

# Sea Hares Use Novel Antipredatory Chemical Defenses

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## Summary

Numerous studies have demonstrated that chemical defenses protect prey from predation [1–7] and have often assumed that these defenses function by repelling predators. Surprisingly, few have investigated the mechanisms whereby predators are affected by these defenses [8, 9]. Here, we examine mechanisms of chemical defense of sea hares (*Aplysia californica*), which, when attacked by spiny lobsters (*Panulirus interruptus*), release defensive secretions from ink and opaline glands [10, 11]. We show that ink-opaline facilitates the escape of sea hares by acting through a combination of novel and conventional mechanisms. Ink-opaline contains millimolar quantities of amino acids that stimulate chemoreceptor neurons in the spiny lobster's nervous system. Ink stimulates appetitive and ingestive behavior, opaline can elicit appetitive behavior but can also inhibit ingestion and evoke escape responses, and both stimulate grooming. These results suggest that these secretions function by “phagomimicry,” in which ink-opaline stimulates the feeding pathway to deceive spiny lobsters into attending to a false food stimulus, and by sensory disruption, in which the sticky and potent secretions cause high-amplitude, long-lasting chemo-mechanosensory stimulation. In addition, opaline contains a chemical deterrent that opposes appetitive effects. Thus, chemical defenses may act in more complex manners than palatability assays of prey chemistry may suggest.

## Results and Discussion

To investigate the survival value of the secretions, we presented to spiny lobsters (*Panulirus interruptus*) sea hares (*Aplysia californica*) with and without opaline and/or ink glands (Figure 1). Sea hares with both opaline and ink glands and sea hares with only opaline glands escaped predation in 60% and 67%, respectively, of the encounters with spiny lobsters, whereas sea hares with neither opaline nor ink glands and sea hares with only ink glands escaped in only 19% and 17%, respectively, of the encounters (Figure 1A). This

statistically significant protective effect of secretions containing opaline is striking given that these experimental conditions decidedly favored the predators. In encounters in which sea hares released secretions and survived, spiny lobsters showed several behaviors suggestive of the mechanisms of chemical defense. These include digging with the legs into the substrate covered by the secretion (“digging,” Figure 1B) and moving the first two pairs of legs to the mouth (“grabbing,” Figure 1C), behaviors similar to that produced when spiny lobsters are chemically stimulated to search for and sample food items [12]. Other behaviors exhibited by spiny lobsters in encounters in which sea hares released secretions and survived were grooming of the antennules (Figure 1D) and grooming of the mouthparts (Figure 1E), behaviors associated with cleaning the sensory organs after chemical or mechanical fouling [13]. Opaline, either alone or with ink, caused spiny lobsters to tailflip (Figure 1F), a defensive behavior produced by aversive stimuli [14]. (Three videos of attacks by spiny lobsters on sea hares, as well as descriptions of the behaviors described above, are included in the [Supplemental Data](#) available with this article online.) These experiments suggest that the secretions can defend sea hares against predatory spiny lobsters by stimulating the predator's chemosensory systems and evoking appetitive or ingestive feeding behavior (ink or opaline), cleaning behavior (ink or opaline), and/or aversive behavior (opaline). These observations led us to perform the following chemical analyses and behavioral and electrophysiological experiments.

To identify possible feeding stimulants in secretions, we analyzed *A. californica* ink and opaline for free amino acids, ammonium, and urea (AA/NH<sub>4</sub><sup>+</sup>/Urea) because these are known to be potent excitants of chemosensory neurons (CNs) and feeding behavior of spiny lobsters and other crustaceans [15, 16]. Opaline and ink from either field-caught or mariculture-raised sea hares contain enormous concentrations of AA/NH<sub>4</sub><sup>+</sup>/Urea—319 and 54 mM, respectively (Figure 2; for complete data set, see [Table S1](#)). Taurine is the dominant amino acid in opaline (at 231 mM, it constitutes 72% of the total AA/NH<sub>4</sub><sup>+</sup>/Urea). Opaline is also high in lysine (65 mM, 20%) and histidine and ammonium (each at 7 mM, 2%). In ink, ammonium is the dominant component (at 24 mM, it is 44% of the total AA/NH<sub>4</sub><sup>+</sup>/Urea); cysteine (15 mM, 28%) and taurine (8 mM, 15%) are also abundant components. The high levels of taurine in opaline and ink are striking because taurine is one of the most potent stimulants of crustacean feeding [15]. To test whether these high levels of AA/NH<sub>4</sub><sup>+</sup>/Urea in ink and opaline simply reflect high levels in other body tissues of *A. californica*, we analyzed hemolymph and found only 2 mM AA/NH<sub>4</sub><sup>+</sup>/Urea, of which over 50% was urea (Figure 2). This total level is only 0.6% and 3.7% of that in opaline and ink, respectively, showing that ink and opaline glands secrete very high levels of specific feeding stimulants.

Next, we performed behavioral experiments to determine whether the secretions induce a feeding response

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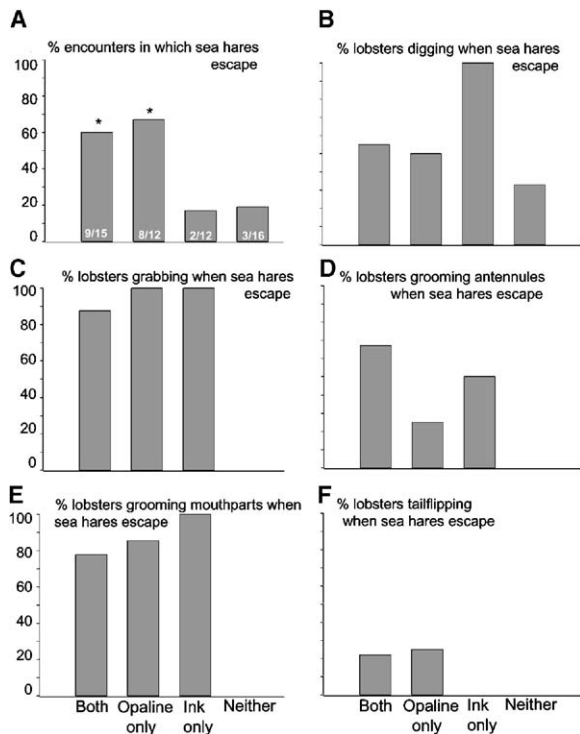


Figure 1. Effect of Ink and Opaline Secretions on Survival of Sea Hares and Spiny Lobster Behavior in Attacks by Spiny Lobsters

(A) Percentage of trials in which sea hares escape being eaten by spiny lobsters. Numbers within each bar represent the number of escaping sea hares followed by the number of trials. \* indicates significant difference from the “neither” group (Fisher’s Exact Test,  $p < 0.05$ ).

(B–F) For encounters in which sea hares escape, % of spiny lobsters showing digging in substrate (B), grabbing (C), antennule grooming (D), mouthpart grooming (E), and tailflipping (F).

(grabbing and ingestion) in spiny lobsters (Figure 3). We also tested artificial ink and opaline mixtures, which contained the seven most-concentrated components identified in the secretions at their natural concentrations. Ink-opaline, ink, artificial ink, and artificial opaline induced significantly more grabbing than did the negative control (sea water) and as much grabbing as did natural food (squid juice) (Figure 3A). Interestingly, artifi-

cial opaline elicited significantly more grabbing than did sea water, but natural opaline did not, suggesting the presence of a feeding deterrent in opaline. Tannic acid was included in our experiment as a potential negative (aversive) control because it is a feeding deterrent to clawed lobsters [17]; in our study, tannic acid, like sea water, elicited very little grabbing. To examine ingestion, we compared spiny lobsters’ ingestion of ink-opaline, ink, and opaline to that of natural foods (squid juice and freeze-dried shrimp) and sea water. Ink elicited the same amount of ingestion as squid juice did and more ingestion than sea water did (Figure 3B). When added to ink, opaline inhibited ingestion (Figure 3C). In fact, ingestion of natural food (freeze-dried shrimp) was inhibited when it had been soaked in opaline taken from either field-caught or mariculture-raised (on the red alga *Gracilaria ferox*) sea hares (Figure 3D). These results demonstrate that ink is a feeding excitant that elicits both grabbing and ingestion. Opaline contains feeding excitants, but it also has a feeding inhibitor present even in sea hares fed a limited diet. We are currently investigating the molecular identity of this inhibitor.

To determine whether ink and opaline mimic the activity of food odors in the spiny lobster’s neural pathway, we examined the responses of chemosensory neurons (CNs) in the spiny lobster’s antennules and second maxillipeds; we thereby took advantage of the fact that spiny lobsters are model systems in chemosensory neurobiology [15–18]. Because these experiments were conducted at two different locations, we used the local sympatric species of spiny lobster and sea hare. Thus, antennule data were taken from *P. argus*, with secretions from *A. dactylorella* (which are similar in amino acid composition to *A. californica*; see Table S1), whereas second-maxilliped data were taken from *P. interruptus*, with secretions from *A. californica*. Both antennular and mouthpart CNs were highly excited by 0.1% opaline and 1% ink (Figure 4A). Even at 0.01% of full strength, secretions elicited significant responses, especially in antennular CNs. We examined two response properties of these cells: response intensity (Figure 4B) and across-neuron patterns (ANPs) (Figure 4C), which are the neural codes for stimulus quantity and quality, respectively. Ink, opaline, artificial ink, and artificial opaline were more excitatory (i.e., they evoked a higher frequency of action potentials, or “spiking”) than sea water and were similar to shrimp

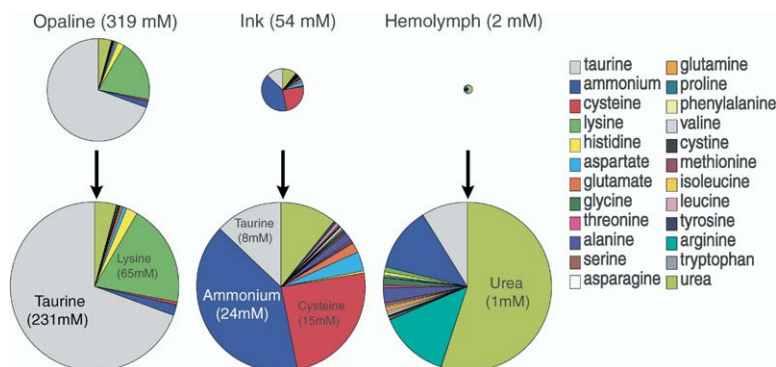


Figure 2. Composition of Opaline, Ink, and Hemolymph of Sea Hares

Samples of ink and opaline were collected from dissected glands of 15 field-collected *A. californica*, and hemolymph was collected from 5 individuals. Concentrations of 22 free amino acids, as well as ammonia and urea, were analyzed for pooled samples via an ion exchange, post-column ninhydrin-detection system (Beckman Model 6300/7300 Amino Acid Analyzer, The Scientific Research Consortium: <http://www.aminoacids.com>). The three pie charts in the top row represent absolute amounts on the same scale; pie charts in the bottom row show the same results but on a relative scale.

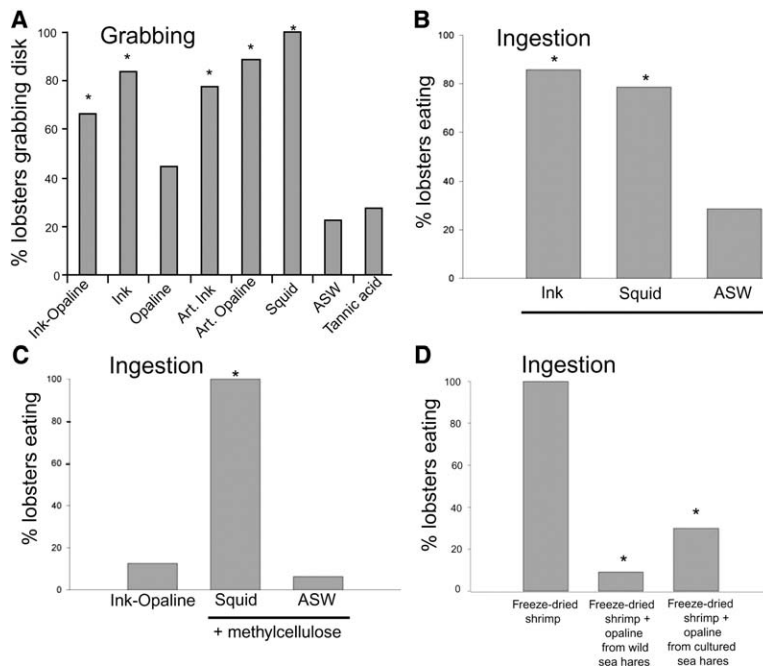


Figure 3. Behavioral Responses of Spiny Lobsters to Defensive Secretions of Sea Hares

(A) Grabbing of ink-opaline, ink, opaline, artificial ink, and artificial opaline (all at 50% of full strength); squid juice (500 g/l); artificial sea water (ASW: negative control); and tannic acid (100  $\mu$ M).

(B–D) Ingestion. In (B) and (C), substances (except ink-opaline) were mixed in 20 mg/ml carboxymethylcellulose. N (of spiny lobsters tested) = 19 (A), 14 (B), 16 (C), 13 (D). Bars with an asterisk above them are significantly different from ASW (A–C) and freeze-dried shrimp (D) [ $p < 0.05$ , Cochran Q test for (A), McNemar test for (B)–(D)].

juice and major components of the secretions (such as taurine and ammonium) (Figure 4B). Analysis of ANPs shows that secretions and artificial mixtures produce ANPs similar to each other and to those produced by shrimp, and it also shows that the components of ANP-producing secretions that are the most similar to the secretions and mixtures are taurine and ammonium. These predicted results are based on the compositions of these stimuli and support the conclusion that these defensive secretions may mimic food odors. These results also suggest that the inhibitor (which deters ingestion) in opaline does not function by inhibiting the activity of neurons activated by amino acids and other feeding excitants that may evoke appetitive behavior in spiny lobsters, but may function instead by activating a different population of neurons. Thus, by sending contradictory messages to spiny lobsters opaline may excite different neuronal populations. We identified one candidate neuron: an antennular chemosensory neuron that was excited by opaline but not by artificial opaline or any other stimulus. However, the conclusive identification of neurons mediating this inhibition requires the isolation of deterrent compounds in opaline.

Our results show that sea hares contain not only unpalatable, aversive chemicals that appear to repel spiny lobsters from feeding on sea hares but also chemicals that protect them by more-novel mechanisms. One is a previously undescribed form of chemical defense, “phagomimicry,” in which secreted substances mimic the stimulatory properties of food to divert predators; this mechanism is suggested by the observed digging and grabbing of the spiny lobsters. The enormous difference in concentration of free amino acids and ammonia in opaline and ink versus in hemolymph suggests that defensive secretions function as a supernormal stimulus (a stimulus that is more effective than the typical stimulus) [19]. To be effective as a phagomimic, the

secretion should be a supernormal stimulus because the prey itself is food to the predator and would release hemolymph when bitten, and a supernormal stimulus is necessary to direct the predator away from the prey. This phagomimic also functions as a sensory trap [20] because the spiny lobster’s chemosensory system is “trapped” to respond in a certain way. The detection of high concentrations of free amino acids typically signals to spiny lobsters the presence of food. Sea hares exploit this property of their predator’s nervous system by releasing secretions that mimic stimulatory properties of food and thereby divert the attention of the attacker. The highly viscous nature of opaline may create a tactile sensation of food, contributing to the mimicry. Sea hares normally release both ink and opaline at about the same time, and the ink binds to the sticky opaline, thus keeping the concentrated stimulus near the attacker. This likely explains why sea hares with only ink glands escaped in only 17% of encounters with spiny lobsters; the less-viscous ink rapidly diffused into the water column, away from the spiny lobsters. Anecdotal reports suggest other candidates for phagomimicry [21–23]. Because the use of false scents of food to attract mates, prey, and pollinators has evolved in many species, [24], phagomimicry may be a strategy used by many species and serving as an alternative to chemical defenses that harm or deter predators.

Finally, the defensive ink-opaline secretion may also function through sensory disruption or desensitization, which would occur when the sticky ink-opaline coats the spiny lobster’s sensory and feeding appendages with concentrated chemical stimuli. The resulting massive and sustained excitation of the chemosensory neurons would produce confusing sensory messages and inappropriate behaviors, such as extensive grooming, and it would possibly be followed by chemosensory desensitization or adaptation. Although sensory

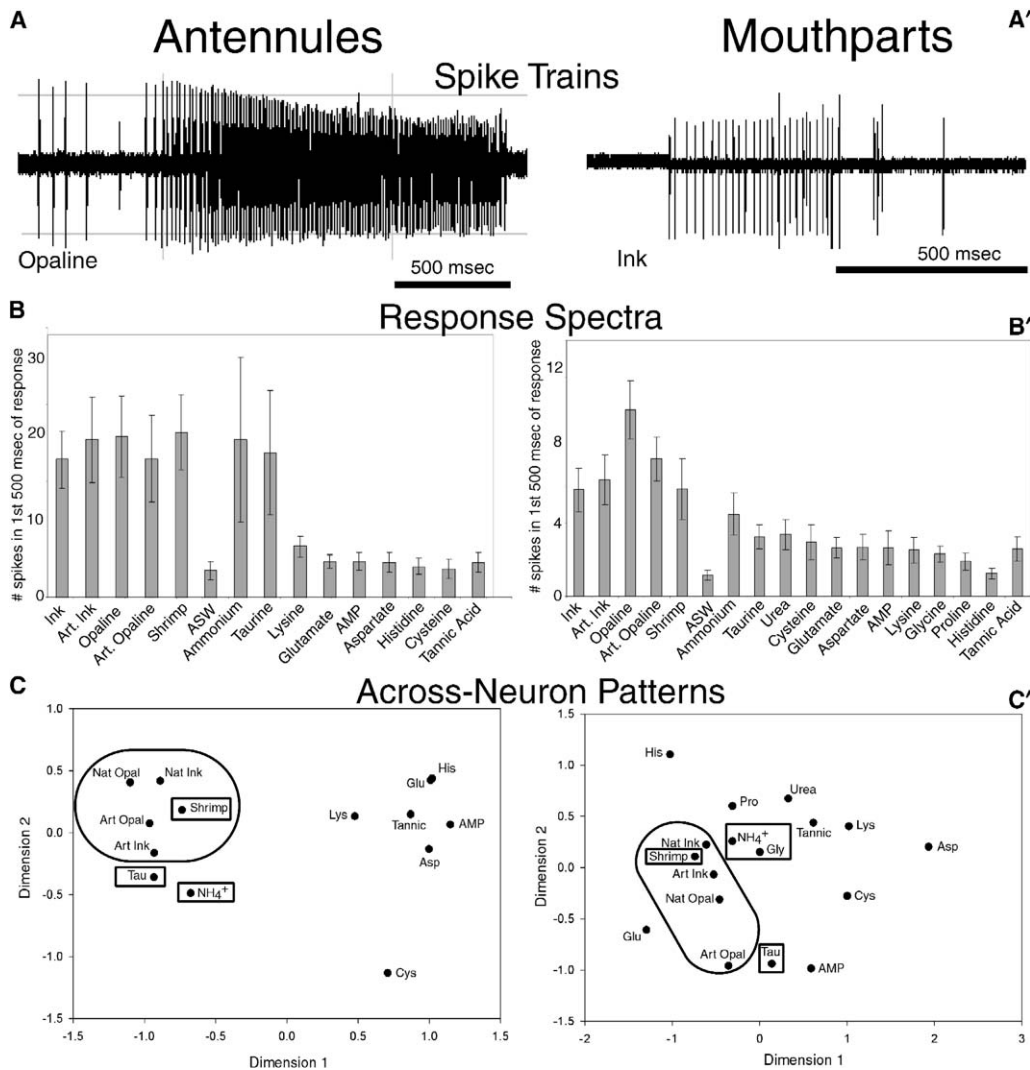


Figure 4. Responses of Antennular and Mouthpart Chemoreceptor Neurons of Spiny Lobsters to Sea Hare Defensive Secretions

(A, B, and C) Responses of CNs in the antennular lateral flagellum of *Panulirus argus*.

(A', B', and C') Responses of CNs in the second maxilliped of *Panulirus interruptus*. Examples of single-unit responses of antennular CN to 0.1% opaline (A) and of mouthpart CN to 1% ink (A'). Population response intensity for (B) 12 antennular CNs from 10 different preparations from as many animals, after stimulation with 0.1% secretions and the artificial mixtures; single compounds at 10  $\mu$ M, and for (B') 30 mouthpart neurons from 11 different preparations from as many animals in response to 1% secretions and artificial mixtures; single compounds at 100  $\mu$ M. Responses were expressed as mean  $\pm$  standard error of the mean number of spikes in the first 500 ms of response. Across-neuron patterns (C) for the same 12 antennular CNs and same 15 stimuli as in (B) and (C') for the same 30 mouthpart CNs and same 18 stimuli as in (B) are shown. Across-neuron patterns were analyzed with the first 500 ms of response in multidimensional scaling (Statistica, StatSoft) and with similarities determined by Pearson correlation coefficients [15]. These two-dimensional solutions account for 94% (C) and 84% (C') of the variance in the data.

disruption (or related phenomena, such as startle or sensory irritation) has been previously suggested as a potential mechanism of antipredatory chemical defense [8–11], ours is the first neurophysiological support in sea hares and, to our knowledge, any animal.

In conclusion, the ink-opaline secretion of sea hares protects them through a combination of mechanisms, including phagomimicry, sensory disruption, and chemical deterrence. This is one of the few studies to demonstrate how predators process a prey's chemical defenses at the neural level, and it illustrates how defenses can have multiple physiological effects on a

given predator. This multitude of active chemical defensive mechanisms involving ink-opaline, together with other known passive chemical defenses and other behavioral strategies [11, 25–29], likely provides highly effective protection against not only spiny lobsters but other predators as well.

#### Experimental Procedures

##### Animals and the Collection of Ink

California spiny lobsters (*Panulirus interruptus*) and sea hares (*Aplysia californica*) were either collected in the field or provided by the National Institutes of Health National Resource for *Aplysia*. Un-

less stated otherwise, results are from field-caught hares. Caribbean spiny lobsters (*Panulirus argus*) and sea hares (*Aplysia dactylomela*) were collected in the Florida Keys and Bermuda. Sea hares were fed red alga, *Gracilaria ferox*. Ink and opaline secretions were collected from dissected ink and opaline glands. Ink glands were gently squeezed to release ink. Unless otherwise indicated, opaline glands were centrifuged at 30,000 × g for 1 hr at 4°C to separate opaline secretion from gland tissue. Opaline was also collected by squeezing the glands. Secretions were frozen at -20°C until needed. Although opaline obtained by centrifugation is less sticky than that obtained by squeezing the glands, spiny lobsters find both types of opaline unpalatable.

#### Assay of the Role of Ink in Success of Predation by Spiny Lobsters on Sea Hares

The effects of ink and opaline on the survival of a total of 55 sea hares in the presence of crustacean predators were analyzed with the sympatric predator-prey pair *P. interruptus* and *A. californica*. Sea hares (40–50 g) were randomly assigned to one of the following four treatment groups (and were balanced according to sea-hare size): both ink and opaline (no glands removed), opaline only (ink gland surgically removed), ink only (opaline gland removed), and neither ink nor opaline (both ink and opaline glands removed). To control for effects of handling and surgery, we handled sea hares in the “both” group as those in the other groups, except that we performed a sham surgery in which a portion of the parapodia was instead removed. Glands were removed the day before the experiment, and each sea hare was used only once. Animals in all groups appeared to be in good health on the day of the experiment. Each spiny lobster was used one time and was tested in an 80-liter aquarium (60 cm L × 30 cm W × 45 cm H) and recorded with a digital video camera. Only spiny lobsters that were motivated to feed (as determined by the production of a feeding response to sea hare juice [thawed body-wall tissue prepared by the same method as squid juice; see below]) were included in the data analysis. Interactions were recorded for 5 min after the spiny lobster attacked, and digging, grabbing, antennule grooming, mouthpart grooming, and tailflipping were quantified. Sea hares were scored as “eaten” if the spiny lobster had eaten or was in the process of eating 10 min after attack. Some spiny lobsters dropped partially eaten dead sea hares less than 10 min after attack. These were scored as eaten. If the spiny lobster dropped the (live) sea hare within 10 min of attack, the sea hare was scored as “escaped.”

#### Assay of Responses of Spiny Lobsters to Ink, Opaline, and Other Chemicals

We examined feeding responses (grabbing and ingestion) of *P. interruptus* to *A. californica* ink, opaline, and ink-opaline in three different assays. To standardize hunger level, we fed spiny lobsters a piece of shrimp 3–5 hr before starting feeding assays. In the first assay, grabbing was examined with a previously described procedure [17]. Filter-paper disks (Fisherbrand P8, 2.5 cm diameter) soaked in stimuli were presented to the legs of spiny lobsters. Grabbing was defined as taking the disk in its legs and transferring it to its mouthparts. Stimuli included: ink, opaline, ink-opaline, artificial ink, and artificial opaline, each at 50% of full strength; squid juice (squid soaked in sea water) as a positive control; artificial sea water (ASW) as a neutral control; and tannic acid as a possible negative (aversive) control [17]. Squid juice was made by homogenizing a thawed piece of squid mantle in a volume of water equivalent to the volume of the squid piece and then filtering the homogenate through a coffee filter. Squid juice was the fluid that passed through the filter. All spiny lobsters received each type of disk, one disk per trial, randomly presented.

In a second assay, the ability of chemicals to elicit ingestion was examined by presenting to the legs and mouthparts of spiny lobsters a 1 ml stimulus via a syringe. Ink-opaline was viscous enough to be presented au naturel (because the opaline obtained by squeezing the opaline glands was very viscous); ink, squid, and sea water were mixed in 20 mg/ml carboxymethylcellulose to have viscosity similar to opaline. Ink and opaline were presented at full strength.

In a third assay, the ability of opaline to inhibit ingestion of food

was examined by evaluating the effect of adding opaline to freeze-dried shrimp. Spiny lobsters were first offered a palatable control food (freeze-dried shrimp soaked in 500 μl sea water). If this was consumed, spiny lobsters were offered a piece of freeze-dried shrimp soaked in 500 μl full-strength opaline. Spiny lobsters that rejected opaline-soaked shrimp were offered a control shrimp to ensure that rejection was not due to satiation, and spiny lobsters that did not consume either the initial or control shrimp were excluded from analysis. This experiment was performed for opaline from both field-caught and mariculture-raised animals.

#### Electrophysiological Recordings from Chemoreceptor Neurons

Single-unit, extracellular electrophysiological techniques were used to record responses of individual chemoreceptor neurons of the spiny lobster's lateral flagellum of the antennule and second maxilliped. For stimulus delivery, we used a perfused preparation in an olfactometer with electronically driven valves, and we used fine-tipped glass electrodes to make recordings from CN axons [30, 31]. CNs from second maxillipeds of *P. interruptus* and from antennules of *P. argus* were tested with glandular secretions of sympatric *Aplysia* species. CNs were identified with 300 mg/l homogenized shrimp or 0.1% of full-strength ink-opaline. We measured responses to ink, opaline, artificial ink, and artificial opaline (1% for second-maxilliped CNs and 0.1% for antennular CNs); to the major single compounds in secretions and their artificial mixtures (taurine, lysine, glutamate, aspartate, histidine, cysteine, ammonium, and urea); to tannic acid and adenosine-5' monophosphate (10 μM for second-maxilliped CNs and 100 μM for antennular CNs); to shrimp juice (3000 mg/l for second-maxilliped CNs and 300 mg/l for antennular CNs); and to ASW (negative control). Higher concentrations were tested for second-maxilliped CNs because these neurons have lower sensitivity and higher thresholds than antennular CNs [31]. For each neuron, response intensity was quantified as the number of spikes in the first 500 ms of response. Two response features were quantified for all stimuli: population response intensity, which represents the relative efficacy of stimuli, and across-neuron pattern (or “ensemble-response patterns”), which represents the ability of the population to discriminate between stimuli (see Figure 4 for description).

#### Supplemental Data

Three supplemental videos of spiny lobsters attacking sea hares, one supplemental figure of a sea hare releasing ink, and one supplemental table of the compositions of secretions from *Aplysia californica* and *A. dactylomela* are available with this article online at <http://www.current-biology.com/cgi/content/full/15/6/549/DC1/>.

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