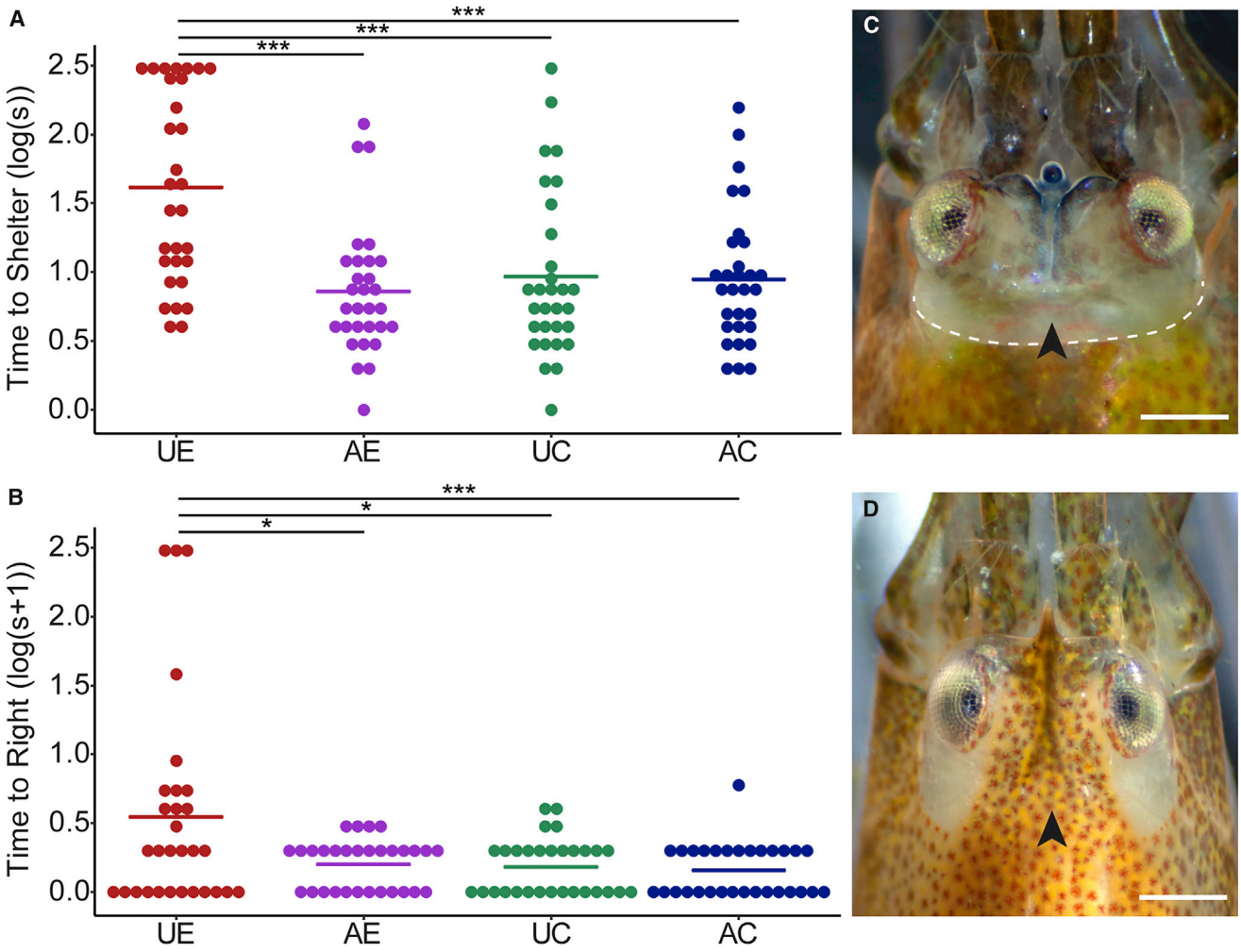

Figure 2. Orbital hoods protect *A. heterochaelis* from short-term behavioral effects of shock wave exposure

(A) We compared how long it took shrimp from four treatment groups to contact shelter ("Time to Shelter") after being placed in an unfamiliar environment (Data S1A). Shrimp without orbital hoods that were exposed to shock waves (unarmored experimental or "UE") took longer to contact their burrows than shrimp with orbital hoods that were exposed to shock waves (armored experimental or "AE"), shrimp without orbital hoods that were not exposed to shock waves (unarmored control or "UC"), or shrimp with orbital hoods that were not exposed to shock waves (armored control or "AC"). Animals in the AE, UC, and AC treatments did not differ in how long they took to contact their burrows.

(B) We measured how long it took individuals to achieve a normal upright posture ("Time to Right") following their release into the behavioral arena (Data S1B). Shrimp in the UE treatment took longer to become upright than animals in the AE, UC, or AC treatments. Animals in the AE, UC, and AC treatments did not differ in how long they took to achieve a normal posture.

In (A) and (B), each colored dot represents a single animal (n = 30 per treatment), and the colored bars represent the mean times it took animals in (A) to contact their burrows and animals in (B) to achieve an upright posture.

(C) Example of *A. heterochaelis* with a surgically removed orbital hood (treatment groups UE and UC) in which the dashed line marks the site of incision between the orbital hood and the carapace.

(D) Example of *A. heterochaelis* with an unaltered orbital hood (treatment groups AE and AC).

In (C) and (D), arrowheads indicate the location of the brain in each animal.

Scale bars, 1 mm. *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$.

See also Videos S1, S2, S3, S4, S5, and S6.

indicating orbital hoods protect snapping shrimp from potentially injurious shock waves.

Orbital hoods dampen shock waves

Shock waves with greater magnitudes (i.e., those with greater differences between their peak overpressures and peak underpressures) tend to inflict greater amounts of barotrauma.[3,32] We propose that orbital hoods protect snapping shrimp from blast-induced neurotrauma by dampening shock waves so that less kinetic energy is transferred to their eyes and brains. If orbital hoods function in this manner, shock waves recorded underneath orbital hoods near the brain (internal recordings) should have significantly lower magnitudes than the same shock waves recorded outside and just above orbital hoods (external recordings). We

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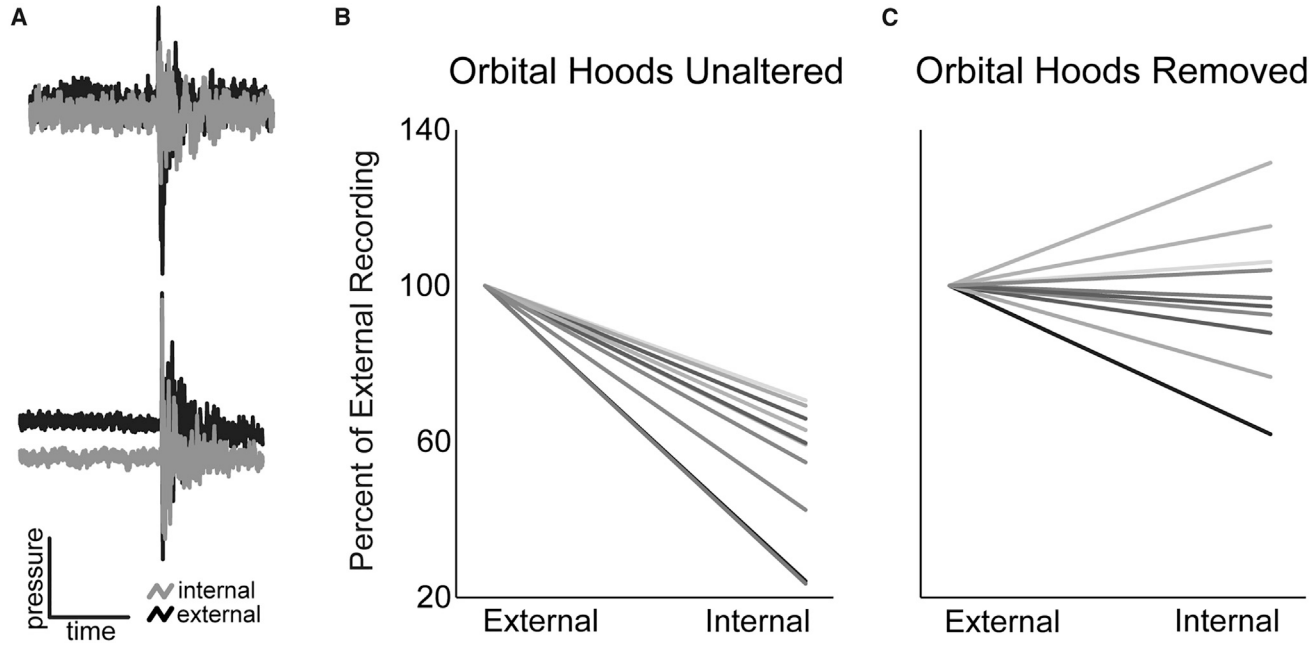

Figure 3. The orbital hoods of *A. heterochaelis* dampen shock waves

(A) Pressure recordings of shock waves (measured in Pa) from a test subject with an unaltered orbital hood (above) and the same test subject with its orbital hood removed (below). We took simultaneous recordings of shock waves from underneath the orbital hood ("internal") and from just above the orbital hood ("external") (Figure S1A). Each pressure recording = 1 s, the time scale bar = 0.3 s, the pressure bar = 18 Pa for the upper trace, and the pressure bar = 42 Pa for the lower trace.

(B) In test subjects with unaltered orbital hoods, shock waves recorded internally always had lower magnitudes than those recorded externally (Data S1C).

(C) When we removed orbital hoods from test subjects, shock waves varied in whether they had higher magnitudes internally or externally (Data S1C).

In (B) and (C), the external recordings are plotted as one and the internal recordings are plotted as proportions of the corresponding external recordings.

tested our hypothesis by taking internal and external recordings of shock waves using pressure sensors with an atmospheric reference. We placed probes attached to these sensors so that they were parallel to each other and 1 cm away from the outstretched snapping claw of the shrimp we used to produce shock waves (Figure S1A). We took these recordings under two conditions: first in *A. heterochaelis* with unaltered orbital hoods and then in the same test subjects after we surgically removed their orbital hoods (Figure 3A).

The orbital hoods of *A. heterochaelis* dampen shock waves. In shrimp with unaltered orbital hoods, shock waves had lower magnitudes when recorded internally than when recorded externally. Every shock wave we recorded from shrimp with unaltered orbital hoods had a lower magnitude internally than externally. On average, orbital hoods cut the magnitudes of shock waves in half: shock waves recorded internally had magnitudes that were only 53% ± 16% (n = 10) of the magnitudes of the same shock waves recorded externally (Figure 3B; Data S1C). In these trials, shock waves recorded by the internal and external probes had magnitudes of 102 ± 114 and 211 ± 216 Pa, respectively. When we removed orbital hoods from shrimp, the magnitudes of shock waves no longer varied by recording location. In the absence of orbital hoods, shock waves recorded internally had magnitudes that were 97% ± 19% (n = 10) of the magnitudes of the same shock waves recorded externally (Figure 3C; Data S1C). In these trials, shock waves recorded by the internal and external probes had magnitudes of 43 ± 15 and 46 ± 18 Pa, respectively. Relative to external recordings, internal recordings of shock wave magnitudes were lower when shrimp had unaltered orbital hoods than after we removed their orbital hoods (Wilcoxon's signed-rank test, $Z = 2.75$, $p < 0.002$). We propose that the dampening of shock waves by orbital hoods explains the results of our behavioral experiment: following shock wave exposure, shrimp with unaltered orbital hoods behaved normally because their orbital hoods protected them, whereas shrimp from which we had removed orbital hoods demonstrated short-term effects of blast-induced neurotrauma because they lacked such protection.

Snapping shrimp experience shock waves from their own snaps

The results of our first two experiments indicate orbital hoods protect *A. heterochaelis* from shock waves produced by nearby conspecifics, an ecologically relevant scenario because *A. heterochaelis* live in dense populations in which their frequent conflicts over territories and mates often involve snapping.[18,22–25] Orbital hoods may also protect snapping shrimp from the shock waves they generate with their own claws. The ecological relevance of this is uncertain, however, because snapping shrimp may not experience shock waves from their own snaps with as much force as the targets of their snaps. Reasons for this include the magnitudes of shock waves diminishing with distance and snapping shrimp producing toroidal cavitation bubbles that may not release shock waves of similar magnitudes in all directions when they collapse.[5,8] To test how

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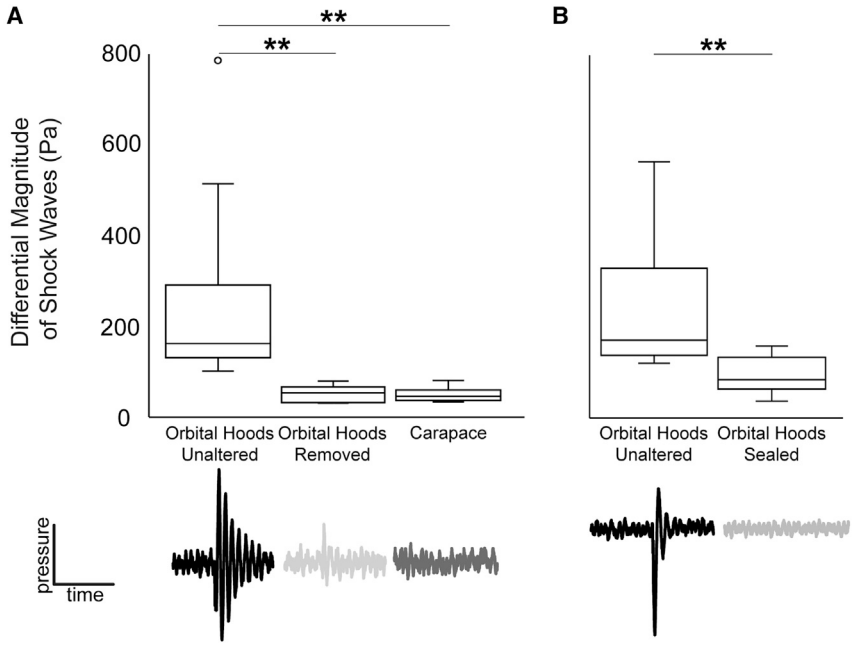

Figure 4. Structural properties of orbital hoods influence their interactions with shock waves

(A) The orbital hoods of *A. heterochaelis* alter the magnitudes of shock waves produced by conspecifics, but their carapace does not (Data S1E; Figure S1). The differential magnitudes of shock waves recorded simultaneously at internal and external locations were significantly greater when test subjects had unaltered hoods ("orbital hoods unaltered") than when they lacked orbital hoods ("orbital hoods removed") or when the internal probe was repositioned underneath the carapace ("carapace").

(B) Sealing orbital hoods diminishes how much they alter the magnitudes of shock waves (Data S1F; Figure S1). The differential magnitudes of shock waves recorded simultaneously at internal and external locations were significantly greater in test subjects when their orbital hoods were unaltered ("orbital hoods unaltered") than when the anterior openings of their orbital hoods were sealed shut ("orbital hoods sealed").

Below (A) and (B) are representative traces (1 s in duration) of the differential magnitudes of shock waves we recorded (as pressure in Pa) for each of the treatments in the two experiments. *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$.

A. heterochaelis experience shock waves from their own snaps, we used the same pressure sensors and probes from the preceding experiment. For each test subject, we placed the probe from a first pressure sensor outside and immediately above its orbital hood (about 1 cm from the tip of the snapper's snapping claw), and then placed the probe from a second pressure sensor at an ecologically relevant distance to be a target of a snap (also about 1 cm from the tip of the snapper's snapping claw) (Figure S1B). We then enticed test subjects to snap and recorded the magnitudes of shock waves at both recording positions.

The shock waves *A. heterochaelis* experience from their own snaps have magnitudes indistinguishable from those experienced by the targets of their snaps (Figure S2; Data S1D). Shock waves recorded directly above the heads of shrimp had magnitudes of 59 ± 25 Pa and the same shock waves recorded near the tips of their snapping claws had magnitudes of 50 ± 31 Pa ($n = 10$ for each recording location), a non-significant difference (paired t test, $t(9) = 2.62$, $p = 0.199$). The results from this second experiment reveal that when snapping shrimp snap, they expose themselves to shock waves powerful enough to stun or kill other crustaceans.[18–20] Orbital hoods may thus protect snapping shrimp from their own shock waves, in addition to those produced by conspecifics.

Orbital hoods alter the magnitudes of shock waves, but the carapace does not

Like all crustaceans, snapping shrimp have a hardened dorsal section of their thoracic exoskeleton termed the carapace. The orbital hoods of snapping shrimp are attached to their carapace (Figure 1C), so we asked if dampening shock waves is a specific feature of the orbital hood or a more general feature of the snapping shrimp exoskeleton. We addressed this question by taking internal and external recordings of shock waves using probes attached to the two recording ports of a differential pressure sensor. We compared the differential magnitudes of shock waves recorded simultaneously by the two probes when each test subject experienced three conditions in sequence: first, with their orbital hood unaltered; second, with their orbital hood removed; and third, with the probes re-positioned so that the internal probe was underneath the carapace rather than the orbital hood and the external probe remained parallel to it (Figure S1C). The internal probe served as the reference in all of the differential recordings.

The orbital hoods of *A. heterochaelis* alter the magnitudes of shock waves, but the carapace does not (Figure 4A; Data S1E). The differential magnitudes of shock waves recorded simultaneously by the internal and external probes were 251 ± 211 Pa when test subjects had unaltered orbital hoods, 52 ± 17 Pa after we removed orbital hoods, and 49 ± 14 Pa after we repositioned the internal probe underneath the carapace ($n = 10$ for each recording condition). The differential magnitudes of shock waves varied significantly across the three test conditions (Friedman test, $\chi^2(2) = 13.56$, $p < 0.001$). Post hoc analysis with Wilcoxon signed-rank tests indicates pressure differentials were significantly greater when test subjects had unaltered hoods than when they lacked orbital hoods ($Z = 2.75$, $p < 0.002$) or when the internal probe was underneath the carapace ($Z = 2.75$, $p < 0.002$). The differential magnitudes of shock waves did not vary significantly between test subjects when they lacked orbital hoods or when the internal probe was underneath the carapace ($Z = 0.61$, $p = 0.557$). By showing the orbital hoods of *A. heterochaelis* alter the magnitudes of shock waves, the results of this experiment support the results of our first pressure-sensing experiment. Further, we find the carapace of *A. heterochaelis* does not alter shock waves. Consequently, the orbital hoods of *A. heterochaelis* must have structural or material properties that cause them to interact with shock waves differently than other parts of the exoskeleton.

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Orbital hoods may dampen shock waves by trapping and expelling water

How do the orbital hoods of *A. heterochaelis* dampen shock waves? Orbital hoods are open at their anterior end[33] (Figure 1C) and a layer of water lies between their interior surface and the eyes beneath. We propose that when a shock wave strikes an orbital hood, the rapid changes in pressure cause the water underneath it to be expelled through the anterior opening, away from the head of the shrimp. Through the expulsion of water, some of the kinetic energy of the shock wave may be redirected and released. We tested our hypothesis by comparing the magnitudes of shock waves recorded simultaneously by internal and external probes attached to a differential pressure sensor (Figure S1A). We took recordings when test subjects experienced two conditions in sequence: first, with their orbital hood unaltered and second, with the anterior opening of their orbital hood sealed shut.

Sealing the orbital hoods of *A. heterochaelis* diminished how much they altered the magnitudes of shock waves produced by a conspecific (Figure 4B; Data S1F). In test subjects with unaltered orbital hoods, the differential magnitudes of shock waves were 232 ± 135 Pa; after we sealed the anterior openings of orbital hoods, the differential magnitudes of shock waves were 94 ± 37 Pa (n = 10 per recording condition). The differential magnitudes of shock waves were significantly greater when test subjects had unaltered orbital hoods than when their orbital hoods were sealed shut (Wilcoxon's signed-rank test, $Z = 2.75$, $p < 0.002$). From this, we learn that the anterior opening of the orbital hood is a critical component of a snapping shrimp's defense against shock waves. The mechanism of protection against shock waves in snapping shrimp may not be merely the cushioning provided by the layer of water held between the orbital hood and the eyes, but also the release of pressure by water expelled from underneath the orbital hood. When water cannot be expelled through this opening, it appears less kinetic energy from shock waves is redirected and released.

Conclusion: A biological armor system that protects brains from shock waves

The orbital hoods of *A. heterochaelis* are the first biological armor system shown to dampen shock waves and in doing so protect an animal from negative short-term behavioral consequences of blast-induced neurotrauma. Species of snapping shrimp have orbital hoods that vary in shape and the degree to which they cover the underlying eyes.[26] By comparing the morphologies of orbital hoods to their abilities to dampen shock waves, we will learn more about the function and evolution of these structures. We are also interested in the co-evolution of weapons and armor in snapping shrimp. Like their orbital hoods, the snapping claws of alpheids vary in size and shape, and it has been suggested that some species may be able to generate more powerful snaps than others.[34] Do snapping shrimp species that produce more powerful shock waves tend to have orbital hoods that provide greater protection against shock waves? Or could other factors (e.g., territoriality and frequency of interspecific conflict) influence how effectively the orbital hoods of different species protect against blast-induced neurotrauma?

Learning more about the structure and function of orbital hoods may help us design helmets that better protect the heads of humans from blast-induced neurotrauma. Shock waves, such as those produced by explosions, are a persistent and widespread threat to human health. Compared to other types of soft tissue, neural tissues appear to be particularly vulnerable to short- and long-term damage from shock wave exposure. Even when they are not deadly, shock waves can cause long-term harm such as neural degeneration and persistent cognitive deficits.[14,15,35,36] Preventing blast-induced neurotrauma in humans has been challenging, in part because we have yet to design and deploy helmets that effectively prevent the transfer of energy from shock waves to neural tissues.[2,37] Our results indicate orbital hoods redirect and release kinetic energy from shock waves by expelling water through their anterior openings. The redirection of kinetic energy from shock waves via the release of hydraulic energy has been explored as a method for constructing armor systems that dampen shock waves.[38] In these human-engineered armor systems, water inside capped tubes absorbs kinetic energy from shock waves and then redirects and releases this energy by dislodging the caps and exploding out of the tubes.[38] The parallels between orbital hoods and experimental, water-based armor systems suggest that discoveries related to shock wave mitigation in snapping shrimp may be applicable to future efforts at designing armor systems that protect humans from shock waves.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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  - Data and code availability
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- METHOD DETAILS
  - Equipment and procedures for behavioral trials
  - Equipment and procedures for pressure-sensing experiments
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.06.042.

A video abstract is available at https://doi.org/10.1016/j.cub.2022.06.042#mmc10.

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AUTHOR CONTRIBUTIONS

Conceptualization, A.C.N.K. and D.I.S.; methodology, validation, formal analysis, resources, data curation, writing – original draft, writing – review & editing, and funding acquisition, A.C.N.K., D.I.S., S.A.W., and D.S.W.; investigation, A.C.N.K. and D.I.S.; visualization, A.C.N.K. and D.I.S.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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REFERENCES

1. Ling, G., Bandak, F., Armonda, R., Grant, G., and Ecklund, J. (2009). Explosive blast neurotrauma. J. Neurotrauma *26*, 815–825. https://doi.org/10.1089/neu.2007.0484.
2. Phillips, Y.Y., and Richmond, D.R. (1991). Primary blast injury and basic research: a brief history. In Conventional Warfare: Ballistic, Blast, and Burn Injuries, R.F. Bellamy, and R. Zajtchuk, eds. (Office of the Surgeon General of the US Army), pp. 221–240.
3. Finkel, M.F. (2006). The neurological consequences of explosives. J. Neurol. Sci. *249*, 63–67. https://doi.org/10.1016/j.jns.2006.06.005.
4. DePalma, R.G., Burris, D.G., Champion, H.R., and Hodgson, M.J. (2005). Blast injuries. N. Engl. J. Med. *352*, 1335–1342. https://doi.org/10.1056/NEJMra042083.
5. Versluis, M., Schmitz, B., von der Heydt, A., and Lohse, D. (2000). How snapping shrimp snap: through cavitating bubbles. Science *289*, 2114–2117. https://doi.org/10.1126/science.289.5487.2114.
6. Lohse, D., Schmitz, B., and Versluis, M. (2001). Snapping shrimp make flashing bubbles. Nature *413*, 477–478. https://doi.org/10.1038/35097152.
7. Kaji, T., Anker, A., Wirkner, C.S., and Palmer, A.R. (2019). Parallel saltational evolution of ultrafast movements in snapping shrimp claws. Curr. Biol. *28*, 106–113.e4. https://doi.org/10.1016/j.cub.2017.11.044.
8. Koukouvinis, P., Bruecker, C., and Gavaises, M. (2017). Unveiling the physical mechanism behind pistol shrimp cavitation. Sci. Rep. *7*, 13994. https://doi.org/10.1038/s41598-017-14312-0.
9. Clemedson, C.-J. (1956). Blast injury. Physiol. Rev. *36*, 336–354. https://doi.org/10.1152/physrev.1956.36.3.336.
10. Cernak, I. (2015). Blast injuries and blast-induced neurotrauma: overview of pathophysiology and experimental knowledge models and findings. In Brain Neurotrauma: Molecular, Neurophysiological, and Rehabilitation Aspects, F.H. Kobeissy, ed. (CRC Press/Taylor & Francis).
11. Beamer, M., Tummala, S.R., Gullotti, D., Kopil, C., Gorka, S., Abel, T., Bass, C.R.D., Morrison, B., Cohen, A.S., and Meaney, D.F. (2016). Primary blast injury causes cognitive impairments and hippocampal circuit alterations. Exp. Neurol. *283*, 16–28. https://doi.org/10.1016/j.expneurol.2016.05.025.
12. Cernak, I., Wang, Z., Jiang, J., Bian, X., and Savic, J. (2001). Ultrastructural and functional characteristics of blast injury-induced neurotrauma. J. Trauma Inj. Infect. Crit. Care *50*, 695–706. https://doi.org/10.1097/00005373-200104000-00017.
13. Koliatsos, V.E., Cernak, I., Xu, L., Song, Y., Savonenko, A., Crain, B.J., Eberhart, C.G., Frangakis, C.E., Melnikova, T., Kim, H., and Lee, D. (2011). A mouse model of blast injury to brain: Initial pathological, neuropathological, and behavioral characterization. J. Neuropathol. Exp. Neurol. *70*, 399–416. https://doi.org/10.1097/NEN.0b013e3182189f06.
14. Appelboom, G., Han, J., Bruce, S., Szpalski, C., and Connolly, E.S. (2012). Clinical relevance of blast-related traumatic brain injury. Acta Neurochir. *154*, 131–134. https://doi.org/10.1007/s00701-011-1210-3.
15. Eierud, C., Nathan, D.E., Bonavia, G.H., Ollinger, J., and Riedy, G. (2019). Cortical thinning in military blast compared to non-blast persistent mild traumatic brain injuries. Neuroimage Clin. *22*, 101793. https://doi.org/10.1016/j.nicl.2019.101793.
16. Mac Donald, C.L., Johnson, A.M., Cooper, D., Nelson, E.C., Werner, N.J., Shimony, J.S., Snyder, A.Z., Raichle, M.E., Witherow, J.R., Fang, R., et al. (2011). Detection of blast-related traumatic brain injury in U.S. military personnel. N. Engl. J. Med. *364*, 2091–2100. https://doi.org/10.1056/NEJMoa1008069.
17. Mishra, V., Skotak, M., Schuetz, H., Heller, A., Haorah, J., and Chandra, N. (2016). Primary blast causes mild, moderate, severe and lethal TBI with increasing blast overpressures: experimental rat injury model. Sci. Rep. *6*, 26992. https://doi.org/10.1038/srep26992.
18. MacGinitie, G.E., and MacGinitie, N. (1949). Natural History of Marine Animals (McGraw-Hill), pp. 276–279.
19. MacGinitie, G.E. (1937). Notes on the natural history of several marine crustacea. Am. Midl. Nat. *18*, 1031. https://doi.org/10.2307/2420601.
20. Herberholz, J., and Schmitz, B. (1999). Flow visualisation and high speed video analysis of water jets in the snapping shrimp (*Alpheus heterochaelis*). J. Comp. Physiol. *185*, 41–49. https://doi.org/10.1007/s003590050364.
21. Mathews, L.M. (2002). Territorial cooperation and social monogamy: factors affecting intersexual behaviours in pair-living snapping shrimp. Anim. Behav. *63*, 767–777. https://doi.org/10.1006/anbe.2001.1976.
22. Nolan, B.A., and Salmon, M. (1970). The behavior and ecology of snapping shrimp (Crustacea: *Alpheus heterochelis* and *Alpheus normanni*). Forma Functio *2*, 289–335.
23. Schein, H. (1977). The role of snapping in *Alpheus heterochaelis* Say, 1818, the big-clawed snapping shrimp. Crustaceana *33*, 182–188. https://doi.org/10.1163/156854077x00089.
24. Hughes, M. (1996). The function of concurrent signals: visual and chemical communication in snapping shrimp. Anim. Behav. *52*, 247–257. https://doi.org/10.1006/anbe.1996.0170.
25. Schmitz, B., and Herberholz, J. (1998). Snapping behavior in intraspecific agonistic encounters in the snapping shrimp (*Alpheus heterochaelis*). J. Biosci. *23*, 623–632. https://doi.org/10.1007/BF02709175.
26. Anker, A., Ahyong, S.T., Noel, P.Y., and Palmer, A.R. (2006). Morphological phylogeny of alpheid shrimps: parallel preadaptation and the origin of a key morphological innovation, the snapping claw. Evolution *60*, 2507–2528. https://doi.org/10.1111/j.0014-3820.2006.tb01886.x.
27. Monczak, A., Mueller, C., Miller, M.E., Ji, Y., Borgianini, S.A., and Montie, E.W. (2019). Sound patterns of snapping shrimp, fish, and dolphins in an estuarine soundscape of the southeastern USA. Mar. Ecol. Prog. Ser. *609*, 49–68. https://doi.org/10.3354/meps12813.
28. Mishra, V., Skotak, M., Schuetz, H., Heller, A., Haorah, J., and Chandra, N. (2016). The curious acoustic behavior of estuarine snapping shrimp: temporal patterns of snapping shrimp sound in sub-tidal oyster reef habitat. PLoS One *6*, 26992. https://doi.org/10.1038/srep26992.
29. Lillis, A., and Mooney, T.A. (2018). Snapping shrimp sound production patterns on Caribbean coral reefs: relationships with celestial cycles and environmental variables. Coral Reefs *37*, 597–607. https://doi.org/10.1007/s00338-018-1684-z.
30. Knowlton, R.E., and Moulton, J.M. (1963). Sound production in the snapping shrimps *Alpheus* (Crangon) and *Synalpheus*. Biol. Bull. *125*, 311–331. https://doi.org/10.2307/1539406.
31. Atkinson, R.J.A., and Eastman, L.B. (2015). Burrow dwelling in Crustacea. In The Natural History of the Crustacea: Lifestyles and Feeding Biology, M. Thiel, and L. Watling, eds. (Oxford University Press), pp. 78–117.
32. Champion, H.R., Holcomb, J.B., and Young, L.A. (2009). Injuries from explosions: physics, biophysics, pathology, and required research focus. J. Trauma *66*, 1468–1477. https://doi.org/10.1097/TA.0b013e3181a27e7f.

33. Kingston, A.C.N., Lucia, R.L., Havens, L.T., Cronin, T.W., and Speiser, D.I. (2019). Vision in the snapping shrimp *Alpheus heterochaelis*. J. Exp. Biol. *222*, jeb209015. https://doi.org/10.1242/jeb.209015.

34. Hazlett, B.A., and Winn, H.E. (1962). Sound production and associated behavior of Bermuda crustaceans (*Panulirus*, *Gonodactylus*, *Alpheus*, and *Synalpheus*). Crustaceana *4*, 25–38. https://doi.org/10.1163/156854062x00030.

35. Arun, P., Wilder, D.M., Eken, O., Urioste, R., Batuure, A., Sajja, S., Van Albert, S., Wang, Y., Gist, I.D., and Long, J.B. (2020). Long-term effects of blast exposure: a functional study in rats using an advanced blast simulator. J. Neurotrauma *37*, 647–655. https://doi.org/10.1089/neu.2019.6591.

36. Sponheim, S.R., McGuire, K.A., Kang, S.S., Davenport, N.D., Aviyente, S., Bernat, E.M., and Lim, K.O. (2011). Evidence of disrupted functional connectivity in the brain after combat-related blast injury. Neuroimage *54*, S21–S29. https://doi.org/10.1016/j.neuroimage.2010.09.007.

37. Wightman, J.M., and Gladish, S.L. (2001). Explosions and blast injuries. Ann. Emerg. Med. *37*, 664–678. https://doi.org/10.1067/mem.2001.114906.

38. Chen, Y., Huang, W., and Constantini, S. (2012). Blast shock wave mitigation using the hydraulic energy redirection and release technology. PLoS One *7*, e39353. https://doi.org/10.1371/journal.pone.0039353.

39. Heuring, W.L., and Hughes, M. (2019). It takes two: seasonal variation in sexually dimorphic weaponry results from divergent changes in males and females. Ecol. Evol. *9*, 5433–5439. https://doi.org/10.1002/ece3.5136.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data: Shelter-seeking behavior	This paper	Data S1A
Data: Time-to-right behavior	This paper	Data S1B
Data: Hood off pressure-sensing	This paper	Data S1C
Data: Target vs self pressure-sensing	This paper	Data S1D
Data: Carapace pressure-sensing	This paper	Data S1E
Data: Hood glued pressure-sensing	This paper	Data S1F
Experimental models: Organisms/strains		
Bigclaw Snapping shrimp (*Alpheus heterochaelis)*	Georgetown, SC	N/A
Software and algorithms		
R-project	R Core Team	https://www.r-project.org/
Signal Express	National Instruments	https://www.ni.com/en-us/support/downloads/software-products/download.signalexpress.html#322415

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Alexandra Kingston (alex-kingston@utulsa.edu).

Materials availability

This study did not generate new unique reagents.

Data and code availability

Data have been deposited in the supplemental information and details are listed in the key resources table. Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We collected *A. heterochaelis* from two locations in North Inlet Estuary (Georgetown, SC USA) that are about one mile apart: Clambank Creek (33°20.05'N 79°11.6'W) and Oyster Landing (33°21.1'N 79°11.2'W). We transported animals to the University of South Carolina (Columbia, SC, USA), where we held them individually in natural seawater (NSW) at room temperature (~22°C) and a salinity of 35 ppt. We fed animals shrimp pellets twice per week.

METHOD DETAILS

Equipment and procedures for behavioral trials

We used behavioral trials to ask if orbital hoods protect snapping shrimp from two short-term effects of blast-induced neurotrauma: disorientation and loss of motor control. We used shelter-seeking behaviors for these trials because *A. heterochaelis* dwell in burrows and, like many other snapping shrimp,[31] seek burrows when they are in unfamiliar surroundings (Videos S1, S2, S3, S4, S5, and S6). We constructed artificial burrows for *A. heterochaelis* from pieces of PVC pipe (with internal diameters of 1.5 cm and lengths of 5 cm) closed at one end with a round piece of black felt. We housed shrimp individually and allowed them to acclimate to their artificial burrows for a minimum of 48 hours. All shrimp began spending time in their artificial burrows within 24 hrs.

We used four treatment groups of 30 specimens each: (1) Unarmored Experimental (UE) – shrimp without orbital hoods that we exposed to shock waves produced by a conspecific; (2) Armored Experimental (AE) – shrimp with unaltered orbital hoods that we exposed to shock waves produced by a conspecific; (3) Unarmored Control (UC) – shrimp without orbital hoods that we did not expose to shock waves; and (4) Armored Control (AC) – shrimp with unaltered orbital hoods that we did not expose to shock waves. We used fine surgical tools to remove orbital hoods from specimens in the UE and UC groups (Figure 2C). We performed sham

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surgeries on specimens in the AE and AC groups (Figure 2D). In these sham procedures, we handled test subjects as we did during surgical procedures but did not remove their orbital hoods. These procedures included wrapping each animal in Parafilm (Bemis Company, Neenah, WI, USA), placing it under a brightly lit dissecting microscope, rotating it for ~ 3 minutes, and gently touching forceps to its orbital hood. After surgeries and sham surgeries, we allowed animals to recover for 24 hours.

The four treatment groups did not differ significantly in sex ratio or in the mean size of individuals. We estimated sex ratios by scoring as female any shrimp with embryos on their pleopods or developing eggs underneath their dorsal carapace. These indicators should reliably distinguish females from males because we conducted this experiment in the middle of the *A. heterochaelis* reproductive season.[39] Outside of these indicators, *A. heterochaelis* do not have obvious sexual dimorphisms: males and females appear to have similar ranges of both body and claw size. The sexes included in each treatment group were as follows: UE 13 f/17 m; AE 15 f/15 m; UC 15 f/15 m; AC 15 f/15 m. We measured the size of each individual from the tip of its rostrum to the end of its telson. Mean and standard deviation for body size for each treatment group were as follows: UE 2.2 ± 0.2 cm; AE 2.2 ± 0.3 cm; UC 2.2 ± 0.3 cm; and AC 2.2 ± 0.3 cm. We found no significant difference in body size among the groups (one-way ANOVA, $F(3, 116) = 0.575$, $p = 0.633$).

Our behavioral arena consisted of a clear acrylic tank (27.5 cm L x 17 cm W x 16.5 cm D) placed inside a white styrofoam box, housed inside a frame draped in a double layer of black felt. We lit the behavioral arena from above using a single, centrally-mounted Aqua Illumination Prime HD LED fixture (C2 Development, Ames, IA, USA; output 400–700 nm) whose broad-spectrum light we diffused with two filters mounted in series (3000 Tough Rolux and 3027 Half Tough White Diffusion; Rosco Laboratories, Stamford, CT, USA). We recorded the behavioral trials using a GoPro Hero 6 (GoPro, San Mateo, CA, USA).

To begin each shelter-seeking trial, we exposed test subjects to shock waves produced by a conspecific or exposed test subjects to a conspecific that did not produce shock waves. To expose test subjects in the UE and AE groups to shock waves, we held them 1 cm away from the fully extended claw of a conspecific and then enticed the conspecific to snap three times near the test subject's head. We used this distance because shrimp produce cavitation bubbles within 1 cm of the heads of their targets during agonistic interactions.[18] As a sham procedure, we held test subjects in the UC and AC groups in front of a conspecific in a similar fashion to specimens in the UE and AE groups, but we did not entice the conspecific to snap. We used multiple snappers for our behavioral experiment because the claws of snappers appear to be damaged by frequent and rapid snapping. Given the design of our behavioral experiment, each snapper snapped or was presented to a similar number of individuals from the four treatment groups.

After exposing a test subject to a conspecific, we placed its artificial burrow at one end of the rectangular behavioral arena. We then placed the test subject at the opposite end of the behavioral arena and held it under a glass dish for 15 s before releasing it. To account for directional bias, we alternated at which ends of the arena we placed the artificial burrow and the test subject. To prevent shrimp from detecting chemosensory cues from other shrimp, we wiped down the surfaces of the acrylic tank and replaced the seawater between trials. From video recordings (Videos S1, S2, S3, S4, S5, and S6), we measured how long it took shrimp to contact their artificial burrows following their release (Data S1A) and how long it took for shrimp to achieve an upright walking or swimming position (Data S1B). Trials lasted for 300 s. If a shrimp failed to contact its burrow during the trial, we assigned a time-to-contact of 300 s. Following a Shapiro-Wilk test for normality, we used a Kruskal-Wallis test to determine if there was a significant difference in how long shrimp from the four treatments took to contact their artificial burrows. We then made pairwise comparisons between treatments using Dunn's test with Bonferroni correction. Following a Shapiro-Wilk test for normality, we applied Mood's median test to determine if there was a significant difference in how long it took animals to achieve an upright position. We then made pairwise comparisons between treatments using pairwise Mood's median tests.

Equipment and procedures for pressure-sensing experiments

To measure the magnitudes of shock waves from the snaps of *A. heterochaelis*, we used a pressure-sensing system that included an INA125 power amplifier board (Texas Instruments/Burr Brown, Dallas, TX, USA) and a USB-6215 data acquisition device (National Instruments, Austin, TX, USA) operated using Signal Express software (National Instruments). We used two types of 26PC Series miniature pressure sensors (Honeywell, Charlotte, NC, USA), both encased in waterproof rubber. The first type of pressure sensor (26PCAFA6G) had one recording port and one reference port (hereafter termed "single-port pressure sensors"). These single-port pressure sensors provide voltage proportional to the difference in pressure between their recording and reference ports. The second type of pressure sensor (26PCAFA6D) had two recording ports (hereafter termed "differential pressure sensors"). These differential pressure sensors provide the absolute difference of the voltages reported by their two recording ports.

The single-port and differential pressure sensors both have response times of 1 ms. We acquired pressure recordings at a rate of 20 kHz for both types of sensors. Shock waves produced by the claws of snapping shrimp have an approximate duration of 0.05 ms.[5] The shock waves we recorded from *A. heterochaelis* appear to have lower magnitudes than those recorded previously[5] because the durations of these shock waves were briefer than the response times of the sensors we used in our experiments.

As probes, we used 5 cm of stainless steel intramedic tubing attached to the ports of the pressure sensors by 60 cm of flexible polyethylene intramedic tubing filled with bubble-free water with the same salinity and temperature as the aquarium water. We quantified the magnitudes of shock waves as the differences between their peak overpressures and peak underpressures. We calibrated pressure sensors to convert our recordings from millivolts (mV) to pascals (Pa). With the probes in the water, we raised and lowered the sensors outside of the tank to relate mV readings to centimeters of water, which we then converted to Pa. In our trials, we generated shock waves by enticing specimens of *A. heterochaelis* to snap by gently brushing their snapping claw with a paintbrush.[5] Within each experiment, we used the same snapper for every trial. The magnitudes of shock waves produced by snapping shrimp varied within and between individuals.

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In our first pressure-sensing experiment, we tested if orbital hoods dampen shock waves. To do so, we placed the recording probe from a single-port pressure sensor (hereafter the ''internal probe'') underneath a test subject's orbital hood near its brain. We positioned the internal probe by feeding the steel intramedic tubing through the test subject's posterior cephalothorax from its thoracic-abdominal divide (Figure S1A). We then placed the recording probe from a second single-port pressure sensor (hereafter the ''external probe'') just above the test subject's orbital hood and held it there by gluing the steel intramedic tubing to the carapace. We placed the internal and external probes so that they were parallel to each other and equidistant from the point of origin of shock waves. We positioned each test subject (the target) 1 cm away from the fully extended claw of a conspecific (the snapper) by attaching both animals to a metal frame using neodymium magnets (Figure S1A). In our first treatment, we recorded shock waves experienced by ten targets with unaltered orbital hoods. In our second treatment, we removed the orbital hoods of these test subjects with fine surgical tools without disturbing the placement of the probes and again recorded shock waves produced by a conspecific. We recorded three shock waves for each of ten test subjects under both test conditions and compared the mean values per individual for a total of ten independent values per recording location per treatment (Data S1C). Following a Shapiro-Wilk test for normality, we used a Wilcoxon's signed rank test to compare between the two treatments.

In our second pressure-sensing experiment, we compared how the targets of the snaps of *A. heterochaelis* experience shock waves to how these shrimp experience shock waves from their own snaps. To do so, we placed the recording probe from a single-port pressure sensor 1 cm away from the tip of a shrimp's fully extended snapping claw. We then placed the recording probe from a second single-port pressure sensor directly above the same shrimp's head, approximately 1 cm away from the tip of its extended snapping claw (Figure S1B). We positioned test subjects by using neodymium magnets to attach them to a metal frame. We recorded five shock waves for each of ten test subjects and compared mean values per individual for a total of ten independent values per recording location (Data S1D). Following a Shapiro-Wilk test for normality, we used a paired sample t test to compare the magnitudes of shock waves at the two recording locations.

In our third pressure-sensing experiment we asked if orbital hoods interact with shock waves differently than other parts of the exoskeleton. Following procedures similar to those described above for our first pressure-sensing experiment, we placed the two recording probes from a differential pressure sensor so that one functioned as the internal probe and the other functioned as the external probe. In all trials, we placed the internal and external probes so that they were parallel to each other and equidistant from the point of origin of shock waves. We positioned each test subject (the target) 1 cm away from the fully extended claw of a conspecific (the snapper) by attaching both animals to a metal frame using neodymium magnets. We recorded shock waves experienced by ten targets under three different test conditions. Each target experienced the test conditions in the same order. First, we recorded shock waves when targets had unaltered orbital hoods (Figure S1A). Second, we removed the orbital hoods from the targets and again recorded shock waves with the internal and external probes in the same positions as before (Figure S1A). Third, we re-positioned the internal probe to be underneath the carapace, near the gills, and re-positioned the external probe so that it remained parallel to the internal probe (Figure S1C). We then re-positioned the target so that both probes faced the snapper and once again recorded shock waves. We recorded three shock waves for each test subject under each condition and compared mean values per individual for a total of ten independent values per condition (Data S1E). Following a Shapiro-Wilk test for normality, we used a Friedman test to compare the differential magnitudes of shock waves among the three test conditions and then used Wilcoxon's signed-rank tests to perform two-way comparisons between results from the three test conditions.

The orbital hoods of snapping shrimp are open to the environment at their anterior end (Figure 1C) and in our fourth pressure-sensing experiment we tested if this feature influences how they interact with shock waves. Following procedures described above for our first and third pressure-sensing experiments, we placed the two probes from a differential pressure sensor so that one functioned as the internal probe and the other functioned as the external probe. In all trials, we placed the two probes so that they were parallel to each other and equidistant from the point of origin of shock waves. We positioned each test subject (the target) 1 cm away from the fully extended claw of a conspecific (the snapper) by attaching both animals to a metal frame using neodymium magnets (Figure S1A). We recorded shock waves experienced by targets under two different test conditions; first, with their orbital hoods unaltered; and second, after we sealed the anterior opening of their orbital hoods with liquid Superglue (Loctite, Connecticut, USA). We recorded three shock waves for each of ten test subjects under each condition and compared mean values per individual for a total of ten independent values per condition (Data S1F). Following a Shapiro-Wilk test for normality, we used a Wilcoxon's signed rank test to compare the differential magnitudes of shock waves between the two test conditions.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical tests were performed using R (1.2.5001; https://www.r-project.org/) or Microsoft Excel. Statistical tests used and number of individuals per treatment are indicated in the main text and STAR Methods.

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Supplemental Information

Snapping shrimp have helmets that protect their brains by dampening shock waves

Alexandra C.N. Kingston, Sarah A. Woodin, David S. Wethey, and Daniel I. Speiser

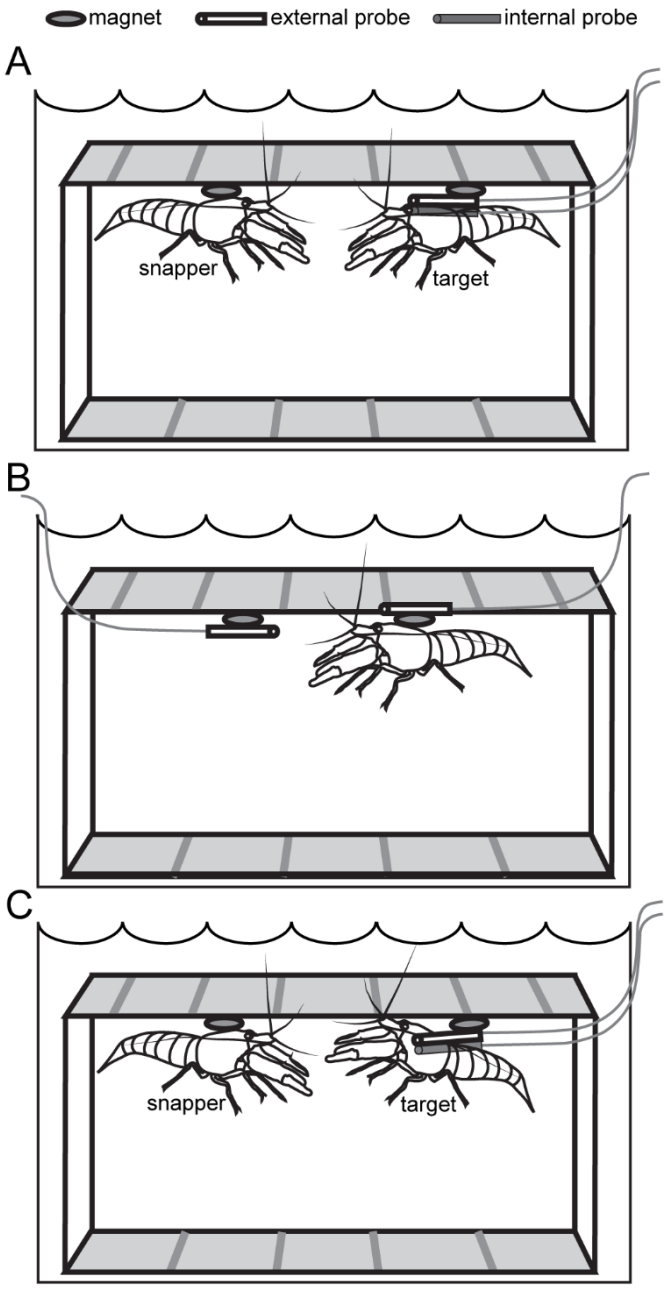

Figure S1. Setups for pressure-sensing experiments with *Alpheus heterochaelis*. Related to Figure 3, Figure 4, and STAR Methods.
(A) Testing if the orbital hoods of snapping shrimp influence the magnitudes of shock waves. Pressure-sensing probes placed beneath (gray) and directly above (white) the orbital hood of a shrimp recorded shock waves produced by a conspecific.
(B) Testing if snapping shrimp experience shock waves from their own snaps by recording pressure at two external locations: 1 cm from the tip of the shrimp's fully extended snapping claw and directly above the same shrimp's head.
(C) Testing if the carapace of snapping shrimp alters the magnitudes of shock waves by positioning pressure-sensing probes beneath (gray) and directly outside (white) the lateral carapace.

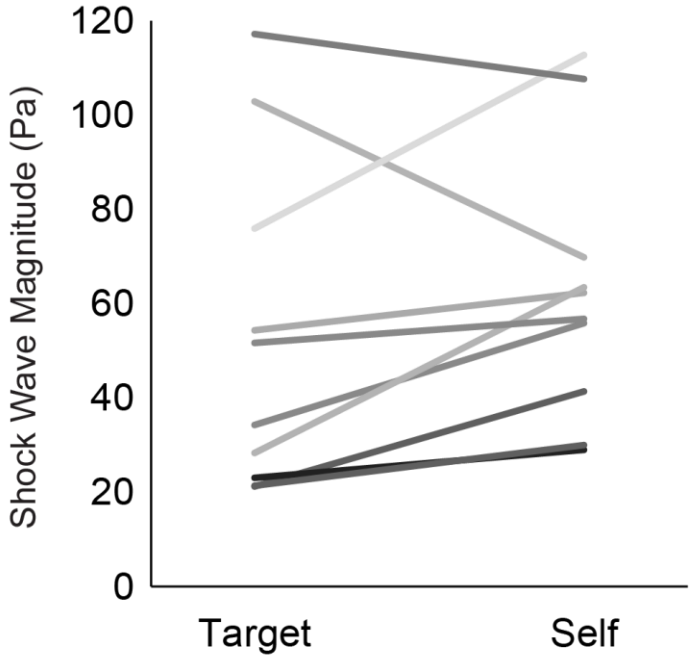

Figure S2. Shock waves produced by *A. heterochaelis* recorded at two locations. Related to Figure 3, Figure 4, and Data S1D.

The shock waves *A. heterochaelis* experience from their own snaps (Self) are indistinguishable in magnitude (paired *t*-test, $t(9) = 2.62$, $p = 0.199$) from those experienced by the targets of their snaps (Target). Each line represents recordings for one individual (with five snaps recorded and averaged at each location).