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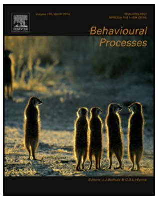

Behavioral evidence illuminating the visual abilities of the terrestrial Caribbean hermit crab *Coenobita clypeatus*

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ABSTRACT

Hermit crabs hide into shells when confronted with potential dangers, including images presented on a monitor. We do not know, however, what hermit crabs can see and how they perceive different objects. We examined the hiding response of the Caribbean hermit crab (*Coenobita clypeatus*) to various stimuli presented on a monitor in seven experiments to explore whether crabs could discriminate different properties of a threatening digital image, including color, brightness, contrast, shape and orientation. We found crabs responded differently to expanding circles presented in wavelengths of light corresponding to what humans see as red, blue, and green. "Blue" stimuli elicited the strongest hiding response (Experiments 1, 2, & 7). "Blue" was also more effective than a gray stimulus of similar brightness (Experiment 3). Hermit crabs were sensitive to the amount of contrast between a stimulus and its background rather than absolute brightness of the stimulus (Experiment 4). Moreover, we did not find evidence that crabs could discriminate orientation (Experiment 6), and mixed evidence that they could discriminate stimulus shape (Experiments 5 & 7). These results suggest that the Caribbean hermit crab is sensitive to color features, but not spatial features, of a threatening object presented on a computer screen. This is the first study to use the hiding response of the hermit crab to examine its visual ability, and demonstrates that the hiding response provides a useful behavioral approach with which to study learning and discrimination in the hermit crab.

1. Introduction

Visual perception provides an important source of information for many animals to find food and mates, detect potential predators and threats, and notice changes in their surroundings (Baldwin and Johnsen, 2009; Kinoshita and Arikawa, 2014). Color and shape are two reliable and useful dimensions in visual signals. The use of color and shape information to make decisions can reduce the uncertainty in the environment and lead to better behavioral adaptation (Behrens et al., 2007).

Color and shape vision have been studied thoroughly in vertebrates, especially in humans (*Homo sapiens*), many primates, and pigeons (*Colomba livia*) (Bovet and Vauclair, 2000; Jacobs, 2013; Lombardi, 2008). While color and shape vision in invertebrates mainly focuses on hexapods and crustaceans (Avarguès-Weber et al., 2011; Gärtner, 2000). The honeybee (*Apis* spp.), bumblebees (*Bombus terrestris*), stingless bee (*Scaptotrigona mexicana)*, parasitoid wasp (Ichneumonidae) and butterflies (Superfamily Papilionoidea) are found to have the ability to perceive color and shape (Ings et al., 2012; Martínez-Harms et al., 2014; Pérez et al., 2012; Sánchez and Vandame, 2012; Stavenga and Arikawa, 2006 Zhang et al., 2004).

Most crustaceans possess only one or two photoreceptor types, which are maximally sensitive to blue/green light between 480 nm and 540 nm (blue/green sensitive R1-7 cells), while in some species a secondary set of UV/blue photoreceptors sensitive near to 400 nm (UV/violet sensitive R8 cells) could also be found (Marshall et al., 1999). However, the stomatopods (mantis shrimps) are found to possess up to 16 different photoreceptor types, which is far exceeding any other animal known (Chiao et al., 2009; Thoen et al., 2014).

Crabs use compound eyes to perceive visual signals, which were thought to have simple apposition eyes like many species of Crustacea, but Nilsson (1988) found that the eyes of many true crabs

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and hermit crabs work as parabolic superposition eyes by employing imaging optics of a conceptually new kind. Color discrimination is found to be not only possible but widespread among many crab taxa at the retinal level, and the discrimination of colors in these taxa is best between blue and yellow, or yellow and ultraviolet (Leggett, 1979). Among crabs, the visual abilities of fiddler crabs (*Uca* spp.) have been most studied, from eye structure, electron micrographs, microvillar banding patterns to functional anatomy. These species are very visual animals which employ a variety of visual signals, from claw-waving displays to brilliant body colors (Alkaladi and Zeil, 2014; Detto, 2007; Zeil and Hemmi, 2006), for social communication.

A number of studies suggest that the hermit crab (Paguroidea) may also have sophisticated visual abilities. One hermit crab species, *Pagurus bernhardus*, has been found to avoid shells that have the greatest contrast with the background, and choose shells that best match the color of their surroundings (Briffa et al., 2008). Another hermit crab, *Clibanarius vittatus*, can discriminate between different geometric shapes with equal surface area, and are also found to be more attracted to horizontal rectangles and less attracted to vertical diamonds (Diaz et al., 1994).

Previous studies in our lab have also found that the terrestrial Caribbean hermit crab (*Coenobita clypeatus*) shows hiding responses to looming visual images (Chan et al., 2010a,b; Stahlman et al., 2011). The methods we have employed consist of presenting visual displays on a monitor designed for human vision to explore simple learning and attention in the hermit crab. Given that the monitor is designed for human vision, it is unclear what aspects of the visual display the hermit crabs are sensitive to. The aim of the experiments reported below was to explore the aspects of the stimuli we typically use, especially color and shape, that the hermit crabs in our experiments can detect and discriminate.

To study hermit crab visual characteristics with the computer monitor, we presented expanding (threatening) images in seven experiments utilizing the procedures previously developed in our laboratory. An expanding image on the monitor is perceived as threatening and causes the crab to hide in its shell. Unpublished experiments from our lab reveal that neither the movement of a visual image across the screen (e.g., from left to right), nor the contraction of an image created by reversing the “looming” image so that it appears to be receding, reliably evoke a hiding response from our hermit crab subjects. These data rule out the role of simple 2D movement cues on the screen as the basis for the effectiveness of our threatening displays. Instead, it appears that a stimulus that simulates the characteristics of a looming image is necessary. We first tested the ability of crabs to detect threatening visual displays consisting of expanding circles presented on an LCD computer screen in each of three wavelengths of light corresponding to the three primary colors, red (700 nm), green (510 nm), and blue (440 nm), as perceived by primates (Experiment 1; for ease of exposition, we will continue to refer to the specific wavelengths of light tested in terms of the corresponding colors as trichromatic humans perceive them). We further assessed the ability of crabs to distinguish between blue and green expanding stimuli using a generalization-of-habituation procedure (Experiment 2). In the third experiment, we tested the ability of crabs to discriminate blue from gray stimuli. In the fourth experiment, we examined whether crabs could discriminate grayscale stimuli with different brightness to test the role of contrast in visual threat detection. We then assessed the ability of crabs to discriminate threatening visual stimuli based purely on shape (Experiment 5) and orientation (Experiment 6). Finally, the seventh experiment directly compared the salience or effectiveness of wavelength of light versus shape in threat detection using the generalization-of-habituation procedure.

2. General methods

2.1. Subjects

Subjects were medium-sized, experimentally-naïve Caribbean hermit crabs (*Coenobita clypeatus*) purchased from a local aquarium store. Upon arrival, they were given a minimum of two weeks to adjust to their new environment. Each crab was marked with a number on the major claw. Crabs were housed in groups of one, two, or four 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 70% humidity in the bins. Plastic lids covered the bins to maintain humidity. Each bin was supplied with Tetrafauna Hermit Crab pellets and new dishes of fresh and salt water three times per week. The coconut substrate was checked regularly and replaced if wet to prevent fungus growth. A heat lamp provided warmth in the room, and room temperature was maintained at 25°C. The room was illuminated on a 14h/10h day-night schedule and room humidity was maintained at 50–75%. Experimental procedures were conducted during the light portion of the cycle. The same subjects participated in several experiments, with a minimum interval of 20 days between experiments to allow rest and recovery.

2.2. Apparatus

The experiment was conducted in a 52 cm × 72 cm × 42 cm open field on a desk surrounded by white wooden planks in a large room (3.7 m × 6.1 m × 2.4 m) lit by two incandescent ceiling lights. Room lights were turned off during experimental procedures. We used a 43 cm Dell LCD monitor (1704FPVt) set at 1024 × 768 resolution to present the visual stimulus. The monitor was set at the default factory settings in all parameters unless otherwise specified. All experimental manipulations of the display and recording of subject response were conducted using Visual Basic 6.0 (Microsoft, Redmond, CA, USA). The crab was secured with ArtMinds Crafty Tack Putty onto a 5.5 cm tall pedestal that was positioned 28.5 cm in front of the LCD monitor. Two Logitech webcams (C250) were used to record all trials. One camera was located 5 cm on the right side of the pedestal to serve as a detector camera to monitor and record the subject's response. The other camera was located on the middle of the top of the wooden plank to record an aerial view of the experiment, including both the subject and the display.

2.3. Procedure

Hiding behavior was scored automatically using the detector camera and a custom automated scoring program. The detector camera's visual field included a 240 × 220 pixel rectangular target region that was used to score the position of the subject with respect to its shell: either hiding inside the shell or emerged from the shell. The computer took a snapshot of this region when the crab was hiding, and then monitored the number of pixels changed relative to this baseline every 0.1 s. At the beginning of each session, after the crab was secured to the pedestal and emerged from its shell, there would be a 90 s period for the program to monitor the amount of pixels that change from when the crab was fully hiding to when the crab was fully emerged. We then established the minimum pixel criterion for scoring the crab's emergence from the shell. This minimum was set as the criterion for scoring the crab as emerged during the session. When the number of changed pixels dropped below 95% of the criterion, the program scored the crab as hiding.

The background of the screen remained black except in Experiment 4 where the screen background was part of manipulation.

On each trial, when the visual stimulus was scheduled to be delivered, at onset it was the size of a single pixel centered at the top of the screen. The stimulus then expanded at a constant rate for 16.4 s until it reached a size of 768 pixels and filled most of the screen. Then the stimulus remained on the screen at full size for 2 s before it disappeared from the screen. An expanding stimulus like this has been used in prior work in our lab to investigate basic behavioral processes of learning and attention in the hermit crab. We took advantage of this natural threat response to probe visual perception in our subjects.

All stimuli were measured at full size on the screen using a photodetector (SpectraScan PR650, Photo Research, Chatsworth, CA) with the camera positioned 10 cm away from and directly facing the monitor to determine the brightness of each image. We report the brightness measures for each stimulus used in each experiment below.

Each trial terminated in one of two ways. If the crab did not hide during the trial, the trial terminated 2 s after the stimulus disappeared from the screen. If the crab hid during the trial, the trial terminated when the crab emerged from the shell again. In either case, the next trial began when the crab emerged from the shell for a consecutive 30 s period. If the crab hid at any time during the 30 s period, the timer was reset until the crab remained out of shell for a consecutive 30 s. Thus, the interval between trials was at least 30 s.

If the hermit crab did not emerge from its shell after 20 min, and had not received any trials in that session, the session was terminated and the crab was returned to its home cage. The crab then participated in the experiment after all other crabs had completed the experiment. If the hermit crab had received at least one trial but did not complete the experiment, its data were not included in the subsequent analysis.

2.4. Analysis

In a pilot experiment and in prior studies, we found by hand scoring the video recordings of each trial that hiding responses could be assorted into four categories: no hide, freezing, partial hide, and completely hiding in the shell. A partial hide accounted for almost half of all hiding responses. Equipment limitations prevented us from automatically recording freezing and partial hides. Freezing and partial hides were thus coded by visual inspection of the video recordings of each trial. Thus, in addition to the automated scoring of hides and no hides, freezing and partial hides were coded by visual inspection of the video recordings of each trial. Freezing was defined as the absence of all observable movement of the limbs, body, and the vibrissae (Ryan et al., 2012). A partial hide was defined as the crab retreating only part of the way into its shell, or rapid jerking movement toward the shell followed by holding still while not completely retracted into the shell. Two independent raters scored freezing and partial hides. Both two raters watched the videos together and whenever there was a discrepancy, they watched the video repeatedly until consensus in scoring was achieved. Thus an inter-rater reliability of 100% was achieved.

All experiments, with the exception of Experiment 1, used a generalization-of-habituation procedure. The generalization-of-habituation procedure has proven very useful for investigating perceptual discrimination. We have previously reported that hermit crabs can habituate to the repeated presentation of a visual threat presented on a computer monitor (Stahlman et al., 2012). The habituation criterion was defined as two consecutive trials on which the subject did not show a complete hide response during the image presentation as determined through automated scoring. Once this criterion was met, the subject then received a test trial with either the same or different stimulus. Note that the automated system scored a freezing response or partial hide as a no hide response, thus, we hand scored the final habituation trial and test trial from the video recordings to determine whether or not the hiding response was the same or different on these two trials. A recovery from habituation due to generalization decrement was recorded for any change in type of response. This included a change from a no hide on the last habituation trial to a partial hide, complete hide, or freezing response on the test trial; and a change from a partial hide or freezing response on the last habituation trial to a complete hide on the test trial.

The threat response system of the terrestrial hermit crab is a complex behavioral system, with different dependent measures differentially reflecting separate factors in the threat-response behavioral system (Watanabe et al., 2012). While our primary interest was the rate of habituation (cf. Stahlman et al., 2011) and recovery from habituation (i.e., generalization decrement) on the generalization tests, where possible, we also collected data on latency to hide (which has proven a useful measure in Chan et al., 2010a,b and Ryan et al., 2012) and hide duration (see Watanabe et al., 2012) measures to more fully explore the behavioral profile in our experiments. We had no *a priori* predictions about the effects of our experimental treatments on latencies to hide or hide durations, thus these measures were collected more for the purpose of exploratory analyses. Shorter latencies to hide have previously been found for more salient stimuli (Chan et al., 2010a,b). Latency to hide was measured for all hiding responses, while hide durations were only measured for complete hides

Latency and duration scores were analyzed with repeated-measures Analysis of Variance (ANOVA). Chi-square tests were used to analyze the proportion of crabs that hid. *t*-tests were used to evaluate habituation rates. All values of dependent variables were presented as untransformed means ± standard error (SE). All statistical tests were two-tailed and $p < 0.05$ was considered statistically significant.

3. Experiment 1

Color is an important factor for object detection in the wild where various wavelengths of light can be found. Many species like the honeybee, butterfly, and parasitoid wasp rely on true color more than shape or brightness for object detection (Desouhant et al., 2010). A recent study indicates that even the nocturnal hawk moth *Deilephila elpenor* can use color vision to discriminate colored stimuli at intensities corresponding to dim starlight (Kelber et al., 2002). Terrestrial hermit crabs vary in colors on their body, legs, claws and shells, and sometimes they change color after molting. They also need to navigate in their environment, such as being required to return to the ocean to reproduce. These factors suggest that color may be important for hermit crab's survival and reproduction.

Visual abilities of organisms tend to be adapted so that the maximum light absorption matches the wavelength(s) of the light with the greatest photon flux in their habitat (Lythgoe, 1979). One possible reason to expect that the terrestrial hermit crab, like many other crustaceans (Marshall et al., 1999), might have a maximum light absorption near wavelengths that correspond what humans see as blue and green is that they are adapted to a coastal environment, and that they have to return to the ocean to reproduce. Thus they should be sensitive to the colors abundant in an ocean and shoreline environment, which tend to be rich in blues and greens but not reds. Also, a prior study found that the maximum absorption of light for the Caribbean hermit crab was near blue and green, which might constrain the ability of this crab to perceive other wavelengths of light (Cronin and Forward, 1988).

This experiment was designed to assess whether crabs could perceive each of three hues: red, green, and blue. We chose these colors because we could use LCD screen technology to present pure wavelengths of light that correspond to these three colors as per-

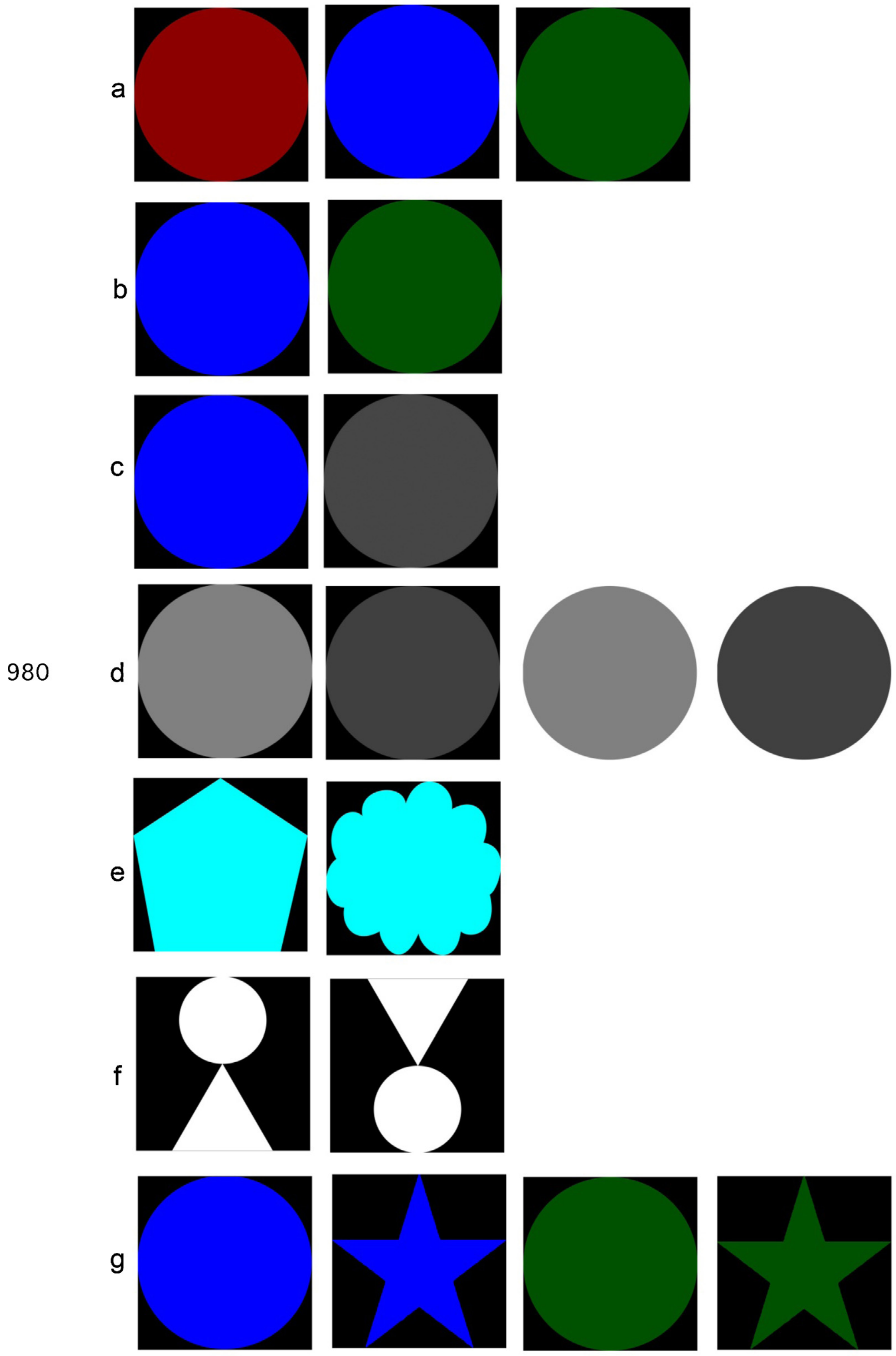

Fig. 1. Stimuli used in the experiments. Stimuli in panel a, b, c, d, e, f, and g were used in experiment 1, 2, 3, 4, 5, 6, and 7, respectively.

ceived by humans. To test for hue perception, we presented each crab with each hue in three separate daily sessions. In the first session, crabs received three consecutive trials with the first color. In the second session, the next color was used, and in the third session the final color was presented. Order of presentation of hue was counterbalanced across subjects so that each hue was equally often the first, second, and third hue presented to individual crabs. On each trial, a circle of the target hue was presented in the manner described in the Procedure section above. If the crab could perceive the stimulus, it should hide into its shell as the circle expands on the screen (Chan et al., 2010a). The more salient the hue, the more likely should the crab notice the stimulus and hide. Thus, the percentage of crabs that hide on each trial provides a measure of how salient is each of the hues.

3.1. Procedures

The subjects were 56 experimentally-naïve hermit crabs. Hue order was counterbalanced across subjects with six levels, $N = 9$ or $N = 10$ per level. Orderings were (a) red–blue–green, (b) red–green–blue, (c) blue–red–green, (d) blue–green–red, (e) green–red–blue, and (f) green–blue–red. Hue was set at red (RGB value: 140, 0, 0), blue (RGB value: 0, 0, 255), and green (RGB value: 0, 82, 0). We equated the brightness of each hue by converting each one into grayscale in Adobe Photoshop CS3 and adjusting their brightness to match (Fig. 1a). Photometric measurements determined that the brightness of each hue was highly similar (Red = 7.22, Green = 6.19, and Blue = 7.32, all units in candles/m^2). There were a maximum of three trials per color per subject in each daily session, and nine trials per subject in total across the three sessions.

3.2. Results and discussion

There was no significant difference in proportion of crabs that hid, latency to hide, and hide duration among the six presentation orders, thus, we collapsed across presentation order for the remaining analyses.

Fig. 2a shows that crabs hid more to the blue circle than to the green or red circles during the first trial ($\chi^2_{22} = 36.93$, $P = 0.024$), and fewer crabs hid to red circle than to either the blue or green circles during the second trial ($\chi^2_{22} = 44$, $P = 0.004$). There were no significant differences in latencies to hide (Fig. 2b) or hide durations (Fig. 2c) among the three colored circles on any trial ($Fs < 2.9$, $Ps > 0.1$).

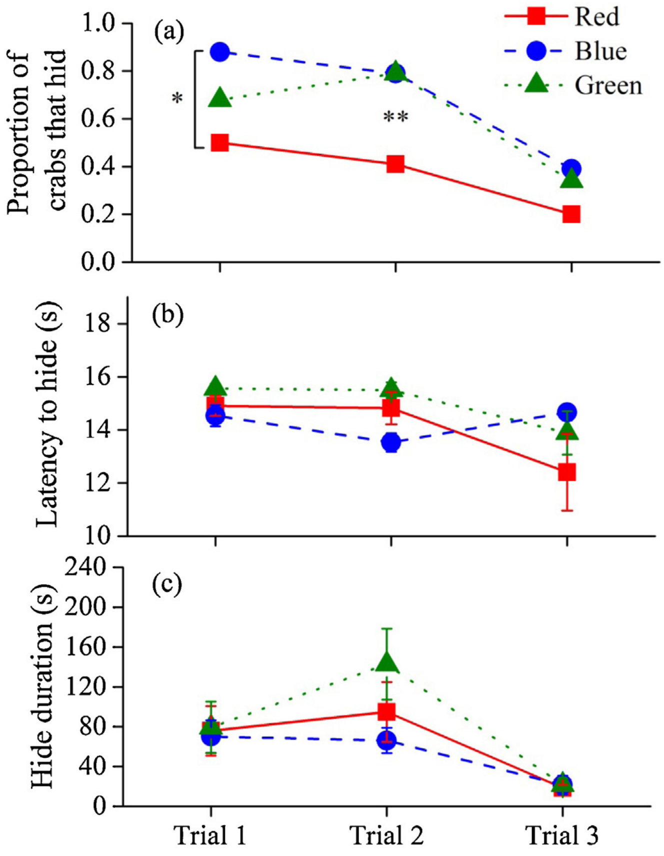

Fig. 2. Proportion of crabs that hid (a), mean latency in seconds to hide (b), and mean hide duration in seconds on each trial (c) for each test condition in Experiment 1. Error bars depict the standard errors of the mean. Red, Blue, and Green in panel a, b, and c denote the color of the stimulus presented during the trial.

Our results indicate that crabs can detect the stimulus presented in each of the individual hues. Moreover, blue seemed to be the most salient hue, while red appeared to be least salient to the crabs. The brightness of each hue tested was very similar, and thus it is very unlikely that the subtle brightness differences contributed significantly to the difference in effectiveness among the hues. In fact, green had the lowest brightness, whereas red and blue were almost the same brightness. So if brightness were contributing to differences in effectiveness of the hues, green should have been less effective than red at eliciting the hide response, which is contrary to what we actually found.

This suggested that the crabs might be able to discriminate between these wavelengths of light, which we directly tested in Experiment 2.

4. Experiment 2

We directly tested the crabs' ability to discriminate between green and blue by presenting one hue repeatedly in a session until the crab reached the criterion for habituation. Following habituation, we presented either the same color again (Group Same) or the other color (Group Different). If crabs could discriminate between green and blue, then a higher proportion of crabs should hide at test in Group Different than in Group Same. That is, once habituated, the crabs should remain habituated to the same stimulus, but should show generalization decrement of habituation to the different color, to the degree that the crabs could perceive the difference.

4.1. Procedure

Fifty-two of the crabs used in Experiment 1 were used as subjects. This experiment used a between-subject design, with Color (Blue or Green) and Group (Same or Different) as factors. Blue (RGB value: 0, 0, 255) and green (RGB value: 0, 82, 0) circles were used as stimuli (Fig 1b). Thus, the 2 × 2 design resulted in four conditions: Blue–Blue (BB, Group Same), Blue–Green (BG, Group Different), Green–Blue (GB, Group Different) and Green–Green (GG, Group Same), with $N = 13$ per condition. We presented each crab with repeated trials of either the blue or green circle following the procedure described in the General Procedure section until the habituation criterion was reached. After reaching habituation, the subject received two more trials on which the circle was presented in the same color (Group Same) or different color (Group Different).

4.2. Results and discussion

Two crabs died during the experiment and three crabs did not complete the experiment, resulting in a total N=47. There was no significant difference in proportion of crabs that hid ($\chi^2_7 = 7.570$, $P = 0.271$; $\chi^2_5 = 3.606$, $P = 0.607$; $\chi^2_5 = 7.372$, $P = 0.194$, respectively, for the first, second and third trial), latency to hide ($Ps > 0.1$), or hide duration ($t_{15} = 1.749$, $P = 0.101$, Cohen's $d = 0.872$, $t_{14} = 2.066$, $P = 0.058$, Cohen's $d = 1.033$, $P = .814$ for trials 1, 2, and 3, respectively) for crabs that received blue versus green circles during the first three habituation trials (Fig. 3a–c). This partially replicates the results from Experiment 1, though we failed to replicate the difference in proportion of crabs that hid to the blue versus green circles on the first habituation trial as observed in Experiment 1. There was no significant difference in trials to habituate to blue and green circles ($t_{24} < 1.0$) (Fig. 3d).

More crabs in Group Different hid on the test trials than did crabs in Group Same ($\chi^2_3 = 16.43$, $P = 0.001$) (Fig. 3e). This was only true, however, for crabs that were habituated to the green circle

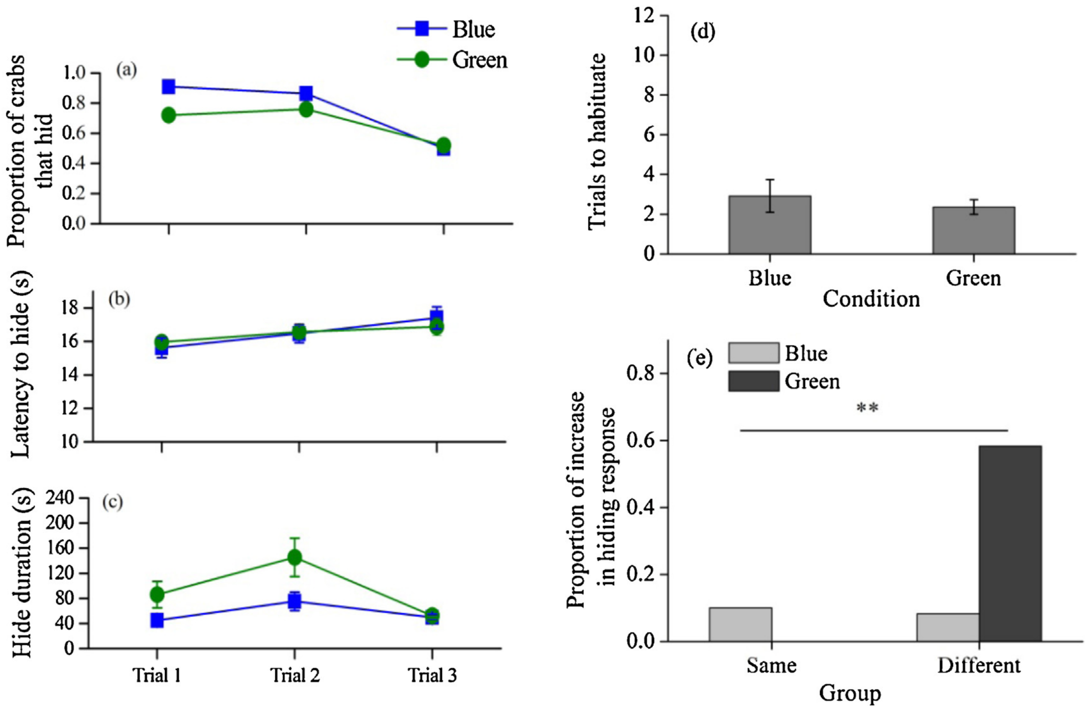

Fig. 3. Proportion of crabs that hid (a), mean latency to hide in seconds (b), mean hide duration in seconds (c) for crabs presented the Blue or Green circles across all three trials of habituation; mean trials to habituate to Blue and Green circles (d), and proportion of increase in hiding response on test trials (e) for each test condition in Experiment 2. Error bars represent standard errors of the mean. Same and Different in panel a denotes that the stimulus used at test was the same as or different from that used during the habituation phase, respectively. Blue and Green in panel b denote the stimulus to which the crab was habituated to during the habituation phase.

and tested on the blue circle. Crabs habituated to the blue circle and tested on the green circle did not hide significantly more than crabs did in Group Same. Thus, the results of the generalization-of-habituation test suggest that blue is significantly more salient than green. The results of Experiments 1 and 2 collectively suggest that the terrestrial Caribbean hermit crab has only one type of photoreceptor that is maximally sensitive to wavelengths of light in the blue spectrum (see General Discussion for elaboration on this point).

5. Experiment 3

This experiment tested the crabs' ability to discriminate between the blue circle and a gray circle of low brightness. We presented a blue or gray circle repeatedly in the session until habituation, then we presented either the same stimulus again (Group Same) or the other stimulus (Group Different). If crabs could discriminate between blue and gray, then a higher proportion of crabs should hide in Group Different than in Group Same.

5.1. Procedure

Thirty-two of the crabs used in Experiments 1 and 2 were used as subjects. This experiment used a between-subject design, with Color (Blue or Gray) and Group (Same or Different) as factors. Blue and gray circles were used as stimuli (Blue: RGB 0, 0, 255, Gray: RGB 70, 70, 70) (Fig. 1c). Photometric measurements determined that the brightness of the gray hue was lower than that of the blue hue (Blue = 7.32 candles/m^2, Gray = 1.06 candles/m^2). The 2 × 2 design resulted in four conditions: Blue–Blue (BB, Group Same), Blue–Gray (BG, Group Different), Gray–Blue (GB, Group Different) and Gray–Gray (GG, Group Same), with $N = 8$ per condition. We presented each crab with repeated trials of either the blue or gray circle following the procedure described in the General Procedure section until the habituation criterion was reached. After reaching this habituation criterion, the subject received two more trials on which the circle was presented in the same color (Group Same) or different color (Group Different). We measured recovery from habituation as an increase in hiding response from the last habituation trial to test trials.

5.2. Results and discussion

Three crabs did not complete the experiment, resulting in a total $N = 29$. Despite having prior experience with the blue but not the gray stimulus, more crabs hid to the blue than gray circle on the first three habituation trials ($\chi^2{}_7 = 16.571$, $P = 0.020$; $\chi^2{}_5 = 14.148$, $P = 0.015$; $\chi^2{}_4 = 14.200$, $P = 0.027$ respectively for the first, second and third trial) (Fig. 4a). Mean latency to hide was shorter to the blue (15.8 ± 0.83 s) than to the gray (18.03 ± 0.45 s) circle during the first trial ($t_{25} = -2.086$, $P = 0.047$, Cohen's $d = 0.83$) (Fig. 4b). Since there was only one crab that showed a complete hide to the gray circle, no statistical analysis could be performed for hide duration, though it appears that the blue circle induced longer hide durations than did the gray circle (Fig. 4c).

Crabs took more trials to habituate to the blue (3.88 ± 1.12) than to the gray (1.47 ± 0.60) circle ($t_{32} = 1.986$, $P = 0.049$, Cohen's $d = 0.70$) (Fig. 4d). In addition, more crabs showed a generalization decrement of habituation on test trials with the blue circle after having been habituated to the gray circle, whereas habituation generalized if they had been habituated to the blue circle and tested on the gray circle ($\chi^2{}_3 = 12.190$, $P = 0.007$) (Fig. 4e). Collectively, these results suggested that crabs could discriminate between blue and gray, and that blue was more salient or threatening than gray.

There are two non-mutually exclusive explanations for the greater effectiveness of the blue than gray stimulus. First, it is possible as suggested by the results of Experiments 1 and 2 that the crab's eye has only a single photoreceptor maximally sensitive to light closest at a wavelength closest to that of our blue stimulus. Alternatively, the greater brightness of the blue than gray

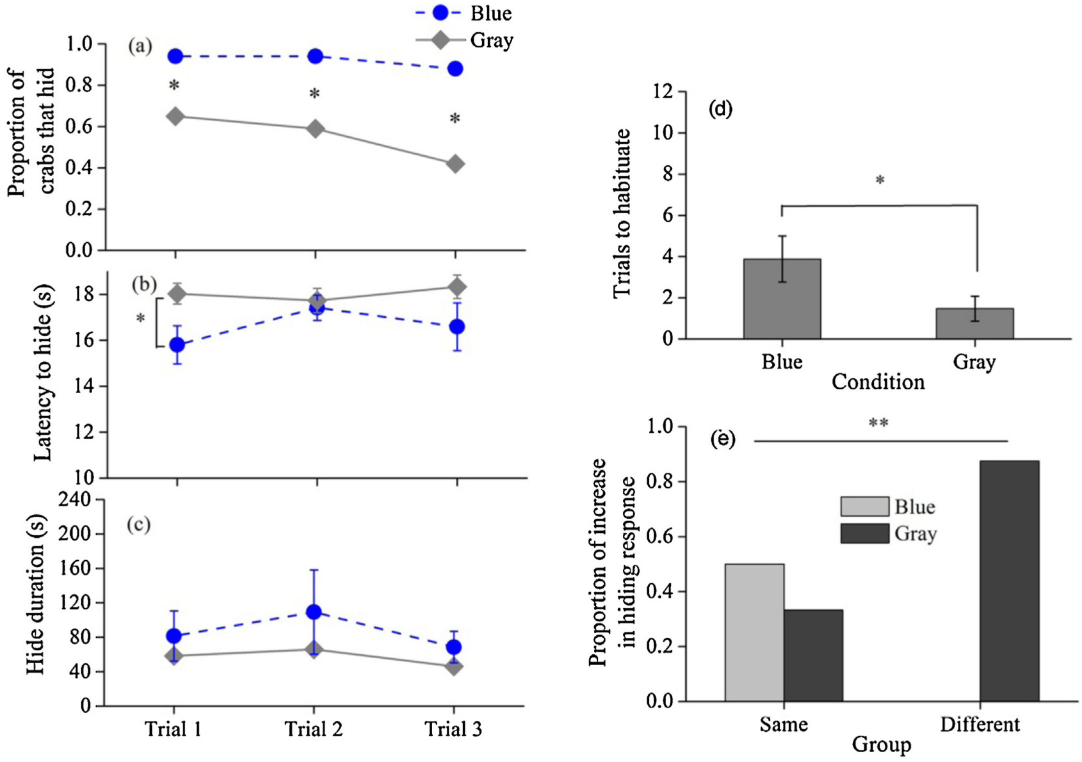

Fig. 4. Proportion of crabs that hid (a), mean latency to hide in seconds (b), mean hide duration in seconds (c) for crabs presented the Blue or Gray circles across all three trials of habituation, mean trials to habituate to the Blue and Gray circles (d), and proportion of increase in hiding response on test trials (d) in Experiment 3. Blue and Gray indicate the stimulus to which the crab was habituated, and Same or Different denote whether the stimulus presented at test was the same or different, respectively, from that used in habituation. Error bars depict standard errors of the mean.

stimulus may have resulted in an increase in perceived salience of the blue stimulus after habituation to the gray stimulus, but a drop in brightness and thus salience, when testing on the gray stimulus after habituation to the blue stimulus. We further explore the role of brightness contrast in Experiment 4.

6. Experiment 4

This experiment assessed whether crabs could discriminate stimuli based on absolute brightness or contrast. We used gray circles of different brightness (bright or dark) and background color (black or white) as stimuli. Crabs were presented with one gray stimulus on a black or white background until habituation; then received test trials with a stimulus of different brightness on the same background. If crabs rely on absolute level of brightness to detect the stimulus, then the light gray circle should always engage more hiding responses than dark gray circle regardless of brightness of the background. If on the other hand, crabs rely on contrast to detect the stimulus, then generalization decrement should be modulated by the absolute amount of contrast between the stimulus and the background.

6.1. Procedure

Thirty-two of the crabs used in Experiments 1–3 were used as subjects. We used bright (RGB: 128, 128, 128) and dark gray (RGB: 64, 64, 64) circles with black or white background as stimuli (Fig. 1d). Photometric measurements determined that the brightness of the light gray hue 25.0 candles/m^2, while dark gray was 1.06 candles/m^2. The white background measured a brightness of 92.6 candles/m^2, whereas a black background was had a brightness of 0 (no pixels illuminated). We used a between-subject design with half of the crabs tested on a Black background and the remaining crabs tested on a White background. During habituation, half the crabs were presented with the bright gray circle, and the remaining crabs were presented with the dark gray circle. Circle brightness (Bright and Dark) and background color (Black and White) were fully counterbalanced, resulting in four conditions (bright gray on black background, dark gray on black background, bright gray on white background and dark gray on white background). For the generalization of habituation test, we used a mixed design. After being habituated to their respective stimulus, crabs then received four trials. The first two trials were control trials and consisted of another presentation of the stimulus to which they had been habituated. The second two trials were test trials that consisted of presentations of the other gray circle to which they had not been habituated. We measured recovery from habituation as an increase in hiding response from the last habituation trial to the control trials and from the last control trial to test trials.

6.2. Results and discussion

A two-way ANOVA with Habituated stimulus brightness (Dark or Bright) and Background (Black or White) as factors revealed a main effect of Background ($F_{1,28} = 9.22$, $P < 0.01$), but no main effect of Habituated stimulus brightness nor an interaction. Thus, crabs took longer to habituate to either stimulus in the presence of the white background than the black background. Crabs took more trials to habituate to the dark gray circle when presented against the white than against the black background ($F_{1,28} = 8.20$, $P < 0.01$), but not significantly more trials to habituate to the bright gray circle when presented against different background colors ($F_{1,28} = 2.05$, $P > 0.16$) (Fig. 5a). The main effect of background may be due to the fact that the crabs were experimentally-naïve with respect to the white background, while the black background had been used in prior experiments in which the crabs had served as subjects. Thus,

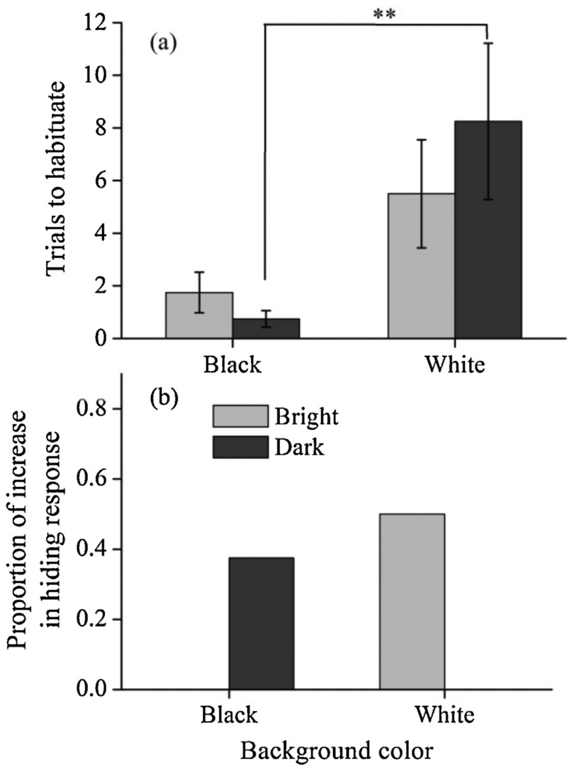

Fig. 5. Mean trials to habituate during the habituation phase (a), and proportion of increase in hiding response on test trials (b) for Bright and Dark gray circles against the Black and White backgrounds in Experiment 4. Bright and Dark in panel b denote the stimulus received during the habituation phase. Error bars depict standard errors of the mean.

the novelty of the white background may have increased sensitization, or reduced transfer of habituation from the familiar black context to the novel white context (Pereyra et al., 2000).

No significant difference was found in proportion of crabs that hid during control trials for either the black or white background conditions ($\chi^2_1 = 1.067$ and 0.410, $Ps > 0.3$).

Three of the eight crabs hid when habituated to the dark gray and tested with the bright gray circle against the black background, while four of the eight crabs hid when habituated to the bright gray circle and tested with the dark gray circle against the white background. By contrast, no crab hid when habituated to the dark gray circle and tested with the bright gray circle against the white background, or when habituated to the bright gray circle and tested with the dark gray circle against the black background (Fig. 5b). Thus, more crabs at test hid when contrast increased ($\chi^2_1 = 8.960$, $P = 0.003$) but not when absolute brightness changed ($\chi^2_1 = 0.183$, $P = 0.669$). This suggested that crabs were sensitive to overall contrast and not absolute level of brightness of the display in preventing generalization of habituation.

These results suggest that the crabs in Experiment 3 were able to discriminate blue and gray circles as a result of the increase in contrast when habituated to gray and tested on blue. This ability may be important since crabs live in coastal areas where weather varies across seasons, and where the sky contains a mixture of grays (clouds) and blues (cloudless). Many species have been found to discriminate color from gray, one species of butterfly, *Papilio xuthus*, was found to be able to discriminate different colors and arrays of grays and also the color contrast and brightness contrast (Kinoshita and Arikawa, 2014). Besides that, the Caribbean hermit crab is mostly nocturnal (Palmer, 1971), and nocturnal species are found to rely on brightness more for object detection (Geisbauer et al., 2004).

7. Experiment 5

This experiment tested whether crabs could perceive differences in object shape. We used a cyan cloud and pentagon as stimuli. We chose to present the shapes in cyan because the crabs had no prior experience in our lab with this hue setting, and as noted below, the brightness was increased relative to our prior experimental stimuli. We presented the cloud or pentagon repeatedly within a session until habituation. Then, at test we presented either the same shape again (Group Same) or the other shape (Group Different). If crabs could discriminate between shapes, then a higher proportion of crabs should hide at test in Group Different than in Group Same.

7.1. Procedure

Thirty-two of the crabs used in Experiments 1–4 were used as subjects. This experiment used a between-subject design with shape (Cloud and Pentagon) and group (Same and Different) as two factors. We equated the surface area, height, and width between the cyan cloud and pentagon. Both stimuli were rendered in the same color (RGB: 0, 255, 255) (Fig. 1e) with a measured brightness of 89.2 candles/m^2. The 2 × 2 design resulted in four conditions: Cloud–Cloud (CC, Group Same), Cloud-Pentagon (CP, Group Different), Pentagon-Cloud (PC, Group Different), and Pentagon–Pentagon (PP, Group Same), with $N = 8$ per condition. We presented each crab over repeated trials of either the cloud or pentagon until the habituation criterion was reached. Then the subject received two more test trials of the same shape (Group Same) or different shape (Group Different). We measured generalization decrement from habituation as an increase in hiding response from the last habituation trial to test trials.

7.2. Results and discussion

Two crabs died during the experiment and two crabs did not complete the experiment, resulting in a final $N = 28$. There was no significant difference in the proportion of crabs that hid ($\chi^2_8 = 10.513$, 3.767 and 2.343, $Ps > 0.2$; Fig. 6a), nor in the latency to hide ($ts < 1$, $Ps > 0.4$; Fig. 6b) for the first three habituation trials. Hide duration was longer to the cloud than to the pentagon on the first trial ($t_{22} = 2.102$, $P = 0.047$, Cohen's $d = 0.90$), but did not differ on the second trial ($t_{11} = 1.802$, $P = 0.099$, Cohen's $d = 1.09$; Fig. 6c). No crab completely hid on the third habituation trial.

Trials to habituate to the cloud (3.33 ± 0.41) and pentagon (2.80 ± 0.66) did not differ ($t_{22} < 1.0$) (Fig. 6d). In addition, there was no difference in proportion of increase in hiding response on the test trials for either stimulus condition (Same or Different) ($\chi^2_3 = 2.30$, $P = 0.513$) (Fig. 6e). These results suggested that crabs either did not perceive the shape of the images, or that shape was not relevant to visual threat detection.

8. Experiment 6

This experiment assessed crabs' ability to discriminate shapes based on orientation. We presented an upright or inverted image repeatedly in a session until habituation. Then, at test we presented either the stimulus in the same (Group Same) or different (Group Different) orientation. If crabs could discriminate between orientations, then more crabs should hide in Group Different than in Group Same.

8.1. Procedure

Thirty of the crabs used in Experiments 1–5, and two crabs used in Experiment 1 were used as subjects. The stimulus was

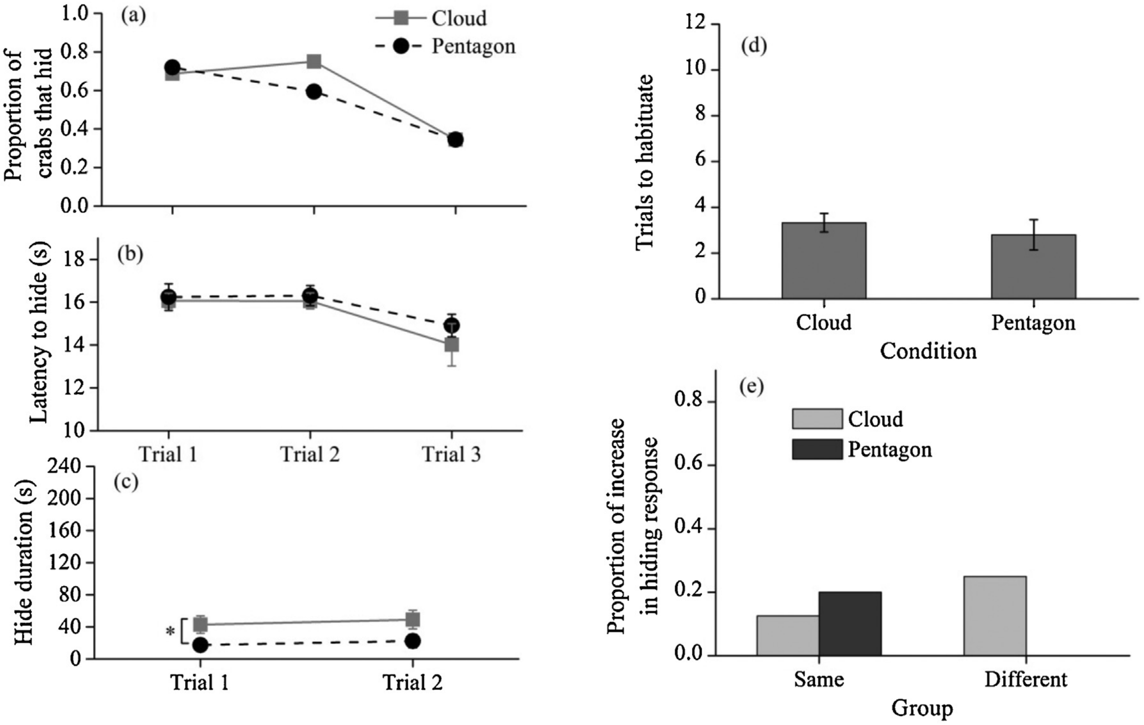

Fig. 6. Proportion of crabs that hid (a), mean latency to hide in seconds (b), and mean hide duration in seconds (c) for the cloud and pentagon during the three habituation trials, mean trials to habituate (d), and proportion of increase in hiding response on test trials (e) in Experiment 5. Cloud and Pentagon denote the stimulus shown during the habituation phase. Same and Different denote whether the test stimulus was the same as or different from, respectively, the habituation stimulus. Error bars denote standard errors of the mean.

a compound of a white circle and triangle presented against a black background (Fig. 1f). The circle above the triangle was arbitrarily referred to as the upright stimulus, while the inversion of this figure was referred to as the inverted stimulus. Both stimuli were equated on all other dimensions (e.g., size, color, brightness, etc.). This experiment used a between-subject design with orientation (Upright and Inverted) and group (Same and Different) as two factors. The 2 × 2 design resulted in four conditions: Upright–Upright (UU, Group Same), Upright-Inverted (UI, Group Different), Inverted-Upright (IU, Group Different), and Inverted–Inverted (II, Group Same), with $N = 8$ per condition. We presented each crab with repeated trials of either the upright or inverted image until the habituation criterion was reached. Then the subject received two more trials of the same orientation (Group Same) or different orientation (Group Different). We measured recovery from habituation as an increase in hiding response on the test trials.

8.2. Results and discussion

One crab did not complete the experiment and was dropped from the analysis, resulting in a final $N = 31$. There was no significant difference in the proportions of crabs that hid ($\chi^2_{15} > 12.601$, $Ps > 0.1$) for the first three habituation trials (Fig. 7a). There was no significant difference in latency to hide to upright or inverted images during the first habituation trial ($t_{26} = 1.059$, $P = 0.300$, Cohen's $d = 0.42$), but approached significance on the second and third trials ($t_{24} = 1.722$, $P = 0.098$, Cohen's $d = 0.70$, and $t_{21} = 1.856$, $P = 0.078$, Cohen's $d = 0.81$ respectively) (Fig. 7b). There was no complete hide for the second and third trial to upright image, thus no statistical analysis was done for hide duration (Fig. 7c). There was no significant difference in trials to habituate to the upright (2.13 ± 0.703) and the inverted images (3.56 ± 0.944) ($t_{29} = -1.201$, $P = 0.239$, Cohen's $d = 0.45$) (Fig. 7d). Finally, none of the test conditions differed in proportion of increase in hiding response ($\chi^2_3 = 3.673$, $P = 0.299$) (Fig. 7e). Thus, we found no evidence that crabs could discriminate stimulus orientation.

Experiments 5 and 6 focused on shape outline and orientation to explore shape discrimination abilities of the hermit crab. We controlled surface area, hue, brightness, and contrast. The null results suggest that hermit crabs might not discriminate among different shapes or orientations. Nevertheless, having compound eyes might affect the capabilities of crabs to discriminate shape as compared to the abilities of the vertebrate eye, and thus caution in generalizing our findings to all cases of shape and orientation is warranted (Horridge, 2012).

9. Experiment 7

We have learned from separate experiments using different stimuli that crabs can discriminate among wavelengths of hue, but little evidence that crabs can discriminate among spatial features of the images such as shape or orientation. A null result for the shape manipulation would be more meaningful in the context of a strong result for the hue manipulation in a single experiment. Thus, this final experiment compared the effect of changing either the color or shape of the habituated stimulus on generalization of habituation at test. We used two colors and two shapes as stimuli. Crabs were divided into two groups: Color or Shape. We presented one stimulus repeatedly in a session until habituation. Then at test, we presented crabs with the stimulus with either a different color (Group Color) or shape (Group Shape). If crabs could discriminate between color or shape, then more crabs should hide on test trials than on control trials.

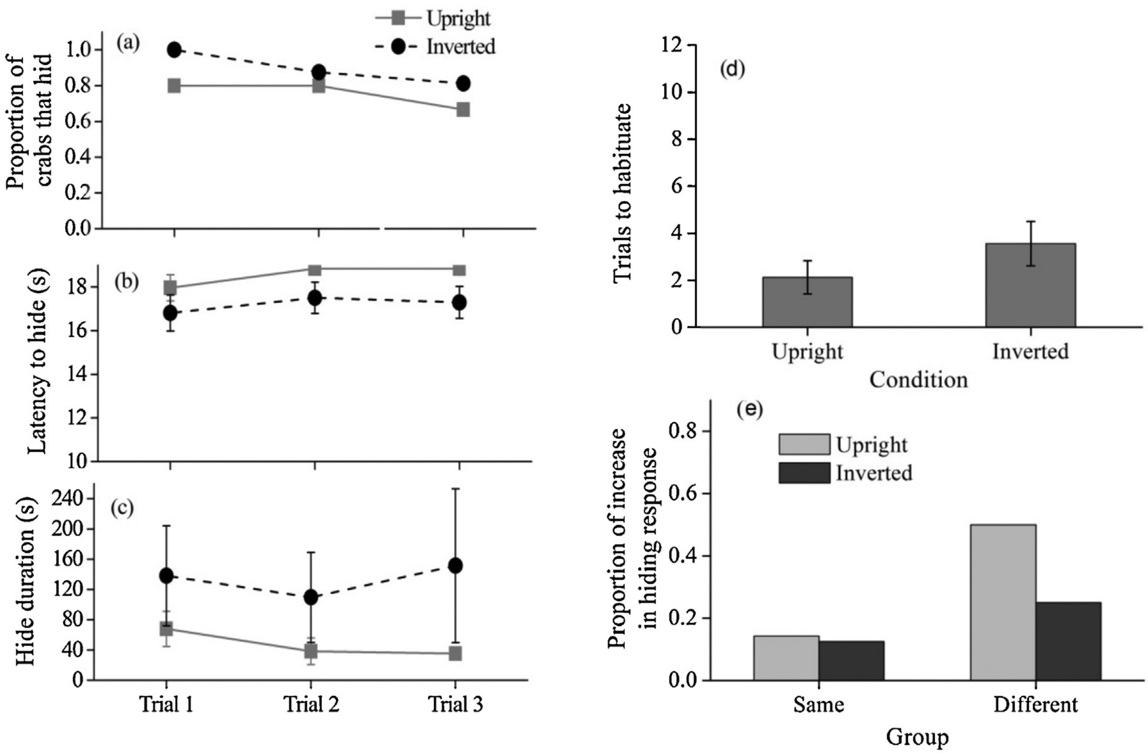

Fig. 7. Proportion of crabs that hid (a), mean latency to hide in seconds (b), and mean hide duration in seconds (c) for the upright and inverted image during the three habituation trials, mean trials to habituate (d), and proportion of increase in hiding response on test trials (e) in Experiment 6. Error bars denote standard errors of the mean. Upright and Inverted denote the orientation of the image to which the crab was habituated. Same and Different denote whether the test stimulus was the same as or different from, respectively, the habituated stimulus.

9.1. Procedure

Thirty of the crabs that used in Experiments 1–6, two of the crabs that used in Experiments 1–4 and 6, and 16 of crabs that used in Experiments 1 and 2 were used as subjects. Blue and green were used as color stimuli and circle and star were used as shape stimuli (Fig. 1g). Blue and green were controlled for brightness, while the circle and star were controlled for height and width. We used a mixed design with crabs divided into two test groups: Color or Shape. We counterbalanced the 16 crabs with less experience and 32 crabs that had more experience to minimize the effect of previous experiment experiences. The crabs were presented with one stimulus first until they were habituated, then two more trials of this same stimulus as control trials (Same test), and then were presented with either the same shape in a different color (Group Color) or the same color in a different shape (Group Shape) for two test trials (Different test). Color (blue and green) and shape (circle and star) were two factors and were fully counterbalanced orthogonal to each other. The 2 × 2 design resulted in four conditions: Blue–Green (BG, Color), Green–Blue (GB, Color), Circle-Star (CS, Shape) and Star-Circle (SC, Shape). We measured generalization of habituation from the last habituation trial to the control trials and from the last control trial to test trials.

9.2. Result and discussion

A 2 × 2 ANOVA conducted on trials to habituate with stimulus color (Blue or Green) and Shape (Star or Circle) as factors revealed main effects of both Color, $F1,_{44} = 6.56$, $P < 0.02$, and Shape, $F_{1,44} = 6.56$, $P < 0.02$, but no interaction (Fig. 8a). As in Experiment 2, blue stimuli were more effective than green stimuli at eliciting hiding behavior. In contrast to Experiment 5, an effect of shape was found, with circle stimuli more effective than star-shaped stimuli.

A 2 × 2 ANOVA conducted on difference for each crab between the number of control test trials with the Same stimulus as used during habituation versus on test trials with a Different stimulus that differed in either Color (blue or green) or Shape (circle or star) found a main effect of Color ($F_{1,44} = 9.32$, $P = 0.004$), but not of Shape nor their interaction (Fs < 1.0) (Fig. 8b and c).

Crabs hid more when color changed but not when shape changed at test, replicating the results of Experiments 2 and 5 within a single experiment. Furthermore, we also replicated the result from Experiment 2 that changing the stimulus wavelength from green to blue, but not from blue to green, resulted in generalization decrement at test. An interesting finding from this experiment was that crabs took more trials to habituate to the circle than to the star. This was not in consistent with the result of Experiment 5 where no difference was found in trials to habituate for cloud and pentagon. Nevertheless, as in Experiment 5, there were no differences in generalization of habituation when the shape was switched at test. One possible explanation for the difference in rate of habitation across the two shapes in Experiment 7 is that, despite the circle and star having the same width and height, the circle had a larger surface area. Thus, the contrast with the background would be different for the circle and star. In general, the visibility of an object depends primarily on the extent to which it contrasts with other parts of the visual field (Fleishman and Endler, 2000). Based on the results of Experiment 4, crabs relied on contrast between the stimuli and the background to discriminate gray circles with different brightness, crabs might also use color/brightness contrast to discriminate different shapes.

10. General discussion

These experiments found that hermit crabs were able to recognize the difference in at least some hues and distinguish hues from

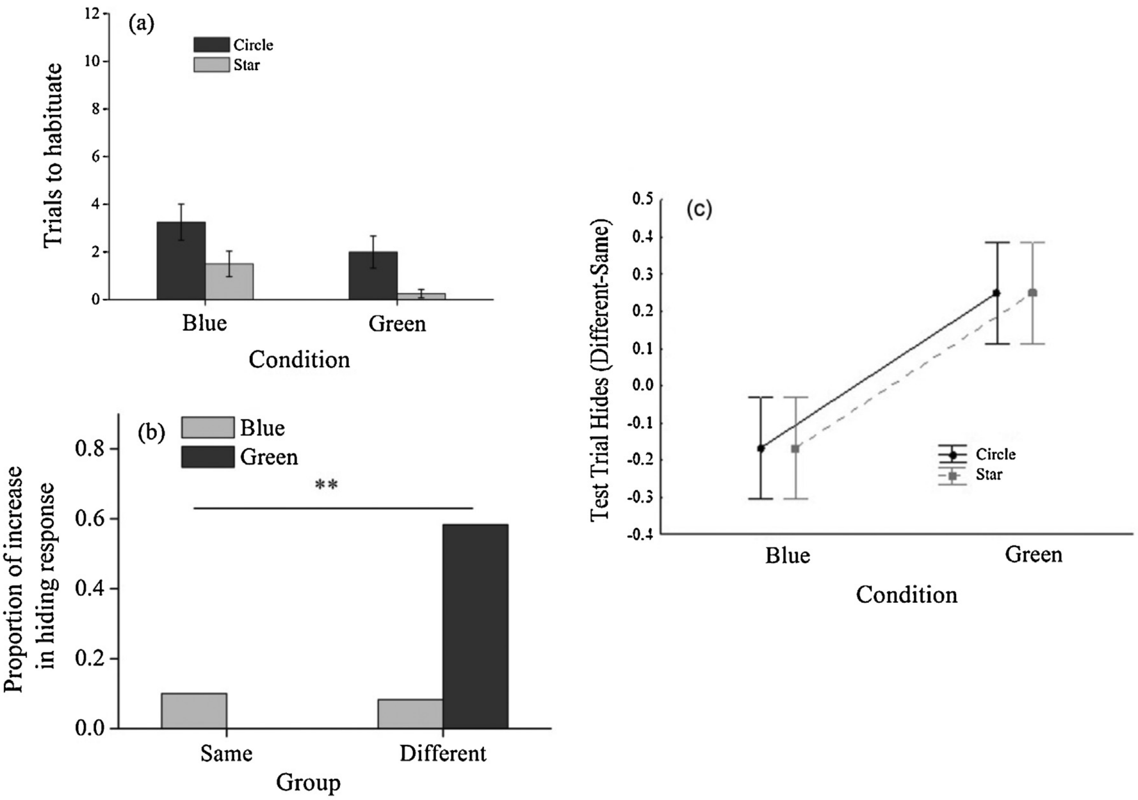

Fig. 8. Mean trials to habituate to each of the four stimuli (blue circle, blue star, green circle, and green star) (a), proportion of increase in hiding response on test trials (b), and test trial hides for each crab between number of hides on test trials with the same stimulus as used in habituation versus a different stimulus as a function of training stimulus color and shape features (c) in Experiment 7. Error bars depict standard errors of the mean. Same means control test trial with same stimulus as used during the habituation phase. Different means test trial with stimulus changed on one dimension (color or shape) from the habituation stimulus.

grayscale images (Experiment 1, 2, 3 and 7). Moreover, crabs could discriminate brightness and used the change in contrast rather than absolute brightness to discriminate images (Experiment 4). When color, brightness, and contrast were held constant, we failed to find evidence that crabs could discriminate different spatial features, such as shape and orientation. However, they might use color/brightness contrast to discriminate shapes (Experiment 5–7).

We must interpret these findings with some restraint. First, the visual system of the hermit crab is quite different from that of a vertebrate. Hermit crabs have compound eyes. Compound eyes have a physiological constraint that has been shown in the honey bee to limit the discrimination of shapes (Horridge, 2012). In addition, we only tested a small number of shapes. Perhaps we would have found greater discrimination if other shapes had been used. Also, unlike humans and other primates which have trichromatic vision, the sensory system's capacity to respond differentially to different wavelengths of light is currently unknown in the species of hermit crab used in these experiments. Our results can only provide clues as to the type of photoreceptor capabilities of the hermit crab eye. Finally, our tests were made using the defensive behavioral system. Given that the type of behavioral system employed in a laboratory experiment can interact with the types of stimuli used (e.g., Garcia and Koelling, 1966; Diaz et al., 1994; Sánchez and Vandame, 2012), perhaps if we had used a different behavioral system, such as feeding, mating, or shell selection, our results may have been different.

The use of video or computer-generated images in place of natural stimuli in our behavioral studies allows for greater precision and experimental control, consistency with stimulus presentation and reliable recording of subject response with minimum disturbance of the subject, which has been usefully applied in many taxa (Bovet and Vauclair, 2000; Death 1998). Nevertheless, the use of such stimuli may have potential drawbacks. It is possible that more naturalistic stimuli would have provided a more ecologically valid preparation with which to study perceptual capabilities of the hermit crab. To this point, however, we have unpublished data collected in our lab showing that hermit crabs fail to respond to naturalistic stimuli, such as photographs of objects in their natural environment, differently than to the highly artificial stimuli used in the current experiments. Finally, the use of a monitor to present stimuli may introduce its own limitations. Computer monitors are designed for human vision, and thus, we cannot be sure that parameters of the monitor setting, such as the rate of flicker, shading of images, reflection and polarization of light, etc., were optimally set for hermit crab vision (Woo and Rieucau, 2011).

We took these points into consideration when designing the experiments. We used primary colors when color was a part of the manipulation tested to be sure that only a single wavelength of light was presented to the subject using the LCD displays. We also restricted shape manipulations to the use of simple shapes to minimize extraneous, non-shape related differences between stimuli. In addition, we used the same monitor, settings, and equipment to conduct all of the experiments to minimize variance due to technique or context. As a caveat, we must acknowledge that what we as humans perceive as red, blue, green, and gray might not be perceived as such by the Caribbean hermit crab. For example, it is possible that crabs have only a single retinal photocell that is sensitive to one wavelength of light closest to the blue color used in our experiments. Such a visual sensory system would account for all of our results manipulating hue. Thus, we cannot claim that the Caribbean hermit crab has color vision, nor that it can discriminate colors, per se. Nevertheless, we can confidently claim that this species of crab can discriminate images that are rendered on an LCD screen in these different colors.

The crabs we used were not laboratory-reared animals, but were wild caught and purchased from a pet-supply company. Thus, their pre-laboratory life experiences were not known and could not be controlled for. We relied on the computer program to automatically detect hiding responses, but some partial hiding and freezing behaviors were too subtle to be detected by the program. Future studies should find more accurate ways to measure these partial hiding and freezing. Nevertheless, we were able to overcome many of these limitations through the careful selection of stimuli, inclusion of control conditions, and careful hand-scoring of video-recorded behavior. This study used behavioral experiments, including simple learning (habituation) to examine the visual ability for object detection in the hermit crab. The design and results of these experiments suggest that the hiding response provides a useful approach to study simple perception, learning, and discrimination in this species.

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