

Changeable cuttlefish camouflage is influenced by horizontal and vertical aspects of the visual background

Alexandra Barbosa · Leonild Litman · Roger T. Hanlon

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Abstract Cuttlefish change their appearance rapidly for camouflage on different backgrounds. Effective camouflage for a benthic organism such as cuttlefish must deceive predators viewing from above as well as from the side, thus the choice of camouflage skin pattern is expected to account for horizontal and vertical background information. Previous experiments dealt only with the former, and here we explore some influences of background patterns oriented vertically in the visual background. Two experiments were conducted: (1) to determine whether cuttlefish cue visually on vertical background information; and (2) if a visual cue presented singly (either horizontally or vertically) is less, equally or more influential than a visual cue presented both horizontally and vertically. Combinations of uniform and checkerboard backgrounds (either on the bottom or wall) evoked disruptive coloration in all cases, implying that high-contrast, non-uniform backgrounds are responded to with priority over uniform backgrounds. However, there were differences in the expression of disruptive components if the checkerboard was presented simultaneously on the bottom and wall, or solely on the wall or the bottom. These

results demonstrate that cuttlefish respond to visual background stimuli both in the horizontal and vertical plane, a finding that supports field observations of cuttlefish and octopus camouflage.

Keywords Visual ecology · Cephalopod behavior · *Crypsis* · Disruptive coloration · *Sepia officinalis*

Abbreviations

| | |
|----------|----------------------------------|
| AHB | Anterior head bar |
| AMB | Anterior mantle bar |
| ATML | Anterior transverse mantle line |
| <i>M</i> | Mean |
| MMS | Median mantle stripes |
| PMS | Paired mantle spots |
| PTML | Posterior transverse mantle line |
| WAT | White arm triangle |
| SE | Standard error |
| WHB | White head bar |
| WMB | White mantle bar |
| WPT | White posterior triangle |
| WS | White square |

Both A. Barbosa and L. Litman are first authors.

A. Barbosa
Institute of Biomedical Sciences Abel Salazar (ICBAS),
University of Porto, Porto, Portugal

A. Barbosa (✉) · R. T. Hanlon
Marine Resources Center, Marine Biological Laboratory,
Woods Hole, MA, USA
e-mail: abarbosa@mbl.edu

L. Litman
Department of Psychology, New York University,
New York, NY, USA

Introduction

To evade visual detection, cephalopods (squid, octopus and cuttlefish—Phylum Mollusca, Order Cephalopoda) have diverse and refined camouflage patterns (cf. Cott 1940; Packard and Sanders 1971; Packard and Hochberg 1977; Hanlon and Messenger 1996). Cephalopod skin can change rapidly in pattern, color, brightness/contrast, and texture, thus allowing the animals to produce a wide variety of body patterns (defined as the total appearance of the animal, to include chromatic, textural, postural and locomotor

components) for both camouflage and communication. This changeable repertoire of adaptive coloration is achieved by a system of dermal-pigmented organs, or chromatophores, accompanied by structural reflectors called iridophores and leucophores (Cloney and Brocco 1983; Messenger 2001; Mäthger and Hanlon 2007). A simplified scheme of the cephalopod neural pathway involved in their dynamic pattern changes is eye–optic lobe–lateral basal lobe–chromatophore lobes–skin (Boycott 1961).

The particular camouflage pattern that an animal produces on a given substrate, and the extent of its expression, depends almost entirely upon visual information in the immediate background (Holmes 1940; Hanlon and Messenger 1988). Thus it is possible in the laboratory to explore how these animals perceive their visual environment by presenting them with controlled visual stimuli and observing the corresponding body pattern (e.g. Marshall and Messenger 1996; Chiao and Hanlon 2001a, b; Barbosa et al. 2004, 2007; Chiao et al. 2005; Mäthger et al. 2006, 2007; Kelman et al. 2007; Shoet et al. 2006).

Cuttlefish live in a wide variety of environments where visual cues often come from sand, gravel, rocks, algae and corals that are underneath or beside the animal. Field observations have also shown that cephalopods pay attention to naturally occurring, vertically oriented backgrounds in their environment (Fig. 1).

Very little is known about the way in which visual cues in the vertical field of view can affect camouflage. Much of the laboratory work done in assessing cuttlefish's visual abilities and camouflage behavior has focused on the visual cues on the substrate below the animal. This is based partly on some initial trials suggesting that vertical "walls" do not exert the primary influence on body patterning of cuttlefish (Hanlon and Messenger 1988). However, Hanlon and Messenger's trials only looked at the effects of uniformly colored dark or light walls. In this study, we revisited this issue since a great deal more research on visual perception of cuttlefish has recently been conducted.

Cuttlefish, *Sepia officinalis*, show an impressive repertoire of camouflage patterns, but these can be synthesized into variations of three pattern types: Uniform (in which contrast variation is minimal or absent), Mottle (defined as small light and dark splotches throughout the skin, with moderate contrast), and Disruptive (characterized by irregular patches of different shape, scale, orientation, contrast and color) (Hanlon and Messenger 1988; Hanlon 2007).

Uniform (or uniformly stippled) body patterns can be elicited on uniform backgrounds, such as plain artificial substrates, or uniformly small-grained sand (Hanlon and Messenger 1988; Chiao and Hanlon 2001a; Langridge 2006; Mäthger et al. 2006, 2007; Kelman et al. 2007).



Fig. 1 Camouflage on *Sepia apama* correlated to the vertical structures of the visual background (photos credits *top* Roger T. Hanlon, and *bottom* Justin Marshall)

Mottle body patterning can be elicited on a black and white checkerboard with a check size of roughly 4 and 12% of the animal's white square (WS) skin component (Barbosa et al. 2004, 2007). Disruptive body patterns can also be evoked by presenting a cuttlefish with a black and white checkerboard substrate, specifically when each individual WS within the checkerboard is between 40 and 120% of the area of the animal's WS (Barbosa et al. 2007).

By taking advantage of knowing which visual stimuli elicit uniform or disruptive patterns, we conducted two experiments to determine if cuttlefish cue visually on vertical background information for camouflage, and to what extent horizontal or vertical cues can influence changeable camouflage patterns.

Materials and methods

Animals and experimental protocol

Nine (Experiment 1, performed in 2003) and eight (Experiment 2, performed in 2004) cuttlefish *S. officinalis* were used for behavioral tests (4.5 and 2.7 cm average mantle lengths, respectively). All cuttlefish were reared and maintained at the Marine Resources Center of the Marine Biological Laboratory.

Each animal was placed randomly inside a black-lined rectangular divider (Experiment 1: 20 × 28 × 11 height) or a circular arena (Experiment 2: 13 cm diameter × 5.6 cm high). Circular arenas offer an advantage by reducing shadows and preventing animals from sitting in a corner, which simplifies image analysis. In this confined area, cuttlefish were presented with the different experimental backgrounds. The rectangular divider/arena was placed inside a running seawater tank (30 cm × 50 cm × 15 cm) enclosed on four sides by a black felt chamber. A Sony digital video camera mounted above the tank recorded the cuttlefish responses on the different experimental conditions over a period of 30 min (record for 2 s every 1 min interval via the camera intervalometer). An external monitor outside the experimental setup allowed remote viewing to reduce experimenter interference. Every animal was allowed a minimum of 5 min acclimation time. An animal was considered acclimated when excessive swimming and hovering movements had ceased and a stable body pattern was shown.

Experimental design

Experiment 1

A uniformly gray substrate was used to elicit uniform coloration and a black and white checkerboard substrate was

used to elicit disruptive coloration. The size of each check was roughly the same as the area of the cuttlefish’s WS skin component (e.g. Mäthger et al. 2006; Barbosa et al. 2007). Both substrate patterns were computer-generated, and the paper on which they were printed was laminated to be waterproof. The animals were tested on three experimental conditions: (1) bottom: checkerboard; wall: black (Check-Black); (2) bottom: gray; wall: checkerboard (GrayCheck); (3) bottom: gray; wall: black (GrayBlack) (Fig. 2a). This experiment was designed specifically to test if vertical backgrounds influence camouflage patterns in cuttlefish. Whereas previous studies have shown that a checkerboard pattern elicits disruptive coloration when it is presented on the bottom of the experimental chamber, we anticipated that a checkerboard pattern would elicit Disruptive coloration whether it was presented vertically or horizontally. In other words, if the bottom substrate were the predominant one, we would expect uniform coloration on the GrayCheck condition. We presented the animals with gray substrate instead of black because it is known that cuttlefish can become stressed and are slower to settle and occasionally show inappropriate patterns on black substrates (Barbosa, personal observation, Hanlon and Messenger 1988).

Experiment 2

Two types of visual backgrounds were used: a white and black checkerboard (to elicit disruptive coloration) and a uniformly brown sand substrate (to elicit a uniform/stipple coloration). Brown sand was glued, with standard acid-free rubber cement, onto a sheet or onto the circular arena of acrylic plastic. We choose sand rather than an artificial laminated substrate because animal acclimation is reduced on natural substrates. Four experimental chambers were constructed from these backgrounds (Fig. 2b), where the checkerboard pattern and the sand substrate were used either as the wall or as the bottom of the arena in the

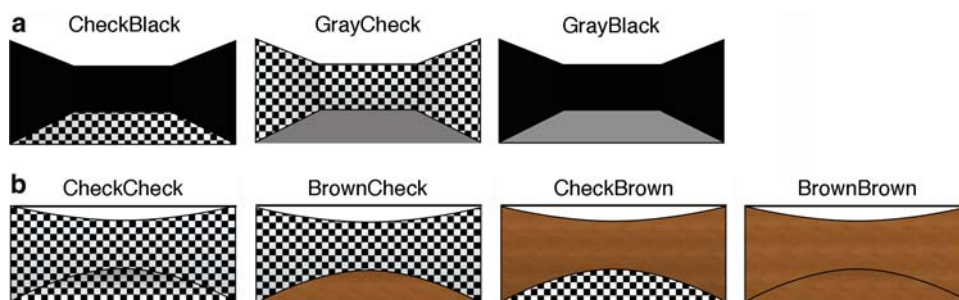


Fig. 2 Schematic representation of the experimental conditions used to determine whether visual cues oriented vertically had an effect on the cuttlefish’s body pattern. **a** Experiment 1: CheckBlack—bottom: checkerboard; wall: black; GrayCheck—bottom: gray; wall: checkerboard; GrayBlack—bottom: gray; wall: black. **b** Experiment 2: Check-

Check—bottom: checkerboard; wall: checkerboard; BrownCheck—bottom: brown sand; wall: checkerboard; CheckBrown—bottom: checkerboard; wall: brown sand; BrownBrown—bottom: brown sand; wall: brown sand

following four combinations: (1) bottom: checkerboard; wall: checkerboard (CheckCheck); (2) bottom: brown sand; wall: checkerboard (BrownCheck); (3) bottom: checkerboard; wall: brown sand (CheckBrown); (4) bottom: brown sand; wall: brown sand (BrownBrown).

Here we tested if animals would differ in the body pattern response when the same cue was presented singly (bottom or wall) or together, which was not addressed in Experiment 1. We expected (1) that strong patterning responses, whether disruptive or uniform, would be elicited when both horizontal and vertical information provided the same visual cue; (2) combinations of uniform and checkerboard backgrounds would evoke disruptive coloration (in accordance with the results from Experiment 1); and (3) that there would be no differences in disruptive coloration whether the visual cue (checkerboard) was presented on the bottom or wall.

Body pattern analysis

For body pattern grading of Experiment 1, one image was taken from the video recording every 6 s, resulting in 10 images per animal per condition. In Experiment 2, one image was taken every 10 s, yielding 6 images per animal per condition, for a total of 270 images for Experiment 1 and 192 images for Experiment 2. To prevent experimenter bias, the background of each image was removed using Photoshop (Adobe Systems, Inc.) before images were graded. These images were named in a random fashion and their origin was only re-established after grading had been completed.

Disruptive patterning in cuttlefish consists of up to 11 individual dark and light skin components (Fig. 3), which are independent physiological units that can be shown singly or in combination with each other (Hanlon and Messenger 1988). The skin components are the result of selective expansion (for dark components) or retraction (for light components) of chromatophores. To determine the responses of the animals to different experimental conditions, the images were graded for disruptiveness using the grading scheme described in Mäthger et al. (2006). All components can be shown with varying intensities, from 0 (no expression) to 1 (weak expression), 2 (moderate expression) or 3 (strong expression). According to this grading scheme, an animal can be given a total grade ranging from 0 (no expression of any disruptive components, or uniform/stipple coloration) to 33 (maximum expression of all 11 disruptive components, resulting in a strongly disruptive body pattern). This method has also been used in other studies (Barbosa et al. 2007; Chiao et al. 2007; Mäthger et al. 2007). The grades of all images obtained for each animal on each condition were averaged. We also analyzed images where cuttlefish showed disruptive coloration for

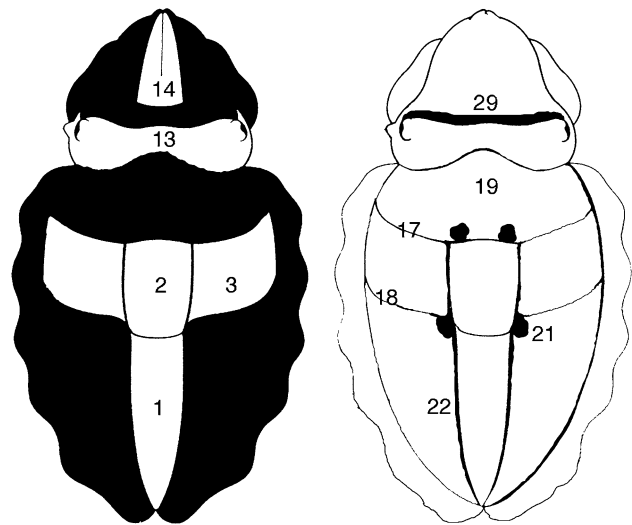


Fig. 3 Eleven chromatic components were analyzed in evaluating body pattern responses of the cuttlefish. Light chromatic components: White posterior triangle (1), White square (2), White mantle bar (3), White head bar (13), White arm triangle (14). Dark chromatic components: Anterior transverse mantle line (17), Posterior transverse mantle line (18), Anterior mantle bar (19), Median mantle stripes (22), Anterior head bar (29), Paired mantle spots (21). These components were originally described and numbered by Hanlon and Messenger (1988). For consistency, we have listed these numbers here. See text for grading method

unilateral or asymmetrical expression of disruptive components.

Results

Cuttlefish response to the different experimental conditions

Cuttlefish showed disruptive coloration on the CheckBlack and GrayCheck conditions (Fig. 4a). On the GrayBlack condition, where no visual stimuli to elicit disruptive coloration were present, cuttlefish showed mostly uniform/stipple body patterns. Figure 4b shows the average disruptive score on each of the experimental conditions. A one-way repeated measures ANOVA showed that there were differences among the experimental conditions, $F(2, 16) = 101.57$, $P < 0.001$. Planned pair-wise comparisons showed further that there was a significant difference between the GrayBlack condition and the CheckBlack condition, $F(1, 8) = 147.44$, $P < 0.001$, and between the GrayBlack and GrayCheck conditions, $F(1, 8) = 188.19$, $P < 0.001$. However, the CheckBlack substrate did not differ significantly from the GrayCheck substrate, $F(1, 8) = 0.241$, $P = 0.63$. The disruptive coloration in response to a checkerboard wall demonstrates that this visual cue can initiate disruptive coloration when presented only in the vertical field of view.

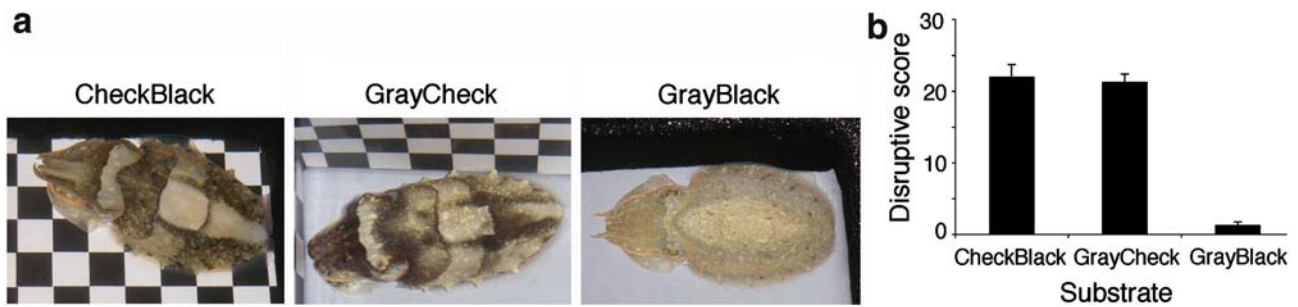


Fig. 4 Experiment 1. Cuttlefish respond to visual background stimuli both on horizontal and vertical surroundings. **a** Disruptive coloration was evoked on both CheckBlack and GrayCheck treatments. A uniform/stipple coloration was evoked on the GrayBlack treatment. **b**

Average disruptive score of cuttlefish on conditions CheckBlack, GrayCheck and GrayBlack. On the GrayBlack condition, due to lack of visual stimuli to trigger disruptive coloration, the disruptive score is almost null. *Error bars* are SE

In Experiment 2, cuttlefish exhibited disruptive coloration whenever a checkerboard pattern was presented in the experimental chamber (Fig. 5; experimental conditions CheckCheck, BrownCheck and CheckBrown). In the BrownBrown condition, cuttlefish showed a uniform or uniformly stippled body pattern (Fig. 5a).

In this analysis, we examined whether a stronger disruptive pattern would be elicited when both the bottom and the wall were checkerboard (CheckCheck) than when checkerboards were not presented simultaneously (BrownCheck and CheckBrown). A one-way repeated measures ANOVA showed that there were significant differences among the four groups, $F(3, 21) = 89, P < 0.0001$. As can be seen in Fig. 5b, the highest averaged disruptive scores were found in the CheckCheck condition. The BrownBrown condition led to an almost null disruptive score. Pair-wise planned comparisons showed that there was a significant difference between the CheckCheck and CheckBrown conditions, $F(1, 7) = 33.2, P < 0.01$. The disruptive scores in the CheckCheck condition were marginally—but not significantly—higher than those on the BrownCheck condition, $F(1, 7) = 5.22, P = 0.056$. There were no significant differences in overall disruptive scores between the BrownCheck and the CheckBrown conditions, $F(1, 7) = 3.47, P = 0.15$.

The cuttlefishes' performance on the BrownCheck condition is best described as being variable. Cuttlefish in this case were sometimes as disruptive as in the CheckCheck condition, and sometimes less disruptive than in the CheckBrown condition. Importantly for characterizing the response on the BrownCheck condition, although the averaged disruptive score quantifies the strength of expression of all disruptive components, it does not provide information about which of the components were shown (i.e., qualitative differences in the disruptive pattern). While the extent of the disruptive response for the BrownCheck and CheckBrown conditions were not statistically different, the animals on the CheckBrown condition, but not in the BrownCheck condition, showed some patches of mottle coloration. In this sense there was a qualitative difference in patterning between the two conditions.

Disruptive component expression according to experimental conditions

To further understand the differences between the overall body patterning in the CheckCheck substrate and the BrownCheck and CheckBrown substrates, we took a closer

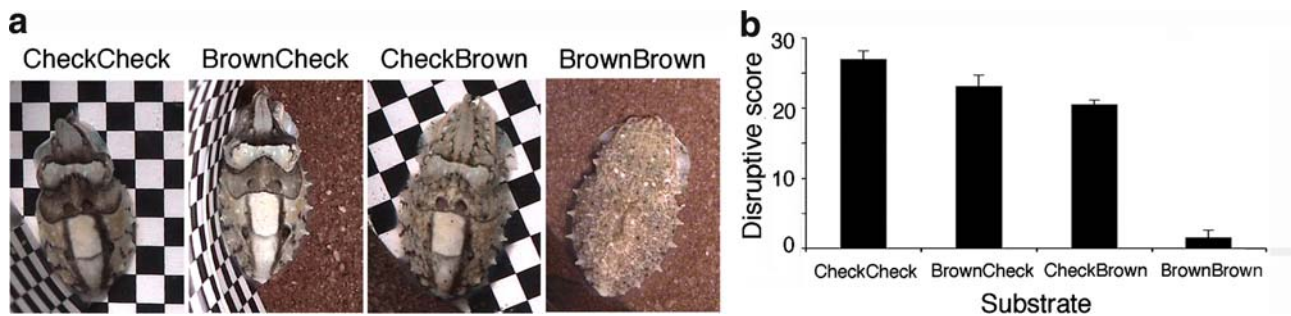


Fig. 5 Experiment 2. **a** Disruptive coloration was evoked whenever a checkerboard was presented either on the wall (BrownCheck), on the substrate (CheckBrown), or both (CheckCheck). A uniform/stipple body pattern was shown when brown sand was presented on both substrate and wall (BrownBrown). **b** Average disruptive score of cuttle-

fish. Disruptive scores were higher when checkerboards were presented simultaneously on the wall and substrate (CheckCheck), than when presented singly on the wall (BrownCheck) or substrate (CheckBrown). *Error bars* are SE

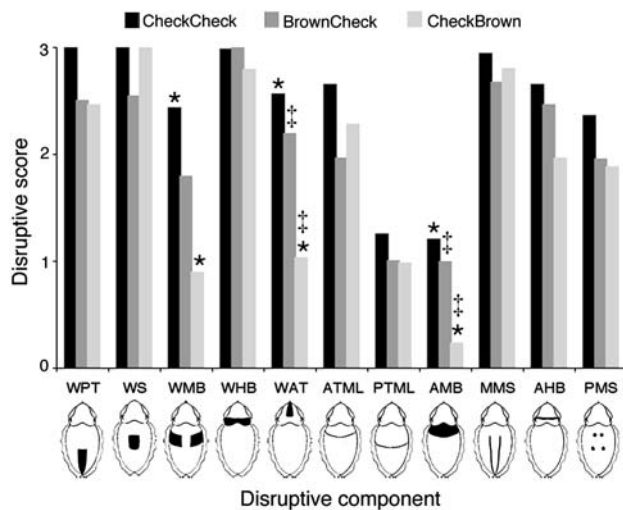


Fig. 6 The expression of three skin components (WMB, WAT, AMB) differed significantly between the CheckCheck and the BrownCheck conditions (*asterisk*) and the CheckBrown and the BrownCheck conditions (*double dagger*). No differences were found between the CheckCheck and the BrownCheck treatments. *WPT* white posterior triangle, *WS* white square, *WMB* white mantle bar, *WHB* white head bar, *WAT* white arm triangle, *ATML* anterior transverse mantle line, *PTML* posterior transverse mantle line, *AMB* anterior mantle bar, *MMS* median mantle stripes, *AHB* anterior head bar, *PMS* paired mantle spots (see Fig. 2 for these skin components)

look at the expression of each of the 11 disruptive components on those 3 substrates.

Figure 6 shows disruptive component grades as a function of substrate. Three disruptive components differed significantly in their expression in the three experimental conditions. The White mantle bar (WMB) component was weakly expressed in the CheckBrown condition ($M = 0.89$) and varied significantly from the mean score in the CheckCheck condition ($M = 2.43$) ($F = 36.19$, $P < 0.01$). There was a statistically significant difference between the White arm triangle (WAT) in the CheckBrown condition ($M = 1.03$) and the BrownCheck condition ($M = 2.19$) ($F = 11.91$, $P = 0.02$). In addition, the WAT score in the CheckCheck substrate ($M = 2.56$) was significantly higher than the mean score in the CheckBrown condition ($F = 31.79$, $P < 0.01$). Finally, there was a statistically significant difference between the Anterior mantle bar (AMB) mean in the CheckBrown ($M = 0.23$) and the BrownCheck ($M = 0.99$) substrates ($F = 27.85$, $P < 0.01$). Also, the AMB mean score in the CheckCheck substrate ($M = 1.20$) was significantly higher than the mean score in the CheckBrown condition ($F = 12.77$, $P = 0.01$).

On the CheckCheck, BrownCheck and CheckBrown substrates, the White square (WS), White head bar (WHB), and Median mantle stripes (MMS) components were strongly expressed across all conditions. The Anterior transverse mantle line (ATML), Anterior head bar (AHB) and Paired mantle spots (PMS) were moderately expressed

across all conditions. The Posterior transverse mantle line (PTML) was weakly expressed across all conditions. For these seven components, means across the three substrates did not differ from each other significantly.

Unilateral and asymmetrical expression of disruptive components

Unilateral or asymmetrical expression of at least one disruptive component was seen in 72% of images in all conditions except BrownBrown (6% of unilateral expression and 94% of asymmetrical expression). Those components were the ATML, PTML, AMB, MMS and PMS (see Fig. 3, components 17, 18, 19, 22 and 21, respectively). Note in Fig. 5 that the expression of the MMS is stronger on the right side of the animal on the CheckCheck, BrownCheck and CheckBrown conditions. Asymmetrical expression of disruptive components was more common on the BrownCheck condition (44%) than on the CheckCheck (37%) or the CheckBrown conditions (20%). Unilateral expression was not observed on the CheckBrown condition and it was twice as frequent on the BrownCheck condition than on the CheckCheck condition. Interestingly, the asymmetrical or unilateral expression of components occurred in 98% of the cases on the side of the cuttlefish that was away from the wall. Furthermore, it was also common for the animals to stretch their skin and move chromatic components away from the wall.

Discussion

We found that visual cues arranged in the vertical field of view are important cues determining the camouflage patterns of cuttlefish. The experiments demonstrated three main points: (1) a checkerboard elicits disruptive coloration when presented either vertically or horizontally; (2) presenting the checkerboard pattern both horizontally and vertically elicits a stronger response than when it is presented only horizontally or vertically; and (3) with this experimental setup, visual cues that elicit disruptive coloration take precedence over those that elicit uniform coloration.

Do vertical cues have a stronger effect on cuttlefish camouflage than horizontal cues?

The variability of the animal's responses in the BrownCheck group precludes us from drawing firm conclusions about whether vertical cues have a stronger effect on disruptive coloration than horizontal ones, but results from Experiment 1, where no differences were found between the disruptive grade from the CheckBlack and the GrayCheck, suggest that there are no such differences. There

was, however, different expression of disruptive components between the CheckCheck and the CheckBrown and the BrownCheck and CheckBrown; furthermore, animals on the CheckBrown condition showed some patches of mottle coloration, which resulted in qualitative differences in patterning between conditions.

As a result of this research, the experimental protocol used in this laboratory since the completion of this study in 2004 has been changed by presenting the cuttlefish with the same visual input both on the floor and wall of the experimental arena (e.g., Mähger et al. 2006; Chiao et al. 2007). Nevertheless, we acknowledge that in this study we only focused on two of the three major body patterns (Uniform and Disruptive, not Mottle) and that the details of how vertical or horizontal stimuli in the animal's visual field evoke a certain body pattern is still not fully understood. Cuttlefish have a highly developed visual system, in ways similar to vertebrates (Packard 1972; Messenger 1991; Muntz 1999; Groeger et al. 2005). The eye has an intriguing W-shaped pupil. How this pupil might influence the extent of the visual field is unknown. So far, we know that *S. officinalis* has a visual field extending over approximately 160°–170° in the horizontal field of view and approximately 70°–80° in the vertical field of view (L. M. Mähger, unpublished data). While these animals do not have a fixed 360° field of view, they can rapidly obtain a 360° field by moving their eyes. Having such a broad field of view may be indicative of their seemingly accurate detection of three-dimensional (3D) objects and predators.

A major focus of cephalopod camouflage research is to develop an understanding of how camouflage decisions are influenced by objects and materials in the animal's immediate visual environment. One could expect that a cuttlefish, if solely paying attention to visual cues derived from the bottom, would show uniform/stipple coloration on the Gray-Check or BrownCheck conditions, and show disruptive coloration on the CheckBlack or CheckBrown conditions. In the same fashion, it could be assumed that a cuttlefish settled near a rock on sand, could resemble the rock or say, possibly the sand. In addition to observations in the wild (Fig. 1), we have seen in the laboratory that cuttlefish preferably position themselves near an object (artificial algae or real rocks). For example, when settled near a smooth rock, they will assume the coloration and texture of the rock, the body shape will be such that the arms are curled underneath the head in an apparent attempt to resemble the rock.

Differential expression of skin components and possible consequences

Overall, the expression of disruptive components in cuttlefish was similar when the checkerboards were part of the vertical field (CheckCheck and BrownCheck conditions).

However, 3 of the 11 disruptive components were more strongly expressed when the checkerboard patterns were placed in the vertical field. Two of these components, WMB and AMB, share a common feature—they are the largest disruptive skin components that make up the disruptive patterns of *S. officinalis*—and they are expressed from the middle of the body to the edge of the cuttlefish's mantle. These two components, along with the WAT (also expressed more strongly when checkerboards presented vertically), would contribute strongly to “disruptiveness” when the animal is viewed from the side. This would presumably aid camouflage via disruptive coloration against a predator viewing the cuttlefish laterally, but this remains speculative.

A study concerning symmetrical crypsis by Langridge (2006) revealed that cuttlefish on the border between two different substrates exhibited a high degree of symmetry, even though each eye received different visual input, suggesting that binocular rivalry does not create asymmetric expression of camouflage patterns. In our experiments, we attained more cases of asymmetrical expression of disruptive components than those reported in the Langridge study. Our results suggest strongly that the rather mild asymmetry is due to a “wall effect” since animals are found most of the time against the wall than in the middle of the experimental chamber which does not seem to be the case in Landridge's study; rather the animals were in a depression in the middle of the experimental chamber, away from the wall. The asymmetrical expression of some disruptive components, especially the MMS on the body away from the vertical substrate, suggests that the animal is creating false edges, concealing its true outline and possibly avoiding a predator's attention.

Some comments on the behavioral ecology of cuttlefish camouflage

No study is complete without thorough evaluation of the animals' behavior in their natural environment. As such, it would be interesting to determine how strong is the cuttlefish preference to position themselves near vertical structures, what body coloration they adopt, how far does a vertical structure influence cuttlefish body patterning, and if they would be as easily detected as if they were in an open space lacking distinct 3D objects. In the same fashion, in an attempt to determine some rules that govern cuttlefish camouflage, it would be instructive to learn how cuttlefish or octopus cope with binocular rivalry when, for example, substrates to the right side might elicit mottle or uniform patterns while those on the left side of the animal might elicit disruptive camouflage.

How a cuttlefish is perceived by a predator depends on the contrast, color and spatial frequency of the body pattern

and the background, the visual ecology of the predator, as well as the cuttlefish's position relative to the predator. A cuttlefish can be viewed against different backgrounds simultaneously depending upon the predator's angle of view—from the top (vertically) or from the side (obliquely or horizontally). If a cuttlefish resembles a rock, then we might think that independently of a predator's angle of view, it could be perceived as an extension or another rock. It is evident that changeable coloration in cuttlefish and octopus is a major advantage that allows environmental exploitation. In a study of *Octopus vulgaris* in the Cayman Islands, Hanlon (2007) showed how the animal sitting on a rock matched the pattern, intensity, color and 3D physical texture of the rock, not the adjacent sand bottom. Hanlon et al. (2008) reported that the so called mimic-octopuses of tropical Indonesia assume body patterns and postures that resembled small sponges, tube-worm tubes, or colonial tunicates, which were among the few objects in the open sand habitat.

These experimental results support our observations in the natural environment [cf. various figures in Hanlon and Messenger (1988); Fig. 1 in Hanlon (2007) of *O. vulgaris* in the Caribbean; Fig. 1 in this paper of *S. apama* in Australia] suggesting that vertically arranged visual stimuli are used by cuttlefish and octopus to achieve effective camouflage, presumably against benthic predators that often attack laterally, and are thus viewing the cephalopod horizontally. The present experiments only begin to tease out the dynamics of how cephalopods make such accurate choices of camouflaged body pattern given the complexity and differing orientations of visual information in natural scenes. We have recent experimental evidence that *S. officinalis* is visually stimulated to raise its arms for a camouflaged posture when vertically oriented objects (or even 2D images of vertical objects) are presented to them. The soft-bodied cuttlefish and octopus are prey to a wide variety of visual predators that approach and attack them from multiple angles, and how cephalopods use visual background information (horizontal and vertical) to regulate and fine tune skin patterns and postures is slowly becoming understood.

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References

- Barbosa A, Florio CF, Chiao C-C, Hanlon RT (2004) Visual background features that elicit mottled body patterns in cuttlefish, *Sepia officinalis*. Biol Bull 207:154
- Barbosa A, Mähger LM, Chubb C, Florio C, Chiao C-C, Hanlon RT (2007) Disruptive coloration in cuttlefish: a visual perception mechanism that regulates ontogenetic adjustment of skin patterning. J Exp Biol 210:1139–1147
- Boycott BB (1961) The functional organization of the brain of the cuttlefish *Sepia officinalis*. Proc R Soc Lond B 153:503–534
- Chiao C-C, Hanlon RT (2001a) Cuttlefish camouflage: visual perception of size, contrast and number of white squares on artificial checkerboard substrata initiates disruptive coloration. J Exp Biol 204:2119–2125
- Chiao C-C, Hanlon RT (2001b) Cuttlefish cue visually on area—not shape or aspect ratio—of light objects on the substrate to produce disruptive body patterns for camouflage. Biol Bull 201:269–270
- Chiao C-C, Kelman EJ, Hanlon RT (2005) Disruptive body pattern of cuttlefish (*Sepia officinalis*) requires visual information regarding edges and contrast of objects in natural substrate backgrounds. Biol Bull 208:7–11
- Chiao C-C, Chubb C, Hanlon RT (2007) Interactive effects of size, contrast, intensity and configuration of background objects in evoking disruptive camouflage in cuttlefish. Vision Res 47:2223–2235
- Cloney RA, Brocco SL (1983) Chromatophore organs, reflector cells, iridocytes and leucophores in cephalopods. Am Zool 23:581–592
- Cott HB (1940) Adaptive coloration in animals. Methuen and Co, LTD, London
- Groeger G, Cotton PA, Williamson R (2005) Ontogenetic changes in the visual acuity of *Sepia officinalis* measured using the optomotor response. Can J Zool 83:274–279
- Hanlon R (2007) Cephalopod dynamic camouflage. Curr Biol 17:R400–R404
- Hanlon RT, Messenger JB (1988) Adaptive coloration in young cuttlefish (*Sepia officinalis* L.): the morphology and development of body patterns and their relation to behaviour. Philos Trans R Soc Lond B 320:437–487
- Hanlon RT, Conroy LA, Forsythe JW (2008) Mimicry and foraging behaviour of two tropical sand-flat octopus species off North Sulawesi, Indonesia. Biol J Linn Soc 93:23–38
- Hanlon RT, Messenger JB (1996) Cephalopod behaviour. Cambridge University Press, Cambridge
- Holmes W (1940) The colour changes and colour patterns of *Sepia officinalis* L. Proc Zool Soc Lond A 110:2–35
- Kelman E, Baddeley R, Shohet A, Osorio D (2007) Perception of visual texture and the expression of disruptive camouflage by the cuttlefish, *Sepia officinalis*. Proc R Soc B Biol Sci 274:1369–1375
- Langridge KV (2006) Symmetrical crypsis and asymmetrical signalling in the cuttlefish *Sepia officinalis*. Proc R Soc B Biol Sci 273:959–967
- Marshall NJ, Messenger JB (1996) Colour-blind camouflage. Nature 382:408–409
- Mähger LM, Hanlon RT (2007) Malleable skin coloration in cephalopods: selective reflectance, transmission and absorbance of light by chromatophores and iridophores. Cell Tissue Res 329:179–186
- Mähger LM, Barbosa A, Miner S, Hanlon RT (2006) Color blindness and contrast perception in cuttlefish (*Sepia officinalis*) determined by a visual sensorimotor assay. Vision Res 46:1746–1753
- Mähger LM, Chiao C-C, Barbosa A, Buresch KC, Kaye S, Hanlon RT (2007) Disruptive coloration elicited on controlled natural substrates in cuttlefish, *Sepia officinalis*. J Exp Biol 210:2657–2666

- Messenger JB (1991) Photoreception and vision in molluscs. In: Cronly-Dillon JR, Gregory RL (eds) Vision and visual dysfunction, vol 2. Evolution of the eye and visual system. CRC Press, Inc., Boca Raton, pp 364–397
- Messenger JB (2001) Cephalopod chromatophores: neurobiology and natural history. *Biol Rev* 76:473–528
- Muntz WRA (1999) Visual systems, behaviour, and environment in cephalopods. In: Archer SN, Djamgoz MBA, Loew ER, Partridge JC, Vallerga S (eds) Adaptive mechanisms in the ecology of vision. Kluwer, Dordrecht, pp 467–484
- Packard A (1972) Cephalopods and fish: the limits of convergence. *Biol Rev* 47:241–307
- Packard A, Hochberg FG (1977) Skin patterning in *Octopus* and other genera. *Symp Zool Soc Lond* 38:191–231
- Packard A, Sanders GD (1971) Body patterns of *Octopus vulgaris* and maturation of the response to disturbance. *Anim Behav* 19:780–790
- Shohet AJ, Baddeley RJ, Anderson JC, Kelman EJ, Osorio D (2006) Cuttlefish responses to visual orientation of substrates, water flow and a model of motion camouflage. *J Exp Biol* 209:4717–4723