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RESEARCH PAPER

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Giant clams discriminate threats along a risk gradient and display varying habituation rates to different stimuli

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Abstract

It is often beneficial for animals to discriminate between different threats and to habituate to repeated exposures of benign stimuli. While much is known about risk perception in vertebrates and some invertebrates, risk perception in marine invertebrates is less extensively studied. One method to study risk perception is to habituate animals to a series of exposures to one stimulus, and then present a novel stimulus to test if it transfers habituation. Transfer of habituation is seen as a continued decrease in response while lack of transfer is seen either by having a similar or greater magnitude response. We asked whether giant clams (*Tridacna maxima*) discriminate between biologically relevant types of threats along a risk gradient. Giant clams retract their mantle and close their shell upon detecting a threat. While closed, they neither feed nor photosynthesize, and prior work has shown that the cost of being closed increases as the duration of their response increases. We recorded a clam's latency to emerge after simulated threats chosen to represent a risk gradient: exposure to a small shading event, a medium shading event, a large shading event (chosen to simulate fish swimming above them), tapping on their shell and touching their mantle (chosen to simulate different degrees of direct attack). Although these stimuli are initially perceived as threatening, we expected clams to habituate to them because they are ultimately non-damaging and it would be costly for clams to remain closed for extended periods of time when there is no threat present. Clams had different initial latencies to emerge and different habituation rates to these treatments, and they did not transfer habituation to higher risk stimuli and to some lower risk stimuli. These results suggest that clams discriminated between these stimuli along a risk gradient and the lack of habituation transfer shows that the new stimulus was perceived as a potential threat. This study demonstrates that sessile bivalves can discern between levels of predatory threat. These photosynthetic clams may benefit from being able to categorize predator cues for efficient energy allocation.

KEYWORDS

habituation, non-consumptive predator effects, plastic defences, predator classification, threat discrimination, *Tridacna maxima*

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1 | INTRODUCTION

Animals encounter threatening stimuli that may be associated with their likelihood of survival, but not all potential threats are equivalent. We expect selection on individuals to accurately evaluate the relative risks associated with different potential threatening stimuli, allowing them to effectively allocate and trade-off resource acquisition against security (Lima & Dill, 1990). Efficient risk assessment requires the differentiation and classification of predatory threats, which may vary along a continuum (Helfman, 1989) or may be qualitatively different (Seyfarth, Cheney, & Marler, 1980; Weightman & Arsenault, 2002).

Virtually all animals (Groves & Thompson, 1970; Rankin et al., 2009) and some plants (Meins & Lutz, 1980; Reed-Guy, Gehris, Shi, & Blumstein, 2017) may habituate to repeated exposures of a non-threatening stimulus. When habituated, further exposures to the same non-threatening stimulus will not lead to a response. By contrast, exposure to a novel stimulus following habituation should lead to a response of similar intensity seen prior to habituation (e.g. Cheney & Seyfarth, 1990). Transfer of habituation from a non-threatening stimulus to a potentially threatening stimulus could be a maladaptive response that could put the individual at risk.

Habituation itself is well studied in many organisms, but less is known about how it functions in nature (Blumstein, 2016). For instance, the physiological mechanisms underlying habituation are extensively studied in California sea hares (*Aplysia californica*) (Bailey & Chen, 1983; Glanzman, 2008). Notably, different threatening stimuli are perceived similarly; sea hares transfer habituation between two types of disturbances—gill and syphon shocks (Goldberg & Lukowiak, 1982). Like many laboratory studies of habituation, stimuli such as shocks are chosen for control and convenience, not biological relevance. Studying habituation in natural conditions, with more natural stimuli, regardless of the taxa, will enhance our understanding of the mechanisms of risk assessment.

Some studies have used biologically relevant stimuli in molluscs to study risk classification. For instance, longfin squid (*Doryteuthis pealeii*) have a variety of antipredator responses to a gradient of sound amplitudes and frequencies that represent different predatory threats (Mooney, Samson, Schlunk, & Zacarias, 2016). Similar studies were conducted in cuttlefish (*Sepia officinalis*) (Samson, Mooney, Gussekloo, & Hanlon, 2014). However, cephalopods are celebrated for their cognitive complexity (Darmaillacq, Jozet-Alves, Bellanger, & Dickel, 2014).

Scallops, a free-living bivalve, also have been reported to have complex predator sensing and escape behaviour (Hutson, Ross, Day, & Ahern, 2005), especially in response to predators with which they share and an evolutionary history (Brokordt, Nunez, & Gaymer, 2011). Blue mussels (*Mytilus edulis*), a more sessile bivalve, possess inducible defences in the presence of predators (Commito, Gownaris, Haulsee, Coleman, & Beal, 2016; Côté & Jelnikar, 1999), and can trigger different responses, which are specific for the attack strategies of different predatory species (Freeman, 2007). Oysters (*Crassostrea virginica*) can detect chemical cues from both predators and injured conspecifics, and grow stronger shells as a result (Scherer, Lunt, Draper, & Smee, 2016). However, this response is enhanced following encounter with predatory cues. Hard clams (*Mercenaria mercenaria*) reduce feeding time and close their shells as an adaptive response to predators (Smee & Weissburg, 2006). Furthermore, some soft-shell clams (*Mya arenaria*) modify their behaviour upon detecting a predator to increase their chances of survival (Flynn & Smee, 2010). Thus, many marine molluscs benefit from having some ability to respond to predators. But how predator-specific can these responses be?

To expand our understanding of threat classification in molluscs, and particularly bivalves, we focused on giant clams (*Tridacna maxima*). Giant clams have pinhole eyes that sense changes in shade (Land, 2002). Giant clams have a simple antipredator response: they retract their mantle and close their shell. However, this is a complex, adaptive response that varies by individual and according to the cost of remaining closed (Johnson, Karajah, Mayo, Armenta, & Blumstein, 2017). By closing their shell and retracting their mantle, giant clams are unable to feed or allow their symbiotic algae to photosynthesize (Soo & Todd, 2014). Johnson et al. (2017) showed that habituation to repeated tapping minimizes the cost of responding to what ultimately was a non-threatening situation. However, in nature, giant clams experience a variety of predator cues and it is not known whether giant clams are able to respond differently to different stimuli. We hypothesize such an ability is advantageous in that individuals could match their response (remaining closed) to the magnitude of threat and remain closed longer for more threatening stimuli. Neo, Eckman, Vicentuan, Teo, and Todd (2015) described different predator cues giant clams encounter, which we simulated with three types of stimuli: shading, shell tapping and mantle touching. Different shade sizes were used to represent different-sized fish swimming over the clam (or a fish at different distances from the clam), taps on the clam's external shell simulated attacks from crabs and sea snails, and touching the clam's mantle mimicked attacks on their soft body parts. We classified the shade stimuli as mildly aversive, tap stimulus as moderately aversive, and mantle touch stimulus as highly aversive because they represented threats at different proximities to the clam's edible mantle.

We habituated individual clams to a simulated predatory stimulus to determine whether they were able to discriminate this stimulus from a different simulated predatory stimulus. If an individual failed to transfer habituation between two stimuli, we could infer that the two stimuli were differentially perceived and classified. Additionally, if the individual consistently responded more to a higher risk stimulus, we can infer that the individual assessed threats along a risk gradient (see Amano, Kitamura, & Hosono, 1999; Mooney et al., 2016). We investigated clam response to a gradient of stimuli to determine whether: (a) clams transfer habituation between categories of stimuli (shade, touch); (b) clams transfer habituation between intensities of stimuli in the same category (shade); and (c) clams habituate to the most risk-intense stimuli (mantle touch).

2 | METHODS

We conducted five experiments between 20 January and 7 February 2018 at Gump Reef, Cook's Bay (17°29025.0″S, 149°49033.1″W) and in between Motu Fareone and Motu Tiahura Islands (17°29021.0″S, 149°54056.3″W) in Mo'orea, French Polynesia. Giant clams were abundant at our two marine protected area study sites. We habituated clams with varying levels of simulated predatory threats and then exposed them to a different type of simulated threat to evaluate whether they classified risks along a biologically relevant gradient. Each experiment tested pairs of five stimuli: small shade, medium shade, large shade, tap and mantle touch. Although the relative intensities of the stimuli were originally assumptions, we confirmed the relative intensities with our initial latency to emerge times. We attached a modified garden rake head covered with tape to a 2 m stick to create a large object that would shade the clam (the 610 cm^2 triangular rake end with the tines removed and covered with duct tape to create a flat triangle) and attached a smaller 36 cm^2 duct-taped rectangle to create the medium shade. The unmodified, 10 cm^2 stick end served as the small shade. We used the non-shade end of the plastic stick to gently tap clam shells from 1 to 2 m away, and we used our fingers to touch the mantle. We practiced our tapping and shading techniques on land and in the water so that tap force would be approximately constant across observers and that shade presentation was constant (25 cm above the clam, pushed 1 m/s through the water, which shaded the clam for about 2 seconds). All observations were conducted while snorkelling in relatively shallow water during periods of time when there was little to no rain and wind was ≤3 on the Beaufort scale. Cloud cover varied during our experiments. Adding cloud cover as a covariate to our formal models did not explain significant variation in response and hence was not considered further.

The three observers conducted pilot trials to ensure they were measuring emergence consistently. Following pilot trials, observers worked independently. Regardless, we included observer as a covariate in subsequent analyses to account for any inter-observer effects (they were significant in some experiments). To avoid resampling clams, we divided the reef into sections and sampled a different section each day. Each observer worked in a different section of the reef on different clams. To habituate clams to a given stimulus, we touched or shaded a clam, waited for the clam to return to its initial relaxed state from the first stimulus, recorded this time as latency to emerge (LTE) in seconds and then waited 2 min before repeating the stimulus. We did this a total of four times. Following the fourth habituation treatment, we tested whether the clam transferred habituation to a novel stimulus. We waited 2 min after the clam returned to its relaxed state, then presented the novel stimulus and recorded the LTE. We measured an additional covariate—maximum shell length—because Johnson et al. (2017) found that clam size influenced a clam's antipredator response. We also measured clam depth—because photosynthetic potential varies with depth.

We tested 81 clams in Gump Reef to determine whether clams transferred habituation between a tap and a large shade. We then tested 73 clams to determine habituation transfer from a large shade to a tap.

We then asked whether clams could discriminate different shade sizes, which is a continuous variable rather than a discrete stimulus, by conducting two different experiments with different size shades—habituating clams to a large shade followed by (a) small shade and (b) medium shade habituations. For the small shade and medium shade habituations, we tested 15 clams and 32 clams, respectively. These clams ranged in size from 8 to 28 cm and were found at depths of 51–142 cm. We conducted both experiments in between the Motu Islands.

Finally, we tested 60 clams for habituation to mantle touch. Individuals ranged from 9.5 to 25 cm and were found at depths of 33–110 cm in Gump reef.

Latency to emerge was $\log_{10}(x + 1)$ transformed to normalize distributions and to account for a lack of response (LTE = 0 s) for some of our small shade experiment. We explored a variety of transformations that did not dramatically improve residual distributions for some models, and thus, we elected to present the slightly improved results by the $\log_{10}(x + 1)$ transformation. We fitted linear mixed-effects models using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) and lmerTest (Kuznetsoza, Brockhoff, & Christensen, 2015) in R version 3.4.3 (R Core Team, 2017) to test for clam habituation and transfer after controlling for potential observer effects as well as giant clam size (Appendices S1 & S2). Models compared the first and fourth stimulus presentation to measure habituation and compared the fourth stimulus presentation and the novel stimulus to test for transfer of habituation. Our alpha for all tests was set to 0.05; we made no adjustments for multiple comparisons and report unadjusted *p*-values because we tested clear a priori hypotheses (e.g. Gotelli & Ellison, 2004).

TABLE 1 Giant clams' response to repeated exposure to threats: mantle touch (MT), shell tap (T), large shade (LS), medium shade (MS) and small shade (SS)

Experiment	Description	*df*	*t*	*p*
MT1-4, T	MT1 and MT4	58.000	−6.724	<0.001[a]
MT1-4, T	MT4 and T	58.000	−5.497	<0.001[a,b]
T1-4, LS	T1 and T4	81.243	−8.779	<0.001
T1-4, LS	T4 and LS	81.540	−8.369	<0.001[a]
LS1-4, T	LS1 and LS4	73.000	−13.224	<0.001
LS1-4, T	LS4 and T	73.000	10.635	<0.001
MS1-4, LS	MS1 and MS4	32.000	−7.009	<0.001
MS1-4, LS	MS4 and LS	32.000	−11.673	<0.001[a]
SS1-4, LS	SS1 and SS4	15.000	−1.703	0.109
SS1-4, LS	SS4 and LS	15.000	−12.47	<0.001

The numbers 1 through 4 represent the habituation treatments for that threat. For instance, MT1 represents the first habituation treatment of the mantle touch stimulus

[a] Size effect $p < 0.05$. [b] Observer effect $p < 0.05$.

We asked whether our assumptions about relative risk were supported by analysing all of the habituation data (i.e. the first four treatments of each experiment). We first fitted a random intercept and fixed slope model with the following fixed effects: observer, clam size, trial and the interaction between size and treatment. We then fitted a random intercept and random slope mixed effect model and assessed which was the better model by comparing likelihood ratios.

We tested for assumptions of the mixed models by plotting the distribution of the residuals in QQ plots using ggplot2 (Wickham, 2013). We also examined histograms of the residuals to validate the normality assumption. QQ plots were approximately straight, and residuals were approximately normal but this varied a bit by analysis (no other explored transformations substantially improved the linearity or normality of the distributions—see above) (Appendices S1 & S2).

3 | RESULTS

Table 1 summarizes the results from the different analyses for the first and last stimulus presentation of each threat, as well as analyses between the last stimulus presentation and the novel stimulus presentation. After controlling for observer effects and clam size, we found that giant clams always had a lower LTE in response to subsequent presentations of the same stimulus and had a higher LTE in response to all novel stimuli except for the mantle touch to tap experiment where the tap, a putatively lower risk stimulus, elicited a further reduced response (Figure 1). To help interpret this, we note that the mean LTE for the tap following the mantle touch habituation (10.13 ± 0.64 *SE*) did not differ significantly ($p = 0.116$) from the average LTE of the first tap in the tap habituation trials (11.57 ± 0.78 *SE*). When we looked at the habituation curves across all treatments, we found that the random intercept and random slope model best explained data ($p < 0.001$). Specifically, after controlling for significant observer effects, where observers 2 and 3 were different ($p = 0.001$), and non-significant clam size effects ($p = 0.095$) all intercepts were significantly different and some slopes were significantly different (Figure 2). Many of the clams did not respond to any of the small shading experiments, and thus had 0 LTE. If we remove these non-responding individuals, the curve shifts upwards and resembles other shading slopes (Figure 3). In 11 analyses, clam depth did not

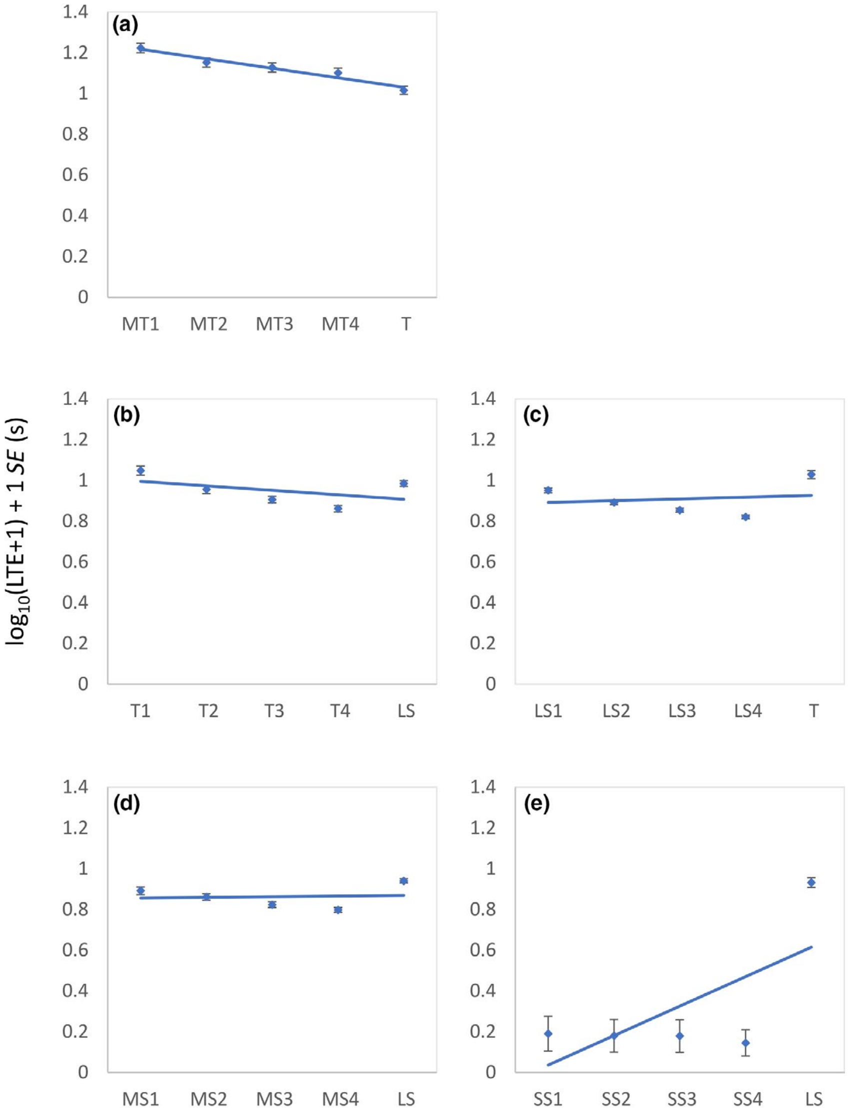

FIGURE 1 Habituation by giant clams to repeated stimulus presentation followed by lack of habituation transfer to a novel probe. Plotted are changes in the average (±*SEM*) latency to emerge (in seconds, $\log_{10}(x + 1)$ transformed). Stimulus sets include the following: (a) mantle touch to tap, (b) tap to large shade, (c) large shade to tap, (d) medium shade to large shade and (e) small shade to large shade [Colour figure can be viewed at wileyonlinelibrary.com]

significantly (all $p > 0.083$) explain variation in LTE. In the four analyses where it did significantly explain variation (all $p < 0.029$), the main conclusions were unmodified and the significance remained the same, as shown in Table 1.

4 | DISCUSSION

Giant clams habituated to repeated presentations of all stimuli in that their fourth response was significantly lower than their first response with the exception of the small shade, which was not significant but showed a trend (Table 1). Additionally, with one exception, they did not transfer habituation in that the novel stimulus elicited higher responses than the last of the habituation trials. In the case of the mantle touch to tap experiment (Figure 1a), the novel stimulus was less aversive than the initial stimulus. Moreover, the average latency to emerge for the tap following the mantle touch habituation was not significantly different than the average initial LTE that a clam had after being tapped for the first time. Together, this suggests that clams were able to discriminate between mantle touch and tap despite a lack of increased response from the fourth repetition of the mantle touch to the new stimulus. For all stimuli, the average LTE times were significantly different from each other and in the order of threat levels that we predicted (Figure 2). These results suggest that clams discriminate between different threatening stimuli, and they can assess the level of threat along a gradient and respond accordingly.

Clams also had different habituation slopes for each stimulus (Figure 2). Organisms should habituate more quickly to less harmful stimuli (Groves & Thompson, 1970). Consequently, we expected the shallowest slope for mantle touch habituation because it is the most aversive stimulus. We also expected the slopes to increase as the stimulus becomes more benign. However, the tap habituation curve had a steeper slope than any of the shade habituation curves. This steeper slope may be due to physical constraints clams have on re-emerging after hiding, since clams cannot instantaneously open, which defines a minimum LTE. This constraint would explain

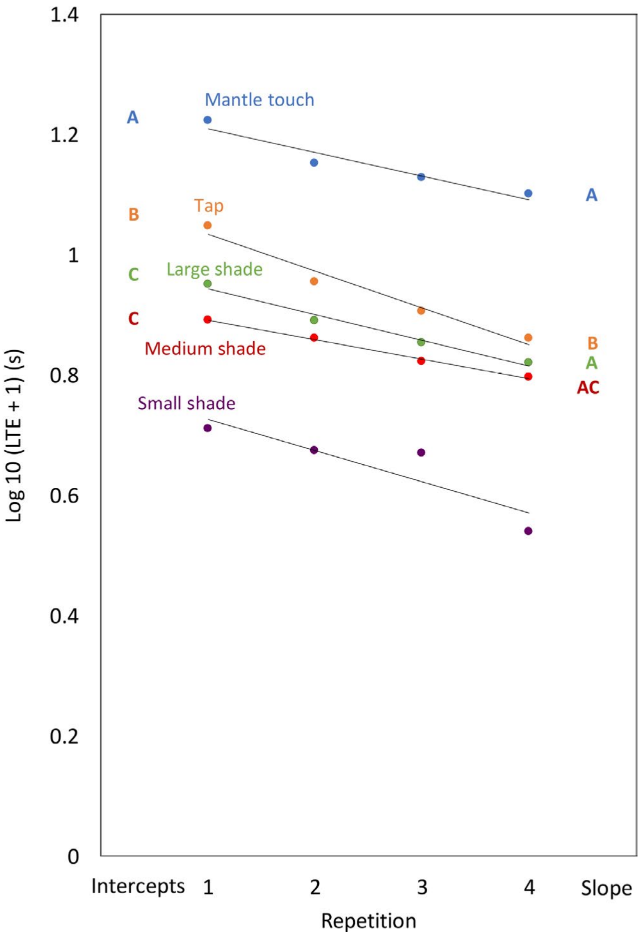

FIGURE 2 Habituation curves of tested stimuli. Plotted are linear regression curves of changes in the average (±*SEM*) latency to emerge (in seconds, $\log_{10}(x + 1)$ transformed). Different letters on the left axis indicate significantly different intercepts. Different letters on the right axis indicate significantly different slopes [Colour figure can be viewed at wileyonlinelibrary.com]

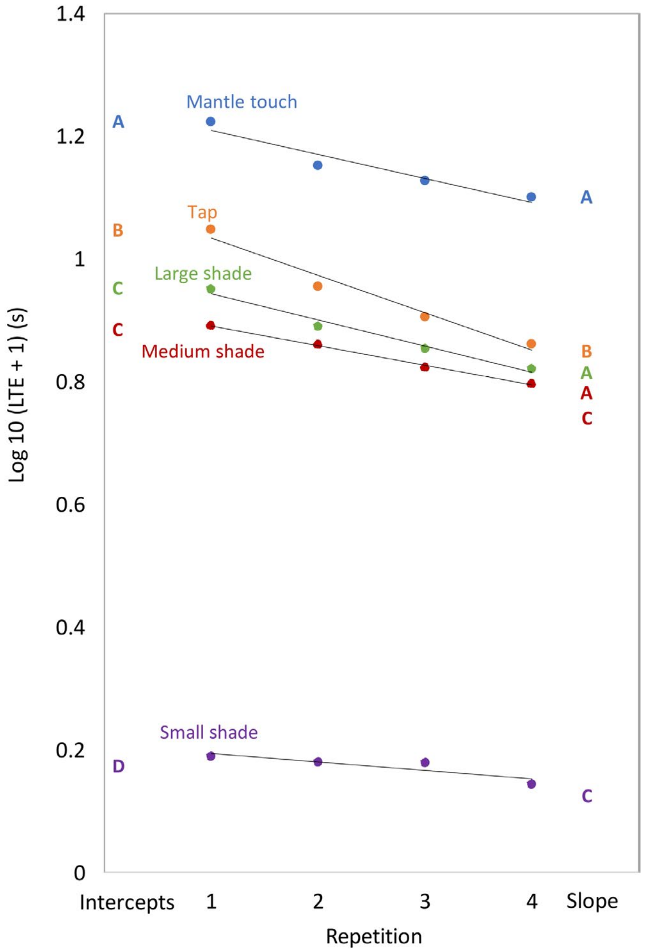

FIGURE 3 Habituation curves of tested stimuli with non-responding individuals (LTE = 0) removed. Plotted are linear regression curves of changes in the average (±*SEM*) latency to emerge (in seconds, $\log_{10}(x + 1)$ transformed). Different letters on the left axis indicate significantly different intercepts. Different letters on the right axis indicate significantly different slopes [Colour figure can be viewed at wileyonlinelibrary.com]

the shallow slopes in response to exposure to less threatening shading, which itself initially has a short LTE. The overall response to the small shade requires explanation. As we noted, removal of non-responding clams that had 0 LTE (which was restricted mostly to small shading events) led to the habituation curve shifting upwards and resembling other shading slopes (Figure 3).

Although molluscs took a different path than other phyla to evolve advanced and, in some species, highly complex nervous systems (Godfrey-Smith, 2013), they have similar abilities to discriminate threats along a risk gradient, and this may reflect an ability to classify threats quantitatively. This pattern is well demonstrated in other species, so it seems to be a common trait. Some species of free-living scallops, bivalves with much more sophisticated escape abilities than giant clams, also have the ability to classify predatory stimuli along a threat gradient (Brokordt et al., 2011; Hutson et al., 2005). In the mollusc phylum, prior work has shown that cephalopods (Mooney et al., 2016; Samson et al., 2014) and gastropods (McCarthy & Fisher, 2000) share this ability. While clams did not evolve advanced sensory systems or complex abilities to move away from predators, they shared this plastic response behaviour with other molluscs.

Although our stimuli were different shapes (the largest was a triangle while the medium and small stimuli were rectangles), they were all relatively two dimensional to avoid creating substantial turbulence that could have otherwise stimulated the clams to close. The largest stimulus, nevertheless, likely created more turbulence than the smallest stimulus. This was unavoidable but we note that because the stimuli were 25 cm above the clams and they were pushed slowly, turbulence reaching the clams was minimized. Additionally, we are unaware of any prior work that has demonstrated that clams (or other bivalves) are able to differentiate different shaped objects. Wilkens (1986) found that giant clams of the genus *Tridacna* reacted to changes in shadows and are sensitive to the movement pattern and the orientation of the shadowing object. Land (2002) further explored *T. maxima*'s pinhole eyes and found that they are most sensitive to the amount of shadowing in their vision field. Since we presented the different shaped stimuli from the same direction and at the same speed, we assumed that the area, and not the shape, of the object explained variation in the clams' responses.

Can our results be used to infer categorical perceptual abilities (Harnad, 1987) by giant clams? Harnad (1987) describes categorical perception as the ability to identify a threshold in stimuli varying along a continuum where then the response changes. These phenomena were classically studied in human infants: infants display categorical perception when they differentiate the sound "ba" from "pa," two sounds lying along an acoustic continuum (Eimas, Siqueland, Jusczyk, & Vigorito, 1971). Despite our best attempts at standardizing our experimental stimulus presentations, inevitably they were not identical. The giant clams seemed to classify variations of the same stimulus into the same category. While we have not shown threshold discrimination, giant clams can make fine-scale discriminations, even of visual objects, despite a limited visual system with pinhole eyes (Land, 2002). At this point, we can infer that giant clams have sophisticated perceptual abilities and future work may illustrate categorical perception.

It may be surprising that giant clams possess well-developed classification abilities since they are sessile and possess a comparatively simple sensory system: they respond to all threatening stimuli superficially in the same way. Additionally, it may be generally costly to maintain cognitive abilities that permit learning (Niven, 2008, Godfrey-Smith, 2013; but see Hollis & Guillette, 2015) and possibly classification. In the case of giant clams, these cognitive mechanisms may be maintained by the cost of making a mistake; when closed, giant clams cannot photosynthesize and hence are deprived of energy. Consequently, the benefits of sophisticated perceptual abilities that permit nuanced threat discrimination may outweigh any costs. Giant clams remind us that simple sensory systems need not necessarily indicate simple cognitive abilities.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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