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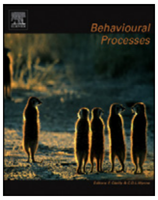

Stimulus concordance and risk-assessment in hermit crabs (*Coenobita clypeatus*): Implications for attention

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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.

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.

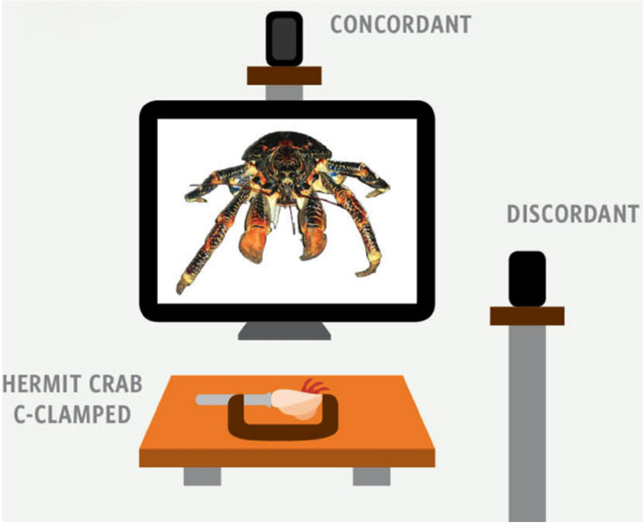

Fig. 1. The experimental apparatus. Concordant and discordant speaker locations are indicated by black boxes. The monitor displays the fully enlarged image of the visual eliciting stimulus, a coconut crab.

The experiment was conducted in a dark 2.5 × 1.5-m soundproof 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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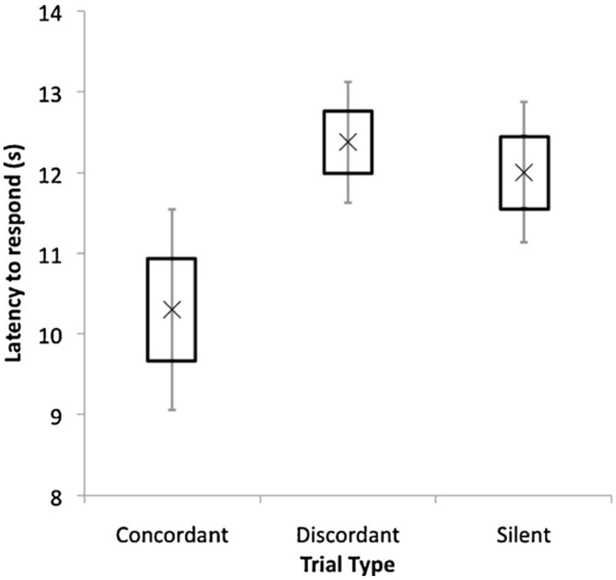

Fig. 2. Mean latency to respond as a function of trial type. The mean latency is indicated by 'x'; the black boxes indicate the standard error of the mean; and the gray error bars indicate the 95% confidence interval of the mean.

where the noise was presented from the speaker behind the crab's position; or (3) *Silent*, where no noise was presented. Thirty seconds after the start of the audio presentation, we presented the visual eliciting stimulus. The visual and audio stimuli co-terminated when the visual stimulus reached its maximum size on the monitor, which took 17 s from onset to termination. The latency to hide, as indicated by a return to baseline pixels, was recorded automatically by the computer. The latency to freeze was scored manually by three raters, two of whom were blind to the experimental conditions. If a minimum of two raters indicated that a crab had frozen during a trial, the crab was recorded as having frozen. An analysis of variance with rater and trial type as factors found no significant differences between recorded reaction latencies over trials (i.e., rater × trial type interaction), $F(4, 156) = 0.36$, $p = 0.84$. Therefore, we calculated the response latency as the average score from all raters on a given trial. Because we made directional predictions, we report one-tailed p values for all pair-wise comparisons.

3. Results

One crab died after its first trial and thus was excluded from all analyses. In the Concordant Condition 13 subjects (57%) exhibited freezing behavior, six froze (26%) in the Discordant Condition, and 14 froze (61%) in the Silent Condition. A Cochran's Q test indicated a significant difference in the number of freezes across the three treatment conditions, $T(2) = 9.5$, $p = 0.009$. Pairwise McNemar's post hoc tests found that the Discordant condition elicited significantly fewer freezes than the Concordant condition ($X^2(1) = 3.27$, $p = 0.035$) and the Silent condition ($X^2(1) = 4.9$, $p = 0.014$). The Concordant and Silent conditions did not produce different levels of freezing behavior, $X^2(1) = 0.00$, $p = 1.0$.

Twelve of the crabs responded in all three conditions. These were the only crabs used when analyzing the measure of response latency. The Concordant condition resulted in a mean response latency of 10.3 s; the Discordant condition resulted in a mean response latency of 12.4 s; and the Silent condition produced a mean response latency of 12.0 s. A repeated measures analysis of variance indicated the crabs' latencies to respond were significantly different across conditions ($F(2, 10) = 5.06$, $p = 0.016$; see Fig. 2). Planned contrasts revealed that crabs responded more quickly in Concordant trials than in both Discordant trials [$F(1, 22) = 8.90$, $p = 0.007$) and in Silent trials ($F(1, 22) = 6.01$, $p = 0.022$)]. Latency to respond was not different between Discordant and Silent trial types, $F(1, 22) = 0.28$, $p = 0.60$).

4. Discussion

We found that the spatial relationship of the auditory distractor to the visual predator modulated the topography of the crabs' defensive behavior. This is a particularly exciting discovery because it is the first time processes resembling spatial cueing and attentional capture (e.g., Posner, 1971, 1980) have been demonstrated in an invertebrate. This study expands our understanding of how components (e.g., duration, loudness) of extraneous acoustic stimuli predictably impact anti-predator behavior, a finding with both theoretical and applied value (Chan and Blumstein, 2011).

A noteworthy finding of this study is that the most rapid reactions were elicited not in the Silent condition, but instead when the white noise was broadcast in a location spatially concordant with the visual stimulus. At first glance, this result appears to be in contrast to previous work. Chan et al. (2010a,b) found that crabs' reactivity was greatest in conditions where there was no extraneous auditory stimulation. However, we can easily resolve this discrepancy by suggesting that the spatial location of an acoustic stimulus is a critical factor in establishing its ability to distract. In the present study, the extreme proximal relationship of acoustic and visual stimuli in the Concordant condition facilitated the crabs' responsiveness to the simulated predator. This is consistent with the operation of an attention process. Prior studies in hermit crabs did not utilize "distracting" noise that was as proximal to the visual target, and therefore they never found acoustic facilitation of visually triggered anti-predator behavior.

An interesting finding of this research was that the spatial relationship between visual and audio stimuli affected not only the speed of the subjects' responses, but also the type of responses elicited. Freezing behavior was more prevalent in the Concordant and Silent conditions than in the Discordant condition. We suspect this is due to the perceived threat of the stimulus at the time of detection. The size of the stimulus was constantly increasing from trial onset to trial termination. Depending on when the subject detected the predator, it appeared on a continuum from very small (a single pixel) to extremely large (the width of the screen). The sooner the visual stimulus was detected, the smaller it appeared. The subjects noticed and reacted to the visual stimulus relatively quickly when it was spatially concordant with the audio stimulus; therefore, the target should have been perceived as a less-imminent threat. A great deal of research suggests that the imminence of predation affects the type of behavior elicited by prey (e.g., Caro, 2005; Fanselow and Lester, 1988; Timberlake and Lucas, 1989). Freezing is an adaptive response to *distant* predators as it eliminates cues, such as movement, that allow the predator to detect prey. Remaining motionless in response to a *nearby* predator, however, may increase the likelihood of being captured. In this situation, it is likely more adaptive for the prey animal to flee or withdraw. Künnapas (1968) noted that the size of an object is one of the most important determinants of distance perception. If the crabs were distracted by the distal acoustic stimulus and therefore were not attending to the visual stimulus, they likely would have first observed the predator later within the trial. At this point, the predator would have been perceived to be much larger (and therefore closer), and would be more likely to elicit withdrawal behavior than freezing. Our results support this hypothesis, since we found that our subjects froze more frequently in the Concordant and Silent conditions than in the Discordant condition.

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This study represents the first time that the spatial relationship between distractor and target has shown to be important to modifying the topography of anti-predator behavior in an invertebrate. Such a result demonstrates the generality of spatial effects on attention-related behavior. This result is perhaps not surprising, given the importance of the spatial relationships between stimulus events in the natural world in assessment operations that are generally critical to animal survival.

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