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Cuttlefish camouflage: The effects of substrate contrast and size in evoking uniform, mottle or disruptive body patterns

Alexandra Barbosa [a,b], Lydia M. Mäthger [b], Kendra C. Buresch [b], Jennifer Kelly [b], Charles Chubb [c], Chuan-Chin Chiao [b,d], Roger T. Hanlon [b,*]

[a] *ICBAS – Institute of Biomedical Sciences Abel Salazar, University of Porto, Portugal*
[b] *Marine Biological Laboratory, Marine Resources Center, Woods Hole, MA, USA*
[c] *Department of Cognitive Sciences & Institute for Mathematical Behavioral Sciences, University of California at Irvine, USA*
[d] *Department of Life Science, National Tsing Hua University, Hsinchu, Taiwan*

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Abstract

Cuttlefish are cephalopod molluscs that achieve dynamic camouflage by rapidly extracting visual information from the background and neurally implementing an appropriate skin (or body) pattern. We investigated how cuttlefish body patterning responses are influenced by contrast and spatial scale by varying the contrast and the size of checkerboard backgrounds. We found that: (1) at high contrast levels, cuttlefish body patterning depended on check size; (2) for low contrast levels, body patterning was independent of "check" size; and (3) on the same check size, cuttlefish fine-tuned the contrast and fine structure of their body patterns, in response to small contrast changes in the background. Furthermore, we developed an objective, automated method of assessing cuttlefish camouflage patterns that quantitatively differentiated the three body patterns of uniform/stipple, mottle and disruptive. This study draws attention to the key roles played by background contrast and particle size in determining an effective camouflage pattern.

Keywords: Color change; Crypsis; Vision; Cephalopod; *Sepia officinalis*

1. Introduction

Cephalopod camouflage is unrivaled in the animal kingdom because in comparison with most animals that have fixed or slightly changeable camouflage patterns, cephalopods can show a variety of camouflage patterns, and they can instantly change them using their neurally controlled chromatophore system in the skin (Hanlon & Messenger, 1988, 1996; Messenger, 2001). In laboratory experiments, research has shown that this camouflage behavior is visually driven, and that animals carefully assess a range of background variables when deciding what camouflage pattern to show (Barbosa et al., 2007; Chiao, Chubb, & Hanlon, 2007; Chiao & Hanlon, 2001a, 2001b; Chiao, Kelman, & Hanlon, 2005; Hanlon & Messenger, 1988, 1996; Holmes, 1940; Kelman, Baddeley, Shohet, & Osorio, 2007; Marshall & Messenger, 1996; Mäthger, Barbosa, Miner, & Hanlon, 2006; Mäthger et al., 2007; Packard & Hochberg, 1977; Shohet, Baddeley, Anderson, Kelman, & Osorio, 2006; Shohet, Baddeley, Anderson, & Osorio, 2007).

Despite variation in the camouflage body patterns shown by cuttlefish, the variations fall into three pattern categories: (1) uniform (or uniformly stippled), (2) mottle, and (3) disruptive (Hanlon & Messenger, 1988); (see Fig. 1), and our research efforts focus on uncovering the visual cues (or "sampling rules") that determine which camouflage pattern is most appropriate on a particular background. Uniform body patterns are characterized by

* Corresponding author. Address: Marine Biological Laboratory, Marine Resources Center, Woods Hole, MA, USA. Fax: +1 508 289 7900.
E-mail address: rhanlon@mbl.edu (R.T. Hanlon).

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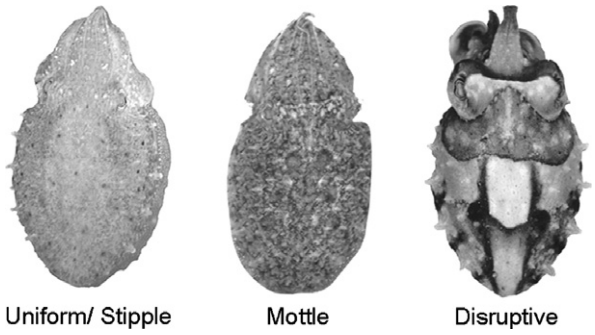


Fig. 1. Three characteristic cuttlefish camouflage patterns. Uniform/stipple pattern: contrast variations are minimal; Mottle pattern: fine/medium-grained contrast variations are activated homogeneously across the body; Disruptive pattern: coarse contrasting skin components of varying shape, size and orientation are expressed.

little or no variation in body pattern contrast. Stipple patterns, grouped under uniform coloration by Hanlon and Messenger (1988), show some small-scale light and dark patches, again with minimal contrast. Mottle patterns have small or large-scale light or dark patches that are largely oval in shape, and show considerable repetition of the pattern across the animal's body. Both uniform and mottle patterns achieve camouflage by the principle of general resemblance to the background (Cott, 1940; Hanlon, 2007). Disruptive patterns, which can achieve some degree of general resemblance, are different in that they are characterized by high-contrast light and dark patches, in a non-repetitive configuration, that also provide camouflage by disrupting the recognizable shape or orientation of the animal (Fig. 1). The mechanisms and functions of disruptive coloration are currently the focus of some lively discussions (Cuthill et al., 2005; Endler, 2006; Hanlon, 2007; Kelman et al., 2007; Merilaita, 1998; Merilaita & Lind, 2005; Schaefer & Stobbe, 2006; Shohet et al., 2007; Stevens, 2007; Stevens & Cuthill, 2006; Stevens, Cuthill, Párraga, & Troscianko, 2006; Stevens, Cuthill, Windson, & Walker, 2006).

Cuttlefish will attempt to camouflage themselves on any substrate they are placed on; thus in the laboratory, we can use this robust behavioral assay to test the animals' visual abilities and investigate the visual cues that drive their camouflage behavior. Cuttlefish are almost certainly color-blind (Marshall & Messenger, 1996; Mäthger et al., 2006), but this does not appear to affect their ability to chromatically camouflage themselves. Recent spectrometer measurements of the animals' skin as well as relevant substrates revealed that the variation in skin and substrate colors is similar, and that cuttlefish can match the colors of the backgrounds that were tested (Mäthger, Chiao, Barbosa, & Hanlon, accepted for publication). It has been shown that cuttlefish cue visually on area, not the shape or aspect ratio, of light objects on a dark background and that substrate edges and contrast are important in eliciting specific body patterns (Barbosa et al., 2007; Chiao & Hanlon, 2001a, 2001b; Chiao et al., 2005; Kelman et al., 2007; Mäthger et al., 2006, 2007; Shohet et al., 2007). Furthermore, Chiao et al. (2007) highlighted the interactions of multiple substrate features such as size, contrast, intensity and configuration of background objects that directly influence which camouflage pattern a cuttlefish will choose.

Experimentally, it has been shown that uniform backgrounds, such as plain artificial substrates, or uniformly small-grained sand, elicit uniform body patterns (Chiao & Hanlon, 2001a; Hanlon & Messenger, 1988; Kelman et al., 2007; Mäthger et al., 2006, 2007). On non-uniform backgrounds, we have learned that large numbers of small black and white checks with areas of roughly 4% and 12% of the animal's White square skin component elicit mottled body patterns (Barbosa, Florio, Chiao, & Hanlon, 2004; Barbosa et al., 2007). The White square (WS) is a light skin component in the middle of the body (Fig. 3, #2). Note that the area of the cuttlefish's WS skin component is the basis of calculations of the check areas likely to evoke different camouflage patterns. Kelman et al. (2007) placed cuttlefish on phase-randomized checkerboards (images that have the same Fourier amplitude spectrum as a checkerboard but whose phase spectra are randomized) and found that these substrates evoked mottle. Unpublished data from this laboratory show that mottle patterns can also be elicited on natural substrates (see a few images in Hanlon, 2007; Hanlon & Messenger, 1988), and we have numerous other examples from underwater photographs. Disruptive body patterning can be elicited on a black and white checkerboard with a check size roughly equal in area to the White square skin component. A natural substrate of high-contrast large rocks of similar size to the White square also elicits disruptive coloration (Chiao et al., 2005; Mäthger et al., 2007).

In this study, we looked in detail at the effect of background contrast on the three camouflage pattern types in cuttlefish. The natural environment in which cephalopods live can be colorful (such as coral reefs, rock reefs and algal habitats) and full of contrast (Marshall, Jennings, McFarland, Loew, & Losey, 2003), and we can therefore expect that contrast is an important visual cue. Since cuttlefish are monochromats (presence of only one visual pigment) (Bellingham, Morris, & Hunt, 1998; Brown & Brown, 1958; Marshall & Messenger, 1996; Mäthger et al., 2006) they will see the world in light and dark shades, rather than in color (for which at least 2 visual pigments are necessary). Mäthger et al. (2006) suggested that *S. officinalis* can detect background contrast differences as low as 15%, although it is likely that the cuttlefish contrast detection threshold is substantially lower.

In this study, we created black and white checkerboards of three sizes known to elicit both disruptive and mottle body patterns. We decreased the contrast between the black and white in known steps until we obtained a low-contrast level checkerboard that would eliminate the expression of disruptive components in the cuttlefish body pattern. We then video-recorded the animals' body patterns in an attempt to unravel the role of contrast and object size in the camouflage behavior of *S. officinalis*.

Importantly, we developed a grading scheme that allows for an objective quantification of cuttlefish camouflage body patterns. Our previous method only allowed us to distinguish between disruptive and non-disruptive body patterns. This newly developed method goes one step farther: it allows us to set apart the three main body patterns used for camouflage—uniform/stipple, mottle and disruptive—and quantify the strength of expression of each body pattern.

2. Materials and methods

2.1. Substrates

We created eighteen checkerboards of varying contrasts (6 different contrast levels) with check sizes equal to 40%, 10% and 3% of the mean area of the cuttlefish's White square skin component (see Fig. 2). In previous studies, we have shown that high contrast black and white checkerboards with a check size of 40% (or greater, up to 120%) successfully evoke disruptive coloration, whereas check sizes of 4% and 12% elicit mottle coloration (Barbosa et al., 2004, 2007). By lowering checkerboard contrast, we presumably make the substrate appear more and more uniform, and previous studies have shown that cuttlefish show uniform coloration on uniform backgrounds. Thus, the rationale behind this study is to test in detail what role contrast plays (especially in relation to size) in evoking a change from disruptive and mottle to uniform.

For each check size, six substrates with different contrasts but the same average intensity were computer-generated, printed, and laminated to be waterproof. For the checkerboards that were 3% of the White square area, the contrast values were 0.88 (black and white), 0.73, 0.63, 0.53, 0.39 and 0.22. For the remaining checkerboards, the contrast levels were 0.80 (black and white), 0.65, 0.60, 0.54, 0.34 and 0.14 (Fig. 2, see below for calculation of contrast). The difference in contrast between the 3% checkerboards and the remaining substrates was due to the use of different paper with different surface properties, which affect absolute reflectance.

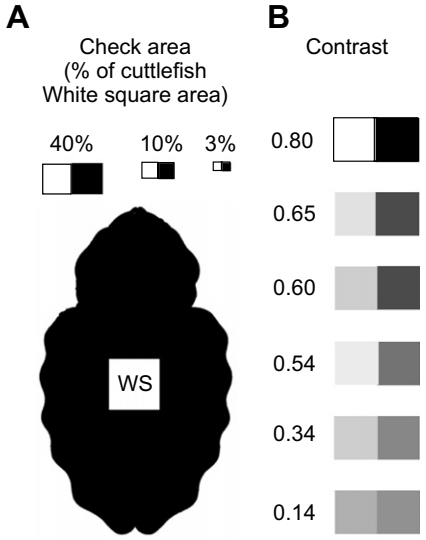


Fig. 2. Stimuli. (A) Checkerboards with checks of three different sizes; small, midsize and large checks had areas equal to 40%, 10% and 3% of the area of the animal's White square (WS), respectively. Note the WS skin component in the center of the animal's mantle. (B) Checkerboards with 10% and 40%-area checks varied in contrast from 0.14, 0.34, 0.54, 0.60, 0.65 and 0.80 Michelson contrast. Checkerboards with 3%-area checks varied in contrast from 0.22, 0.39, 0.53, 0.63, 0.73 and 0.88 Michelson contrast.

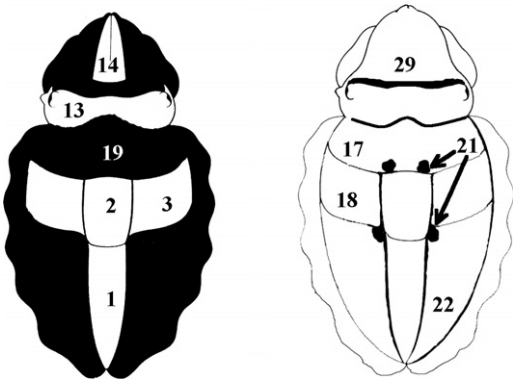


Fig. 3. Manual image analysis of chromatic components used in disruptive coloration. Diagrammatic representation of disruptive components that were graded (see text for detail on grading method). Light chromatic components: 1, White posterior triangle; 2, White square; 3, White mantle bar; 13, White head bar; 14, White arm triangle. Dark chromatic components: 17, Anterior transverse mantle line; 18, Posterior transverse mantle line; 19, Anterior mantle bar; 21, Paired mantle spots; 22, Median mantle stripe; 29, Anterior head bar. The numbers of the components are the same as those used in Hanlon & Messenger, 1988.

2.2. Calculation of contrast

Using a spectrometer (USB2000, Ocean Optics, FL, USA), reflectance spectra were taken of each check shade (black through various shades of grey to white) on the laminated paper. Each check was measured twice and measurements were averaged. A diffuse reflection standard (WS-1, Ocean Optics) was used. The measuring fiber (1000 μm diameter) was held vertically by a micromanipulator (distance of 2.5 cm to laminated sheet). The light source (40 Watt Circline® fluorescent light, Phillips daylight; same as that used during experiments) was arranged so that the laminated substrate was illuminated at an oblique angle, therefore avoiding any specular reflectance from the laminated surface. After measuring the reflectance spectra, the relative photon catch (PC; amount of light absorbed by a photoreceptor and available for vision) was determined. This is given by: $PC = \int(1 - \exp(-k\, S(\lambda)\, l)) \times R(\lambda)\, d\lambda$ (after Warrant, 2004), where $S(\lambda)$ is the spectral sensitivity of the visual pigment, $R(\lambda)$ is the spectral reflectance of the check shade, l is the length of the rhabdom (400 μm; from Hanlon & Messenger, 1996) and k is the quantum efficiency of transduction (0.0067/μm; Warrant & Nilsson, 1998); for further details, see Mäthger et al. (2006). Using the spectral reflectance data from the check shade, we computed Michelson contrast; $MC = (B_{max} - B_{min})/(B_{max} + B_{min})$, where B_{max} is the greater of the quantum catches produced by the lights reflected from the two checks and B_{min} is the lesser. Contrast thus ranges from 0 (0% contrast) to 1 (100% contrast).

2.3. Animals

Ten cuttlefish, *Sepia officinalis* (3.8–4.8 cm mantle length, 1.6 cm^2 average White square area), were used in this experiment. All cuttlefish were raised from eggs at the Marine Resources Center of the Marine Biological Laboratory. Six animals were tested on all checkerboards with check size 3% of the area of the animal's White square. The same six animals were also tested on all of the checkerboards with check size 10% of the area of the animal's White square. Although two of the same six animals served as subjects on the 40% checkerboard, the other four animals tested on the 40% checkerboard were new.

2.4. Experimental procedure

The experimental trials were conducted inside a tent covered by black plastic sheeting. Each animal was placed in a tank with flowing seawater and restricted to a cylindrical arena (25 cm diameter, 11 cm height). In this

confined area, cuttlefish were presented with the different substrates on both the floor and wall of the arena. We used a 40 Watt Circline® fluorescent light source (Phillips daylight; illumination approximately 1000 lx). A digital video camera was mounted above the tank and connected to an external monitor allowing remote viewing. Upon acclimation (i.e., cessation of excessive swimming and hovering movements and expression of stable body pattern) a 20-min trial was recorded. The camera was set to record for 1 s every 30 s, thus yielding 40 s of footage per animal per substrate. From the resulting 40 s of footage, a still image was taken every 4 s yielding 10 images; these 10 images were used to analyze the animal's responses (see below on image analysis). In total, 1080 images were analyzed.

2.5. Image analysis

2.5.1. Disruptive grading (manual method)

Disruptive patterning in *S. officinalis* commonly consists of 11 individual dark and light components, which are independent physiological units that can be shown singly or in combination with each other (Hanlon & Messenger, 1988). The skin components are the result of selective expansion (for dark components) or retraction (for light components) of chromatophores. Eleven skin components of disruptive coloration were graded for each image (Fig. 3). Each component was assigned a grade from 0 to 3 (0, not expressed; 1, weakly expressed; 2, moderately expressed; and 3, strongly expressed). According to this grading scheme, an animal can be given a total grade ranging from 0 (no expression of any disruptive component) to 33 (all disruptive components strongly expressed, i.e., $3 \times 11 = 33$). For further details on this grading method see Mäthger et al. (2006). With this method we can quantify the level of disruptiveness; it does not allow us to distinguish uniform from mottle patterns. This method has also been used by (Barbosa et al., 2007; Chiao et al., 2007; Mäthger et al., 2007). We averaged grades of all 10 images obtained for each animal on each substrate.

2.5.2. Body pattern grading (new automated method)

We also introduce here an automated method to provide a characterization of the pattern produced by an animal that would enable us to discriminate between uniform/stipple, mottle and disruptive patterns. Whereas disruptive patterns are marked by large-scale, bright and dark components, mottle patterns are marked instead by fine-grained light/dark variations. That is, the two pattern types differ in granularity (or spatial scales). We can capture such differences by analyzing the image of the animal in different spatial frequency bands. The protocol underlying this automated method is the following. The image of the pattern deployed by the animal is first "cut out" from its context (i.e., from the checkerboard background on which it appears). The cut-out image is then warped to conform in size and shape to a standard cuttlefish template (to enable comparison of granularity measures across cuttlefish images originally of different scales), and the background (i.e., the remaining area in the fixed size rectangle) is set to a uniform value equal to the mean value of the cuttlefish image (to remove all variations from the image that are not due to the patterning of the cuttlefish itself). We use six, octave-wide, isotropic, ideal filters for our granularity analysis. The standardized image is filtered into each of these six bands. This yields six images that divide the information in the original image into different "granularity bands." Note that these six images can be added together to produce a good approximation of the standardized image (a small amount of information is discarded). The granularities of the six filtered images are reflected by the images on the horizontal axis in Fig. 4. Note that the light and dark blobs in the first image (at the left end of the horizontal scale) of Fig. 4 are comparable in size to the major disruptive components in the animal's patterning repertoire (strongly activated in the disruptive animal of Fig. 1). By comparison, the black and white blobs in the third figure are much finer, corresponding more closely in size to the fine-grained components activated in mottle patterns (such as that shown by the mottle animal of Fig. 1). From each of the six band-pass filtered images we extracted one number: the sum of the squared pixel values in that image. This is the total energy of the original, standardized image in the given spatial frequency band. We refer to these six energies as the "granularity spectrum" of the image. The scale of these numbers is arbitrary. We use a scheme in which energy is expressed as a mean quantity per pixel and is normalized so as to reflect a proportion of the maximum possible energy that could exist in any image.

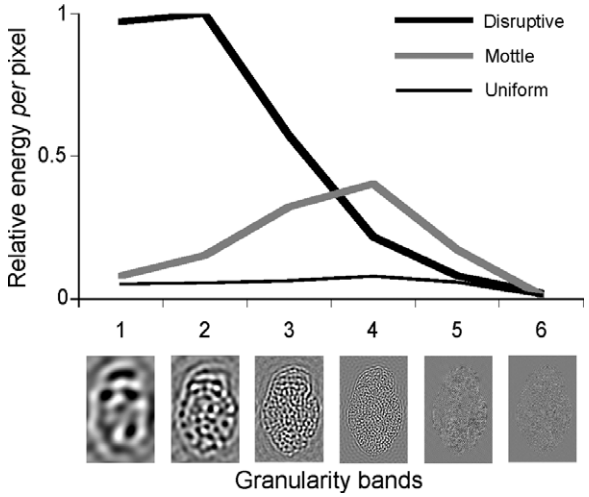


Fig. 4. Automated image analysis. The image of the cuttlefish (following preprocessing—see text) is band-pass filtered into six images corresponding to those shown on the horizontal axis. From each of the six images is extracted the sum of squared pixel values; this is the total energy contributed to the original image by the spatial frequencies isolated in the filtered image. We refer to these six band-specific energies as the "granularity spectrum" of the image. The three spectra shown are typical of uniform/stipple, mottled and disruptive patterns.

Fig. 4 shows the granularity spectra produced by the three animals in Fig. 1. These three granularity spectra are typical of those evoked by uniform/stipple, mottled, and disruptive patterns. Note first that the spectrum of the uniform/stipple response has low energy in all six granularity bands. The mottled pattern yields a spectrum with more energy than the uniform pattern, and this spectrum has highest energy in granularity bands 3 and 4. Finally, the disruptive pattern evokes a spectrum with more total energy than either the uniform or mottled patterns; moreover, most of this energy is in the two coarsest granularity bands 1 and 2.

3. Results

Cuttlefish exhibited all three types of body patterns (uniform/stipple, mottle, disruptive) on substrates differing in contrast level and check size (Fig. 5; see Fig. 1 for typical illustrations of each body pattern type).

3.1. Disruptive grading (manual method)

Disruptive body patterns were found on the 40% check size, with disruptive components being expressed at the 0.80, 0.65 and 0.60 contrast levels (Fig. 6A). On the smaller check areas (Fig. 6B and C) fewer and fewer disruptive components were expressed until the animal showed entirely non-disruptive patterns on the lowest contrast substrates.

3.2. Body pattern grading (new automated method)

Shown in Fig. 7 are the results of the average granularity spectra across the 6 animals tested on each given

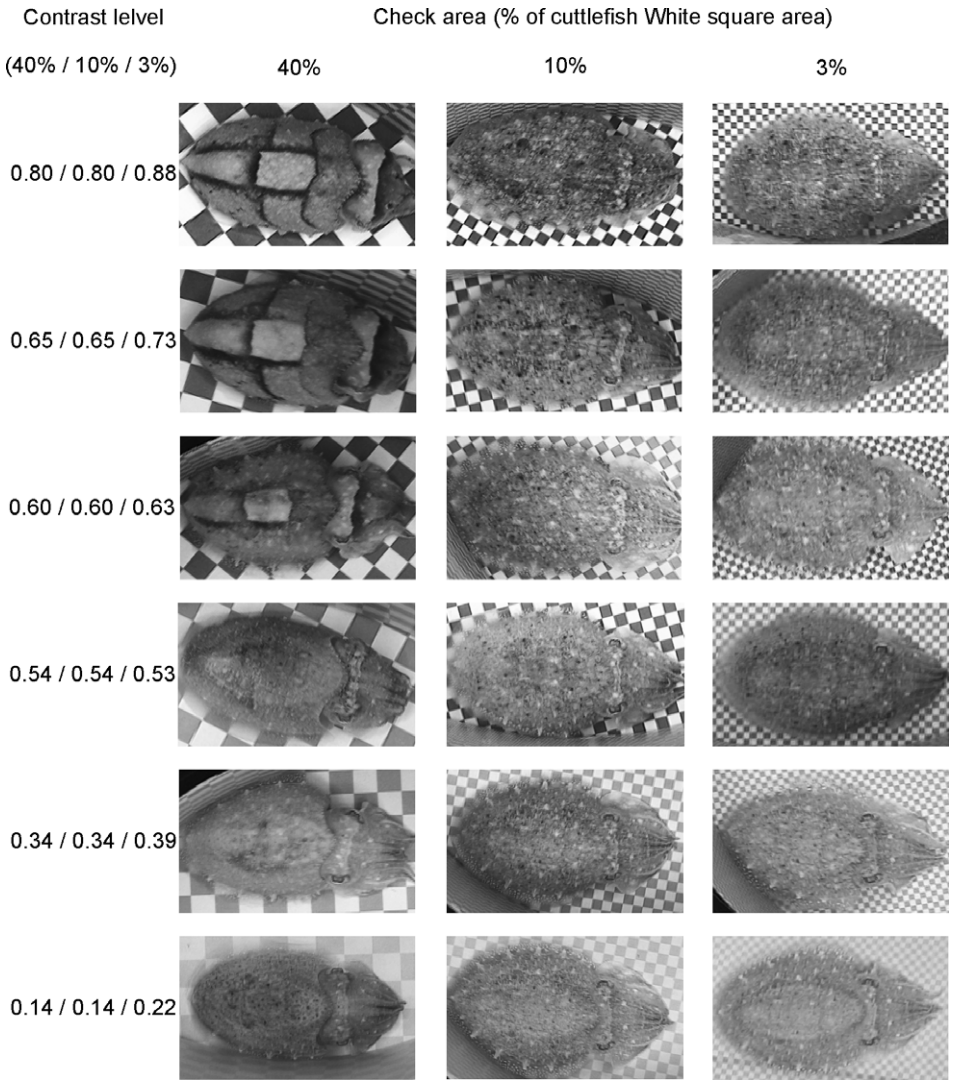


Fig. 5. Contrast and check size influence body patterning in cuttlefish. For high contrast levels, body patterning depends on check size, while for low contrast levels, body patterning is independent of check size. Disruptive coloration was shown on 40% check area with highest contrasts. Uniform/stipple was elicited on all check areas for the lowest contrast levels. Mottle patterning was shown on the 10 and 3% check areas for contrast values higher than 0.39 and 0.53, respectively.

type of checkerboard (error bars, although small, are omitted for clarity). Visual inspection of Figs. 5 and 7 helps interpret this new grading method. Fig. 7A–C give the average granularity spectra for 40%, 10% and 3% checkerboards of various contrasts, respectively. To facilitate comparison of spectra within a given check size condition, the scales for Fig. 7B and C are identical but have been magnified relative to that of Fig. 7A. Each graph in Fig. 7 shows an overall increase in spectrum amplitude with increasing checkerboard contrast. Note that the spectra for the lowest contrast checkerboards (contrast 0.14 for the 40% and 10% checkerboards, and contrast 0.22 for the 3% checkerboard) are very similar across all three check sizes. This is to be expected: as the contrast of any checkerboard decreases near zero, cuttlefish tend to deploy uniform/stipple coloration, regardless of the check size. Thus, in all of Fig. 7A–C, the granularity spectrum for the lowest contrast checkerboard is the spectrum produced by uniform/stipple coloration, which differs not only in amplitude but also in overall curve shape (compare Fig. 4) from the characteristic spectra curves for mottle and disruptive patterns. Note also that the spectra for the maximum contrast in 10% and 3% checkerboards are similar in shape, each assigning peak energy to granularity band 3, whereas the spectrum for maximum contrast on the 40% checkerboard is strikingly different, assigning peak energy to granularity band 1, illustrating that disruptive patterns tend to have more lower spatial frequency energy (due to their relatively large components) than do mottled patterns. This observation indicates that the maximum contrast on the 10% and 3% checkerboards tends to evoke a mottle response, whereas the maximum contrast on 40% checkerboard tends to evoke a disruptive response.

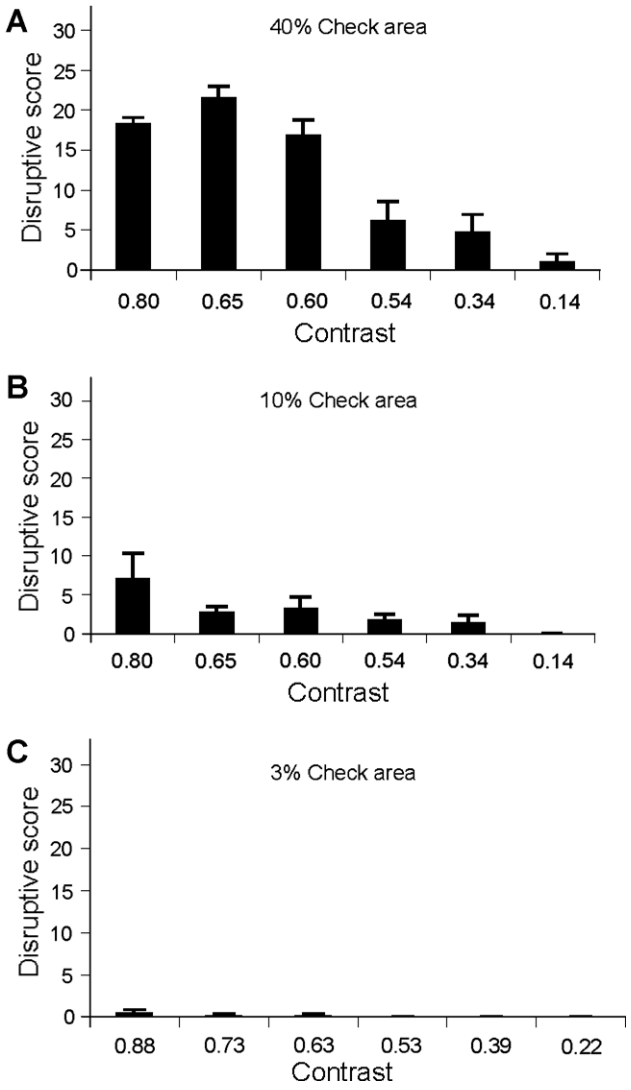


Fig. 6. Expression of disruptive components is influenced by contrast and check size. Disruptive score is higher on the 40% check area compared to the 10% and 3% check areas. As contrast decreases, the expression of disruptive components is reduced. Error bars are ±SE.

A striking feature of the data in each of Fig. 7A–C is that the granularity spectra show a graded increase in amplitude with increasing checkerboard contrast. More specifically, in each of Fig. 7A–C, all of the spectra (except for the spectrum evoked by the lowest contrast checkerboard) appear roughly the same shape but have been multiplicatively scaled to different amplitudes. To investigate this effect more carefully, we need to boil down the granularity spectrum produced by a given animal on a given checkerboard to one number that reflects the overall amplitude of the spectrum. We do this by adding together the 6 granularity spectrum values evoked by that checkerboard.

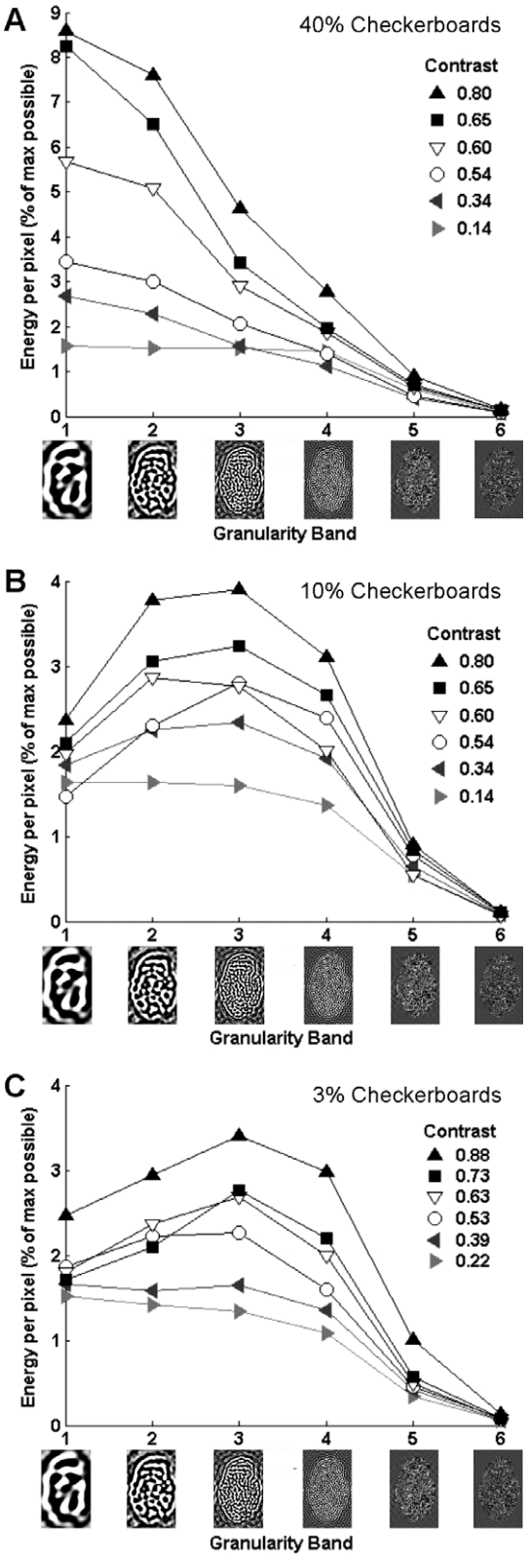


Fig. 7. Mean granularity spectra. (A) Granularity spectra (averaged across 6 animals) for 40% checkerboards (checkerboards whose checks had area equal to 40% of the area of the cuttlefish White square) of different contrasts. (B) Granularity spectra (averaged across 6 animals) for 10% checkerboards of different contrasts. (C) Granularity spectra (averaged across 6 animals) for 3% checkerboards of different contrasts. Note change in vertical scale, as well as the characteristic curve for uniform/stipple, mottle and disruptive pattern types (compare to Fig. 4). In all 3 plots, the overall amplitude of the granularity spectrum tends to increase gradually with increasing checkerboard contrast.

This statistic, which we call the *total energy of the animal's response*, gauges the overall contrast of the pattern deployed by the animal. This will enable us to focus more precisely on how the contrast of a checkerboard influences the contrast of the pattern the animal deploys. For a given animal, let $TE_{K\%}(C)$ be the total energy evoked by the $K\%$ checkerboard of contrast C, for $K = 40$, 10 and 3. Consider first the case of $K = 40$. A within-subjects ANOVA (with contrast C the within-subjects factor) reveals a significant linear trend in $TE_{40\%}(C)$ is significant ($F(1,5) = 69.9$, $p < 0.001$). To take a closer look at just the dependence of $TE_{40\%}(C)$ on contrast, Fig. 8A plots, for each of the 6 animals tested on the 40% checkerboards, $TE_{40\%}(C)$–$MeanTE_{40\%}$, where $MeanTE_{K\%}$ is the average of $TE_{K\%}(C)$ across all contrasts C tested. Why do we subtract out $MeanTE_{40\%}$ for each animal? We anticipate that some animals will have an overall tendency to produce higher contrast response patterns than others. These overall differences in response tendency will produce differences in the values of $MeanTE_{40\%}$ across different animals. Subtracting out $MeanTE_{40\%}$ lets us compare the C-dependent variations in $TE_{40\%}(C)$ for different animals without the vertical shifts between the curves introduced by differences in $MeanTE_{40\%}$. The dashed black line gives the mean of the 6 resulting curves. Here we see how the contrast of the animal's response pattern tends to increase with checkerboard contrast. In fact, all but one of the individual animal curves shows a statistically significant positive correlation with contrast (p-values (for a test of the null hypothesis that the correlation of $TE_{40\%}(C)$ and C is less than or equal to 0) are 0.063, 0.015, 0.014, 0.002, and 0.029). Fig. 8B and C plot the corresponding curves for the 10% and 3% checkerboards. The results for these finer checkerboards parallel those for the 40% checkerboards: for the 10% checkerboards, the linear trend in $TE_{10\%}(C)$ is significant ($F(1,5) = 16.6$, $p < 0.01$). Similarly, for the 3% checkerboards, once again the linear trend in $TE_{3\%}(C)$ is significant ($F(1,5) = 34.2$, $p < 0.002$). To reiterate the main point: for each of the different scale checkerboards we used (the checkerboards whose checks are $K\%$ of the area of the White square of the cuttlefish, for $K = 40$, 10, or 3), animal response patterns increase significantly in contrast (that is, $TE_{K\%}(C)$ increases) as the contrast C of the checkerboard is increased.

Suppose that in response to checkerboards of a fixed check size, a given cuttlefish deploys a fixed pattern that varies only in contrast as checkerboard contrast varies. In this case, the granularity spectra evoked by checkerboards of a fixed check size should all be identical in shape, vary-

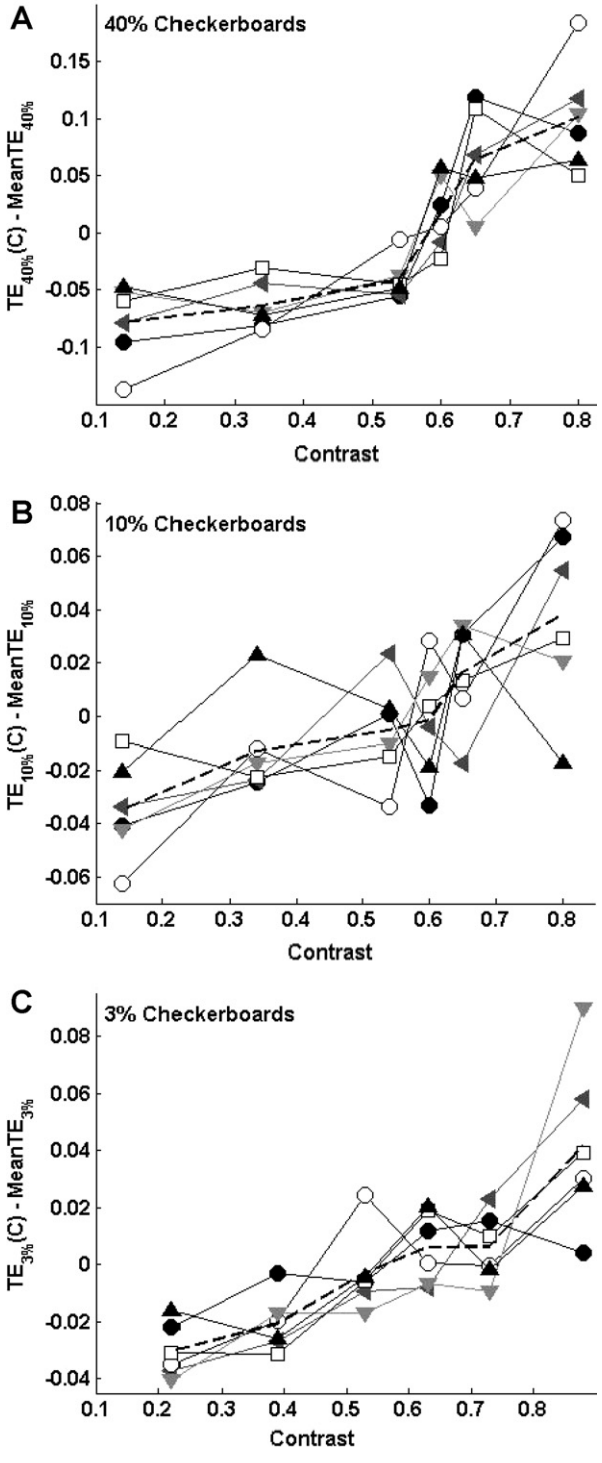
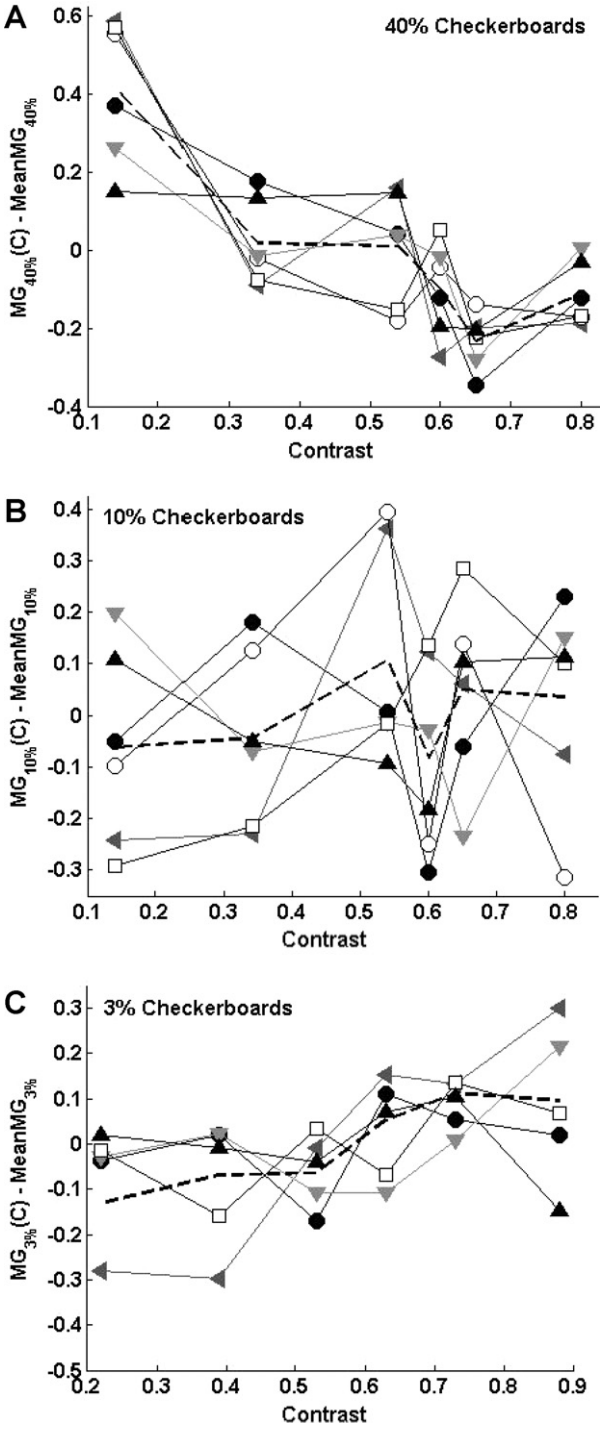


Fig. 8. Total spectrum energy as a function of contrast. For $K = 40$, 10, or 3, and for any of the six contrasts C used to produce the $K\%$ checkerboards, $TE_{K\%}(C)$ is the sum of the six granularity spectrum energies evoked by the $K\%$ checkerboard of contrast C, and Mean $TE_{K\%}$ is the mean of $TE_{K\%}(C)$ across all six contrasts C. Thus, $TE_{K\%}(C)$ reflects the overall amplitude of the granularity spectrum evoked by the $K\%$ checkerboard of contrast C. (A) Plots $TE_{40\%}(C)$–$MeanTE_{40\%}$ for each of the six animals tested on the 40% checkerboards. The dashed, black line gives the mean of the curves. (B) Plots $TE_{10\%}(C)$–$MeanTE_{10\%}$ for each of the six animals tested on the 10% checkerboards. The dashed, black line gives the mean of the curves. (C) Plots $TE_{3\%}(C)$–$MeanTE_{3\%}$ for each of the six animals tested on the 3% checkerboards. The dashed, black line gives the mean of the curves for the 6 individual animals. All three curves show a significant, increasing, linear trend suggesting that checkerboard contrast operates incrementally to control the contrast of the animal's response pattern regardless of the size of the checks in the checkerboard. Each symbol corresponds to a different animal.

ing only in amplitude. We therefore call this the "fixed shape" hypothesis. We anticipate that the fixed shape hypothesis will fail for very low contrast checkerboards (since these all tend to evoke uniform response patterns whose spectra differ in shape from those of mottle and disruptive patterns). However, perhaps the fixed shape hypothesis holds across higher contrasts. To investigate this possibility we boil down the spectra of the response patterns produced by our animals to a single number that is likely to reveal systematic changes in spectrum shape.



For this purpose we focus on the "mean granularity" of the pattern produced by an animal in response to a given checkerboard. We begin by clarifying this concept. Recall that the granularity spectrum S of an animal's response comprises six numbers: $S(1)$, $S(2)$,..., $S(6)$. $S(1)$ reflects the strength of the coarsest granularity information in the animal's response pattern; $S(2)$ reflects the strength contributed by granularities twice as fine as those captured by $S(1)$; $S(3)$ reflects the strength contributed by granularities twice as fine as those captured by $S(2)$; and so forth. So what do we mean by the "mean granularity" of the animal's response pattern? If $S(4)$ were 5, but $S(1) = S(2) = S(3) = S(5) = S(6) = 0$, then the mean granularity of S would be 4. Similarly, if $S(3) = S(4) = 3$, but $S(1) = S(2) = S(5) = S(6) = 0$, then the mean granularity of S would be 3.5. Generalizing this idea, we see that

$$\text{Mean Granularity of } S = \frac{\sum_{g=1}^{6} gS(g)}{\sum_{g=1}^{6} S(g)}, \tag{1}$$

where g is the energy band number in the granularity spectrum. The higher the mean granularity of S, the finer the corresponding response pattern will tend (on the whole) to appear.

To develop mean granularity as a summary statistic for our data set, let $S_{K\%,C}$ be the granularity spectrum evoked in a given animal by the $K\%$ checkerboard ($K = 40$, 10, 3) of contrast C. Note that $\text{TE}_{K\%}(C)$ is equal to $\sum_{g=1}^{6} S_{K\%,C}(g)$. Thus, applying Eq. (1), we define the mean granularity of the response evoked in our animal by the $K\%$ checkerboard of contrast C to be

$$\text{MG}_{K\%}(C) = \frac{\sum_{g=1}^{6} gS_{K\%,C}(g)}{\text{TE}_{K\%}(C)}. \tag{2}$$

Fig. 9. Spectrum mean granularity as a function of contrast. For $K = 40, 10,$ or 3, and for any of the six contrasts C used to produce the $K\%$ checkerboards, $\text{MG}_{K\%}(C)$ is the mean granularity of the spectrum $S_{K\%,C}$ evoked by the $K\%$ checkerboard of contrast C, and g is the energy band number in the granularity spectrum. That is, $\text{MG}_{K\%}(C) = \sum_{g=1}^{6} gS_{K\%,C}(g)/\text{TE}_{K\%}(I)$. In addition, $\text{MeanMG}_{K\%}$ is the mean of $\text{MG}_{K\%}(C)$ across all six contrasts C.A. Plots $\text{MG}_{40\%}(C)$–$\text{MeanMG}_{40\%}$ for each of the six animals tested on the 40% checkerboards. The dashed, black line gives the mean of the curves. Mean granularity shows a significant decrease with increasing C.B. Plots $\text{MG}_{10\%}(C)$–$\text{MeanMG}_{10\%}$ for each of the six animals tested on the 10% checkerboards. The dashed, black line gives the mean of the curves. Mean granularity shows a marginally significant increase with increasing C.C Plots $\text{MG}_{3\%}(C)$–$\text{MeanMG}_{3\%}$ for each of the six animals tested on the 3% checkerboards. The dashed, black line gives the mean of the curves for the 6 individual animals. The increase in the mean curve is marginally significant (see text). These results suggest that as contrast of the (40% and 3%) checkerboards is increased, the animal's response changes not merely in overall contrast but also in granularity. As contrast of 3% checkerboards is increased, the granularity of the response pattern gets finer whereas as contrast of 40% checkerboards is increased, the granularity of the response pattern gets coarser. Each symbol corresponds to a different animal.

We anticipate that some animals will naturally tend generally to produce patterns with higher mean granularities than do other animals. For any given animal, this overall tendency is reflected by the average of $MG_{K\%}(C)$ across all contrasts C tested; let $AvgMG_{K\%}$ be this average. If, for example, one animal has a higher value of $AvgMG_{40\%}$ than does another animal, this means that the first animal has a general tendency to produce finer-grained response patterns on 40% checkerboards than does the second animal, but it does not tell us anything about how either animal's response patterns vary with C. To focus exclusively on these contrast-dependent changes in responding, we need to subtract out $MeanMG_{K\%}$. Accordingly, Fig. 9A plots for each of the 6 animals tested on the 40% checkerboards, $MG_{40\%}(C)$–$MeanMG_{40\%}$. The dashed black line gives the mean of the 6 resulting curves. This figure shows that the mean granularity of a given animal's response decreases with increasing checkerboard contrast, suggesting that (in contrast to the 3% checkerboards), as contrast of 40% checkerboards increases, the response pattern deployed by the animal tends to become coarser in granularity. That this effect is significant is confirmed by a within-subjects ANOVA that yields a highly significant effect of C: $F(5,25) = 15.94$, $p < 0.001$. This effect remains significant when the lowest contrast is dropped from the analysis: $F(4,20) = 4.724$, $p < 0.008$. Fig. 9B plots $MG_{10\%}(C)$–$MeanMG_{10\%}$ for each of the 6 animals tested on the 10% checkerboards. There is no discernable trend in the average of the six curves (the black dashed line), suggesting that mean granularity of the animal's response does not depend on contrast for checkerboards of this scale. This impression is confirmed by a within-subjects ANOVA for the 10% checkerboards. This ANOVA fails to yield a significant effect of C: $F(5,25) = 0.77$, $p < 0.579$. Finally, Fig. 9C plots $MG_{3\%}(C)$–$MeanMG_{3\%}$ for each of the 6 animals tested on the 3% checkerboards. This figure shows that there is a slight tendency for the mean granularity of the animal's response to increase with increasing checkerboard contrast, suggesting that for 3% checkerboards, as contrast increases, the response pattern deployed by the animal changes not merely in overall contrast but also in spatial frequency content; specifically, with increasing contrast, the animal's response pattern tends to shift toward higher spatial frequencies. A within-subjects ANOVA yields a marginally significant main effect of C on $MG_{3\%}(C)$: $F(5,25) = 2.98$, $p < 0.03$. This marginally significant effect persists when the lowest value of C is withheld from the analysis ($F(4,20) = 3.053$, $p < 0.041$). We conclude that increasing the contrast of 3% checkerboards tends to evoke slightly finer response patterns from our animals. We take this as weak evidence against the hypothesis that increasing the contrast of a checkerboard alters only the contrast (and not the form) of the animal's responses pattern.

In summary, the significant main effects of C on $MG_{K\%}(C)$ for $K = 40$ and 3, suggest that as contrast is increased, the response pattern of the animal changes not merely in overall contrast but also in the detailed structure of the pattern employed. On the 40% checkerboards, the pattern deployed by the animal becomes coarser-grained (lower in spatial frequency) as contrast is increased; on the 3% checkerboards, the pattern deployed by the animal becomes finer-grained (higher in spatial frequency) as contrast is increased. Varying the contrast of 10% checkerboards does not produces significant changes in the mean granularity of cuttlefish response patterns.

4. Discussion

These sets of experiments show that substrate contrast and particle/object size play an important role in determining camouflaged body patterning in cuttlefish, *Sepia officinalis*. Since uniform/stipple, mottle and disruptive patterns differ mainly in the size and contrast of the pattern components that make up each pattern type (NB., see Introduction; Hanlon, 2007; Hanlon & Messenger, 1988), it is not surprising that substrate contrast and size are key visual cues for camouflage. On high-contrast checkerboards, cuttlefish body patterning depended on check size (see initial findings in Chiao & Hanlon, 2001a and Barbosa et al., 2007). On low-contrast checkerboards, irrespective of check size, cuttlefish showed low-contrast uniform/stipple patterns. As substrate contrast increased, so did the contrast of the animals' body pattern, until at high contrast, full expression of either mottle (small check size) or disruptive (large check size) were observed. Additional evidence that substrate contrast can be detected and discriminated by cuttlefish, thus affecting body patterning, comes from studies using artificial substrates (e.g., Chiao & Hanlon 2001a; Chiao et al., 2007; Kelman et al., 2007; Mäthger et al., 2006) as well as natural substrates (Chiao et al., 2005; Mäthger et al., 2007).

Experimentally, it was possible to demonstrate that, for a given check size, cuttlefish fine-tune their body patterns (uniform/stipple, mottle and disruptive) in response to rather small changes in background contrast. Such fine changes in body pattern are difficult to perceive with the human eye; our newly devised grading method, however, readily delineated them. Furthermore, with this automated grading method, we can objectively distinguish among the three main camouflaged body patterns without the influence of human judgment.

Disruptive patterning seems inappropriate for contrasting substrates with small particles (e.g., gravel or 3% check area) because the disruptive components are larger compared to the substrate particles, rendering the animal easier to be detected on a spatial scale mis-match by potential predators, than an animal showing uniform/stipple coloration. In studies also performed in this laboratory, we showed that decreasing the size and contrast on both natural and artificial substrates resulted in cuttlefish turning from disruptive to uniform (Mäthger et al., 2006, 2007). Similar results were shown here: on the 40% checkerboard, cuttlefish pattern changed from disruptive to uniform/stip-

ple, with no mottle patterning in between high to low substrate contrast. On the 40% checkerboard, no mottle was observed, presumably because the mottled skin components of cuttlefish were smaller in size compared to the background checks, which, in a natural setting, would not allow the animal to accomplish general background resemblance. Although cuttlefish cannot perfectly match artificial backgrounds such as checkerboards, the animal will process the visual background information and translate it into the most appropriate body pattern. It is therefore possible to take what we have learned from artificial substrates and make inferences about the animals' behavior in nature. This study showed that cuttlefish camouflage by way of (i) "contrast/object size match" to achieve general background resemblance (uniform/stipple and mottle patterns) or (ii) disruptive coloration.

Mäthger et al. (2006) suggested that cuttlefish are able to perceive objects in their background that differ in contrast by approximately 15%. In the current study, with the newly developed automated grading method, we noticed that cuttlefish change their body pattern in response to checkerboards that differ in contrast by 5%. This is particularly obvious in Fig. 8, where small changes in contrast level (e.g., a 5% change from 0.65 to 0.60 in Fig. 8B) result in distinctly different granularity spectrum amplitudes.

Cuttlefish are highly visual animals with very large and developed eyes with high acuity (Groeger, Cotton, & Williamson, 2005; Messenger, 1981, 1991; Muntz, 1999). Visual acuity behaviorally measured as the minimum separable angle was determined by Groeger et al. (2005) to be 34′ of arc (0.57°) at light intensity 15 $\mu W\ cm^{-2}$. From these present results, we cannot make any concrete inferences regarding the contrast sensitivity of cuttlefish vision, because we cannot rely on an animal's body pattern as a direct indication of contrast sensitivity. In their study, Mäthger et al. (2006) showed that there was a strong positive correlation between contrast and strength of disruptive patterning. However, since the body pattern expression cannot be used as a direct indication of visual contrast sensitivity threshold, their and our findings should only be used in the context of camouflage behavior, and not to judge the animals' visual abilities. In a study of octopus vision, Messenger (1973) showed that octopuses have a nystagmus response to grey stripes that differ in brightness by 18%, yielding a Michelson contrast of 8%. Nevertheless, what our study tells us is how substrate contrast affects body patterning and that the animals are capable of detecting the contrast ranges we used.

Few animals are able to rapidly change their camouflage patterns in response to changes in visual stimuli. Studies on flatfish coloration on uniform and contrasting backgrounds showed that different body patterns were expressed for the visual backgrounds presented. Indeed, the expression of light and dark areas in the skin of southern flounder (*Paralichthys lethostigma*) and winter flounder (*Pseudopleuronectes americanus*) (Saidel, 1988) appear to be affected by contrast and size of the background (see images in Saidel, 1988). These also applies to plaice (*Pleuronectes platessa*) (Kelman, Tiptus, & Osorio, 2006), and tropical flounder (*Bothus ocellatus*) (Ramachandran et al., 1996).

Cephalopod camouflage studies thus far have concentrated on camouflage in daylight or crepuscular periods (Hanlon, Forsythe, & Joneschild, 1999; Hanlon & Messenger, 1996). Recently, Hanlon et al. (2007) reported that, at dusk, the giant Australian cuttlefish *S. apama* ceased their day light behavior—sexual signaling and reproductive behavior—to produce night time camouflaged body patterns that were tailored to different backgrounds. This study provided evidence that (i) cuttlefish vision at night is keen, and (ii) cuttlefish camouflage at night is important, undoubtedly because predator vision is excellent at night. It would be interesting to follow-up these night time field studies with controlled experiments under different contrast and lighting conditions (including realistic night levels comparable to field situations).

In summary, we manipulated both the contrast and object size of the background and evaluated cuttlefish responses (the camouflaged body pattern) with a new objective method that allowed us to discriminate between uniform/stipple, mottle and disruptive patterns. This enabled us to detect small changes in cuttlefish body pattern due to changes in substrate contrast. As the current study makes clear, measuring the granularity spectra of cuttlefish responses can be very useful in revealing subtle changes in response tendencies with varying substrate parameters. Granularity spectra do not tell us everything we need to know, however. For example, there are many types of disruptive response pattern; the granularity spectrum does not enable us to discriminate between them (any strongly disruptive response tends to produce the same sort of granularity spectrum, regardless of the particular components activated in the pattern). Additional automated image statistics (tuned to individual disruptive components) will be required to differentiate varieties of disruptive response.

The results show that contrast and object size exert major influences on camouflaged body patterning in cuttlefish, *S. officinalis*. These results contribute to a small but growing body of experimental research aimed at understanding how the camouflaged body patterns of cephalopods are influenced by properties of the visual background, and they provide insight into the visual perception capabilities of the cephalopod eye. Ultimately we wish to relate these findings to the sensory ecology of camouflage in cephalopods under natural field conditions.

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References

Barbosa, A., Florio, C. F., Chiao, C.-C., & Hanlon, R. T. (2004). Visual background features that elicit mottled body patterns in cuttlefish *Sepia officinalis*. *Biological Bulletin, 207*(2), 154.

Barbosa, A., Mäthger, L. M., Chubb, C., Florio, C., Chiao, C.-C., & Hanlon, R. T. (2007). Disruptive coloration in cuttlefish: A visual perception mechanism that regulates ontogenetic adjustment of skin patterning. *Journal of Experimental Biology, 210*(7), 1139–1147.

Bellingham, J., Morris, A. G., & Hunt, D. M. (1998). The rhodopsin gene of the cuttlefish *Sepia officinalis*: Sequence and spectral tuning. *Journal of Experimental Biology, 201*, 2299–2306.

Brown, P. K., & Brown, P. S. (1958). Visual pigments of the octopus and cuttlefish. *Nature, 182*, 1288–1290.

Chiao, C.-C., Chubb, C., & Hanlon, R. T. (2007). Interactive effects of size, contrast, intensity and configuration of background objects in evoking disruptive camouflage in cuttlefish. *Vision Research, 47*(16), 2223–2235.

Chiao, C.-C., & Hanlon, R. T. (2001a). Cuttlefish camouflage: Visual perception of size, contrast and number of white squares on artificial checkerboard substrata initiates disruptive coloration. *Journal of Experimental Biology, 204*, 2119–2125.

Chiao, C.-C., & Hanlon, R. T. (2001b). Cuttlefish cue visually on area—not shape or aspect ratio—of light objects on the substrate to produce disruptive body patterns for camouflage. *Biological Bulletin, 201*, 269–270.

Chiao, C.-C., Kelman, E. J., & Hanlon, R. T. (2005). Disruptive body pattern of cuttlefish (*Sepia officinalis*) requires visual information regarding edges and contrast of objects in natural substrate backgrounds. *Biological Bulletin, 208*, 7–11.

Cott, H. B. (1940). *Adaptive coloration in animals*. London: Methuen& Co. Ltd.

Cuthill, I. C., Stevens, M., Sheppard, J., Maddocks, T., Parraga, C. A., & Troscianko, T. S. (2005). Disruptive coloration and background pattern matching. *Nature, 434*, 72–74.

Endler, J. (2006). Disruptive and cryptic coloration. *Proceedings of the Royal Society B: Biological Sciences, 273*(1600), 2425–2426.

Groeger, G., Cotton, P. A., & Williamson, R. (2005). Ontogenetic changes in the visual acuity of *Sepia officinalis* measured using the optomotor response. *Canadian Journal of Zoology, 83*, 274–279.

Hanlon, R. T. (2007). Cephalopod dynamic camouflage. *Current Biology, 17*(11), 400–404.

Hanlon, R. T., & Messenger, J. B. (1988). Adaptive coloration in young cuttlefish (*Sepia officinalis* L.): The morphology and development of body patterns and their relation to behaviour. *Philosophical Transactions of the Royal Society of London B, 320*, 437–487.

Hanlon, R. T., & Messenger, J. B. (1996). *Cephalopod behaviour*. Cambridge: Cambridge University Press.

Hanlon, R. T., Forsythe, J. W., & Joneschild, D. E. (1999). Crypsis, conspicuousness, mimicry and polyphenism as antipredator defences of foraging octopuses on Indo-Pacific coral reefs, with a method of quantifying crypsis from video tapes. *Biological Journal of the Linnean Society, 66*, 1–22.

Hanlon, R. T., Naud, M.-J., Forsythe, J. W., Hall, K., Watson, A. C., & McKechnie, J. (2007). Adaptable night camouflage by cuttlefish. *American Naturalist, 169*, 543–551.

Holmes, W. (1940). The colour changes and colour patterns of *Sepia officinalis* L. *Proceedings of the Zoological Society of London A, 110*, 2–35.

Kelman, E. J., Baddeley, R., Shohet, A., & Osorio, D. (2007). Perception of visual texture and the expression of disruptive camouflage by the cuttlefish, *Sepia officinalis*. *Proceedings of the Royal Society B: Biological Sciences, 274*(1616), 1369–1375.

Kelman, E. J., Tiptus, P., & Osorio, D. (2006). Juvenile plaice (*Pleuronectes platessa*) produce camouflage by flexibly combining two separate patterns. *Journal of Experimental Biology, 209*(17), 3288–3292.

Marshall, N. J., Jennings, K. J., McFarland, W. N., Loew, E. R., & Losey, G. S. (2003). Visual biology of Hawaiian coral reef fishes. II. Colors of Hawaiian coral reef fish. *Copeia, 3*, 455–466.

Marshall, N. J., & Messenger, J. B. (1996). Colour-blind camouflage. *Nature, 382*, 408–409.

Mäthger, L. M., Barbosa, A., Miner, S., & Hanlon, R. T. (2006). Color blindness and contrast perception in cuttlefish (*Sepia officinalis*) determined by a visual sensorimotor assay. *Vision Research, 46*(11), 1746–1753.

Mäthger, L. M., Chiao, C.-C., Barbosa, A., & Hanlon, R. T. (accepted for publication). Color matching on natural substrates in cuttlefish, *Sepia officinalis*. *Journal of Comparative Physiology A*.

Mäthger, L. M., Chiao, C.-C., Barbosa, A., Buresch, K. C., Kaye, S., & Hanlon, R. T. (2007). Disruptive coloration elicited on controlled natural substrates in cuttlefish, *Sepia officinalis*. *Journal of Experimental Biology, 210*(15), 2657–2666.

Merilaita, S. (1998). Crypsis through disruptive coloration in an isopod. *Proceedings of the Royal Society B, 265*, 1059–1064.

Merilaita, S., & Lind, J. (2005). Background-matching and disruptive coloration, and the evolution of cryptic coloration. *Proceedings of the Royal Society B: Biological Sciences, 272*(1563), 665–670.

Messenger, J. B. (1973). Some evidence for colour-blindness in Octopus. *Journal of Experimental Biology, 59*, 77–94.

Messenger, J. B. (1981). Comparative physiology of vision in molluscs. In H. Autrum (Ed.), *Comparative physiology and evolution of vision in invertebrates. C: Invertebrate visual centers and behavior II* (pp. 93–200). Springer-Verlag.

Messenger, J. B. (1991). Photoreception and vision in molluscs. In J. R. Cronly-Dillon & R. L. Gregory (Eds.). *Vision and visual dysfunction. Evolution of the eye and visual system* (Vol. 2, pp. 364–397). CRC Press Inc.

Messenger, J. B. (2001). Cephalopod chromatophores: Neurobiology and natural history. *Biological Reviews, 76*, 473–528.

Muntz, W. R. A. (1999). Visual systems, behaviour, and environment in cephalopods. In S. N. Archer, M. B. A. Djamgoz, E. R. Loew, J. C. Partridge, & S. Vallerga (Eds.), *Adaptive mechanisms in the ecology of vision* (pp. 467–484). Dordrecht, The Netherlands: Kluwer Academic Publishers.

Packard, A., & Hochberg, F. G. (1977). Skin patterning in *Octopus* and other genera. *Symposia of the Zoological Society of London, 38*, 191–231.

Ramachandran, V. S., Tyler, C. W., Gregory, R. L., Rogers-Ramachandran, D., Duensing, S., Pillsbury, C., et al. (1996). Rapid adaptive camouflage in tropical flounders. *Nature, 379*, 815–818.

Saidel, W. M. (1988). How to be unseen: An essay in obscurity. In J. Atema, R. R. Fay, A. N. Popper, & W. N. Tavolga (Eds.), *Sensory biology of aquatic animals* (pp. 487–513). New York: Springer-Verlag.

Schaefer, H., & Stobbe, N. (2006). Disruptive coloration provides camouflage independent of background matching. *Proceedings of the Royal Society B: Biological Sciences, 273*(1600), 2427–2432.

Shohet, A. J., Baddeley, R. J., Anderson, J. C., Kelman, E. J., & Osorio, D. (2006). Cuttlefish responses to visual orientation of substrates, water flow and a model of motion camouflage. *Journal of Experimental Biology, 209*(23), 4717–4723.

Shohet, A. J., Baddeley, R. J., Anderson, J. C., & Osorio, D. (2007). Cuttlefish camouflage: A quantitative study of patterning. *Biological Journal of the Linnean Society, 92*(2), 335–345.

Stevens, M. (2007). Predator perception and the interrelation between different forms of protective coloration. *Proceedings of the Royal Society B: Biological Sciences, 274*(1617), 1457–1464.

Stevens, M., & Cuthill, I. (2006). Disruptive coloration, crypsis and edge detection in early visual processing. *Proceedings of the Royal Society B: Biological Sciences, 273*(1598), 2141–2147.

Stevens, M., Cuthill, I. C., Párraga, C. A., & Troscianko, T. (2006). The effectiveness of disruptive coloration as a concealment strategy. In S. M. S. Martinez-Conde, L. Martinez, J.-M. Aloso, & P. Tse (Eds.). *Progress in brain research* (Vol. 155, pp. 49–64). Amsterdam: Elsevier.

Stevens, M., Cuthill, I. C., Windsor, A., & Walker, H. (2006). Disruptive contrast in animal camouflage. *Proceedings of the Royal Society B: Biological Sciences, 273*(1600), 2433–2438.

Warrant, E. J. (2004). Vision in the dimmest habitats on earth. *Journal of Comparative Physiology A, 190*, 765–789.

Warrant, E. J., & Nilsson, D.-E. (1998). Absorption of white light in photoreceptors. *Vision Research, 38*, 195–207.