

## Stimulus concordance and risk-assessment in hermit crabs (*Coenobita clypeatus*): Implications for attention

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### ABSTRACT

Recent research has demonstrated that the topography of defensive reactions depends on factors that are extraneous to the stimulus that elicits the defensive response. For example, hermit crabs will withdraw more slowly to the approach of a simulated visual predator (i.e., the eliciting stimulus) when in the presence of a coincident acoustic stimulus. Multiple properties related to the magnitude (e.g., duration, amplitude) of the acoustic stimulus have been found to modulate the crabs' withdrawal response (Chan et al., 2010b). We demonstrate that the proximity in spatial location between a threatening visual stimulus and a potentially distracting extraneous auditory stimulus is an important determinant of anti-predator behavior in hermit crabs. We suggest that a distal relationship between the eliciting stimulus and an unrelated signal may produce greater distraction. This marks the first reported experimental evidence of this relationship in an invertebrate species.

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For most animals, the proper allocation of attentional resources is of critical importance to survival and reproduction (Dukas, 2009). Hungry individuals are often best served by allocating resources related to feeding, while those in danger should direct attention toward potential predators. Attention is not a limitless resource (Broadbent, 1958). It is important that animals properly allocate their limited attention based on current contextual information. The appropriate distribution of attention could very well make the difference between surviving a predator's attack and being eaten.

In the past few decades, psychologists have done a great deal of work in determining the factors that modulate attention. One such factor is the spatial relationship of a cue to a specified target stimulus. For example, Posner (1980) found that humans are relatively slow to respond to a target after being cued to an incongruous spatial location; in a similar vein, people are rapid to detect and respond to a target cue when they are accurately cued to its location prior to its presentation. In Posner's study, subjects were cued with a pointing arrow to expect a target presentation on either the left or right side of a visual field. The cue was accurate on 80% of trials. Once the target was detected, subjects responded by pressing a button. There was an additional control condition in which a neutral cue did not indicate on which side of the visual field the target would occur.

Posner found that subjects responded fastest when the cue was valid and slowest when the cue was invalid. This research clearly indicates that spatial contiguity of a Cue–Target stimulus pair is critically important to the ability to detect and respond to the target (see also Posner, 1971). It is evident that this sort of phenomenon is not limited to humans. Work in non-human primates has found similar results (Mountcastle, 1978; Wurtz and Mohler, 1976). Like primates, rats are slower to respond to a target stimulus when it is cued by an invalid (i.e., spatially non-contiguous) stimulus, as compared to when cue and target are spatially concordant (Ward and Brown, 1996). Similar research extends to various avian species. A distracting task negatively impacts a blue jays' ability to detect a peripheral target – a caterpillar which, when pecked, results in a food reward (Dukas and Kamil, 2000). Pigeons respond more quickly and more accurately to a local or global target (small individual letters or a larger composite shape composed of the smaller individual letters) when primed for that target type, rather than if they are primed for the opposing, distracting target type (Fremouw et al., 2002). Cook et al. (2012) report that localization of a target element in a target-search task in pigeons is impaired by the sudden onset of a distractor element, including evidence for analogous processes (e.g., inhibition-of-return [see Klein, 2000, for a review]) that have been reported in human research.

Recent work has found that anti-predator withdrawal behavior in hermit crabs is negatively impacted by extraneous auditory stimulation (Chan et al., 2010a,b). Hermit crabs are slower to withdraw into their shells in response to a looming visual predator when a non-predictive acoustic signal is also present. Chan et al. (2010b) suggested that the stimulus features of the extraneous

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sound are critical to the modulation of attentional resources; relatively loud and long auditory stimuli produce greater deficits in response latencies to potentially threatening visual signals (see also Stahlman et al., 2011). In the present study, we examine whether the spatial contiguity of a distracting auditory stimulus is critical to the production of anti-predator behavior in the hermit crab. We predict that an audio stimulus broadcast spatially concordant with a threatening visual stimulus may direct the crabs' attention in the direction of the visual stimulus, and thus cause shorter response latencies than when the same audio stimulus is broadcast from a location spatially discordant from the visual stimulus. Such a demonstration would be, to our knowledge, the first analog to Posner's (1980) effect in an invertebrate.

We were interested in two components of anti-predator behavior: response latency and whether the animals exhibit freezing. Latency to withdraw from a threatening stimulus has been suggested to be a valid measure of attention-related behavior in hermit crabs (Chan et al., 2010b). Similarly, freezing in hermit crabs has been reported as being elicited by simulated visual predators (Chan et al., 2010a). Freezing has also been reported in other crab species (Pereyra et al., 2000). Rats will freeze if a predator is far enough away that they may not have been detected, but will attempt to flee if the predator is near and an attack is imminent (Fanselow and Lester, 1988; Timberlake and Lucas, 1989). We predicted that hermit crabs would respond in an analogous fashion to the rats and freeze when a predator appears distant, but withdraw when a predator is more imminent.

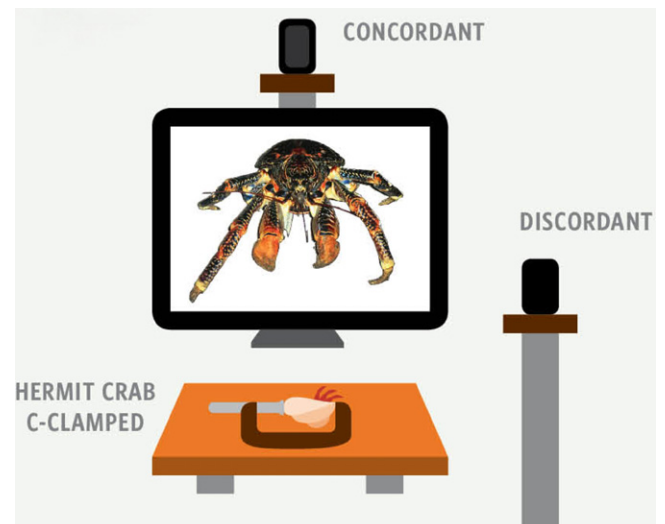
## 1. Method

### 1.1. Subjects

The subjects were 24 medium-sized, experimentally naïve hermit crabs (*Coenobita clypeatus*) purchased from a local aquarium store. Crabs were housed in groups of six and each had its largest claw and shell painted with a unique color of non-toxic nail polish for purposes of identification. Subjects were housed in clear plastic bins (50 cm × 25 cm × 25 cm) lined with coconut fiber substrate (Zoo Med Eco Earth). Each tub contained two ceramic water dishes (one for 1.00% NaCl solution, the other for distilled water), a paper plate, and a moist sponge to maintain a local atmosphere of approximately 70% humidity. Animals were given access to one Tetrafauna Hermit Crab Meal pellet per day per crab (i.e., six pellets) in a plastic cup. Plastic sheets (1/2 cm thick) covered the majority of each bin, with an opening of approximately 2 cm to allow for air circulation. A heat lamp was used to maintain ambient temperatures between 22 °C and 25 °C. There was a 14:10 h light–dark cycle in the vivarium, with experimental procedures occurring during the light portion of the cycle.

### 1.2. Materials

We used a modified automatic withdrawal detector (AWD), which was located 15 cm in front of a 17-in. Dell LCD monitor (see Chan et al., 2010b). The AWD consisted of a 20 cm × 20 cm wooden platform with an adjustable C-clamp that held the crabs in place (see Fig. 1). Attached to the C-clamp were levers that allowed the crab to be moved forward or backward, up or down depending on its shell size to maintain consistent distances from the LCD monitor. Beneath the platform was a foam lining to reduce substrate-borne vibrations. A Logitech Webcam (C250) was used to record video of each trial. Additionally, we used the camera to detect whether a crab was emerged or hiding and to signal the commencement of a trial.



**Fig. 1.** The experimental apparatus. Concordant and discordant speaker locations are indicated by black boxes. The monitor displays the fully enlarged image of the visual eliciting stimulus, a coconut crab.

The experiment was conducted in a dark 2.5 × 1.5-m sound-proof room. There were two speakers (Logitech Z506 5.1) mounted 43.2 cm off the ground with hollow, cardboard poster tubing (7.6-cm diameter). One speaker was centered directly above the computer monitor such that the speaker was 0.25 m from the crab; the other speaker was positioned 0.25 m from the subject at a 30° angle behind the crab (see Fig. 1). The acoustic stimulus was white noise broadcast at 89 dB SPL when measured at 0.25 m (the distance between the speaker and the subject for both conditions) with a RadioShack sound meter (CAT 33-2055). We used the LCD monitor to display a visual stimulus, a claw-spread coconut crab that started as a single pixel at the top and center of the screen, and then expanded and descended at a constant rate for 17 s until it reached a maximum size of screen width (approximately 900 pixels wide) at the bottom of the screen. Pilot tests indicated that this stimulus is particularly effective in eliciting the hermit crabs' withdrawal response.

## 2. Procedure

We used a within-subjects, one-way design with three levels of the independent variable (IV). The experiment consisted of three daily sessions with one trial per crab per session for a total of three trials for each subject. Each trial represented one level of the IV; trial order was counterbalanced across subjects. We measured two dependent variables. The first was *latency to respond* to the visual stimulus that was calculated as the latency to freeze; in the absence of freezing, the value recorded was the latency to hide (cf. Chan et al., 2010a). Our second behavioral measure was simply the presence or absence of the freezing behavior on a given trial.

We began each trial by placing the crab in the AWD so the aperture of its shell faced the ceiling. The webcam was calibrated with respect to the number of detected pixels present. When the crab emerged from its shell, the number of pixels detected would increase which would be translated and recorded by a computer. Pilot work with other crabs demonstrated that an increase of approximately 800 pixels was indicative of an emerged crab. When the pixels returned to baseline this was counted as a hiding response. After a crab had been emerged for 60 consecutive seconds, it was presented with one of three 47-s audio presentations: (1) *Concordant*, where white noise was presented from the speaker that was directly above the computer monitor; (2) *Discordant*,

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