

Edge detection and texture classification by cuttlefish

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Cephalopod mollusks including octopus and cuttlefish are adept at adaptive camouflage, varying their appearance to suit the surroundings. This behavior allows unique access into the vision of a non-human species because one can ask how these animals use spatial information to control their coloration pattern. There is particular interest in factors that affect the relative levels of expression of the Mottle and the Disruptive body patterns. Broadly speaking, the Mottle is displayed on continuous patterned surfaces whereas the Disruptive is used on discrete objects such as pebbles. Recent evidence from common cuttlefish, *Sepia officinalis*, suggests that multiple cues are relevant, including spatial scale, contrast, and depth. We analyze the body pattern responses of juvenile cuttlefish to a range of checkerboard stimuli. Our results suggest that the choice of camouflage pattern is consistent with a simple model of how cuttlefish classify visual textures, according to whether they are Uniform or patterned, and whether the pattern includes visual edges. In particular, cuttlefish appear to detect edges by sensing the relative spatial phases of two spatial frequency components (e.g., fundamental and the third harmonic Fourier component in a square wave). We discuss the relevance of these findings to vision and camouflage in aquatic environments.

Keywords: animal vision, camouflage, cephalopod, texture, edge detection

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Introduction

The common cuttlefish (*Sepia officinalis*) camouflages itself in on the seafloor by the varying the expression of some 40 “chromatic components” on the upper body-surface (Hanlon & Messenger, 1988). These components include local patches of color and visual textures that cover the body (Figure 1). The selection of the coloration pattern, which is under neuromuscular control and visually driven, demonstrates enormous versatility. Cuttlefish vary their appearance with at least six degrees of freedom (Kelman, Osorio, & Baddeley, 2008) by comparison flatfish species mix one to three basic patterns to produce camouflage (Kelman, Tiptus, & Osorio, 2006; Ramachandran et al., 1996). By allowing us to test the image parameters or features that control the expression of the cuttlefishes’ coloration pattern, this remarkable visual behavior offers a unique way to study both camouflage design and vision of a non-human species (Chiao, Chubb, & Hanlon, 2007; Kelman et al., 2008; Zylinski, Osorio, & Shohet, 2009).

Notwithstanding its flexibility, cuttlefish camouflage has been classified into three main classes of “body pattern,” known as Uniform, Mottle, and Disruptive (Figure 1; Hanlon, 2007; Hanlon & Messenger, 1988). The Disruptive pattern, which contains large visual features with clear borders (Figure 1c), is typically used on backgrounds that

include discrete objects—such as pebbles. The Mottle is a more “blurred” pattern, which in nature is probably used on continuous patterned surfaces (Figure 1b). The Mottle and Disruptive patterns are expressed at varying levels and can be mixed (Hanlon et al., 2009). Recent experiments show that several different types of visual information affect expression of the Disruptive pattern, probably because they are associated with the presence of discrete objects. They include light features, visual depth, and texture boundaries (Barbosa et al., 2007; Kelman et al., 2008). Unsurprisingly, visual edges in the background promote the expression of Disruptive patterns (Barbosa, Litman, & Hanlon, 2008; Kelman, Baddeley, Shohet, & Osorio, 2007; Mähger et al., 2007; Zylinski et al., 2009). There is good evidence that, like humans (Georgeson, May, Freeman, & Hesse, 2007; Morrone & Burr, 1988), cuttlefish edge detectors are sensitive to spatial phase; disruption (i.e., randomization) of phase suppresses the expression of Disruptive pattern on both periodic (checkerboard) and aperiodic (randomly placed circles) backgrounds (Kelman et al., 2007; Zylinski et al., 2009).

Here we test a simple model of how cuttlefish classify textures and detect edges. This proposes that visual thresholds are set by a single modulation transfer function (MTF), which is determined by optical and/or neural factors (Campbell & Robson, 1968). Discrimination of a pattern from a Uniform surface requires a single spatial



Figure 1. Cuttlefish body pattern camouflage can be placed in three broad categories, described by Hanlon and Messenger (1988): (a) Uniform, with few or no chromatic components expressed, is used in on visually homogeneous substrates such as fine sand; (b) Mottle, with “small to moderate light and dark” patches of chromatophores, is used on more complex backgrounds including artificial backgrounds with fine checks (Kelman et al., 2007; Zylinski et al., 2009). The details of natural background that elicit Mottle patterns are incompletely understood (Mäthger et al., 2007) but in captivity Mottle is used on coarse textured substrates such as gravel; (c) Disruptive, where “large scale” or coarse light and dark components are used in response to perceived light-colored objects of an area 70–120% of the “white square” component on the animal’s mantle (Barbosa et al., 2007; Barbosa, Mäthger, et al., 2008). These patterns are varied and mixed with great versatility (Hanlon et al., 2009; Zylinski et al., 2009). Body patterns are constrained by the position of the chromatic components on the body, which are fixed.

frequency component, whereas detection of edges (e.g., in a square wave) requires two detectable spatial frequency components (e.g., the fundamental and the third harmonic). A simple phase based edge detector such as this (Georgeson et al., 2007; Kovesi, 2000, 2002; Morrone & Burr, 1988) can be contrasted with other possible models that are proposed for humans and animals and which are used in machine vision (Marr & Hildreth, 1980; Mäthger et al., 2007; Stevens & Cuthill, 2006; Torre & Poggio, 1986). The analysis presented here of the coloration patterns expressed by cuttlefish on checkerboard backgrounds suggests that the simple model (MTF + minimum edge detection) accounts well for the way that cuttlefish classify the background texture to select Uniform, Mottle and Disruptive body patterns for camouflage.

Methods

Stimuli

The experimental design resembles that used recently by Barbosa, Mäthger, et al. (2008). Test stimuli were gray-scale checkerboards of seven sizes (1, 2, 3, 4, 6, 8, and 10 mm), plus a homogeneous gray. These stimuli gave a continuum between Uniform, Mottle, and Disruptive body patterns. Each checkerboard size class was tested at Michelson

Contrasts 0.25, 0.45, 0.63, 0.74, and 0.80 (measured with a spectrophotometer; Ocean Optics S-2000).

Animals and filming tank

Cuttlefish were hatched from eggs collected from the south coast of England and housed in purpose built facilities at the SeaLife center, Brighton, UK. They were fed *ad libitum* on mysids and natantids and maintained under 12:12-hour light–dark lighting. Subjects were aged approximately 5 months at the start of experiments, with mantle lengths 50–60 mm. The animals’ body patterns, produced in response to test stimuli, were photographed in an enclosed tank that minimized disturbance (Kelman et al., 2007). Test stimuli were placed under and around the edges of a test arena of 250-mm diameter, 100 mm deep in seawater. Images were recorded after the animals had settled and the body pattern expressed had remained stable for at least ten minutes. Stimuli were randomly presented, with ten animals tested on each stimulus on a single occasion, giving 360 images in total.

Image processing and data analysis

The images of the cuttlefish were cut from the background and randomized to ensure that the subsequent analysis was blind to both animal and treatment. The

images were graded by eye for the expression of 32 relevant chromatic, textural, and postural components (Hanlon & Messenger, 1988) by a single experienced observer (S.Z.). The expression of each component was scored on a four point scale, from 0 (*not expressed*) to 3 (*strongly expressed*). The resulting data set was reduced using principal component analysis (PCA; Kelman et al., 2007; Zylinski et al., 2009). PC coefficients were rescaled between zero and one for ease of interpretation. MANOVA was used to test for differences between stimuli responses on PCs 1 and 2. Kruskal–Wallis one-way ANOVA was used to test for within-treatment differences. Linear regression was used to test for linearity of responses to contrast modulation at specific check sizes.

Results

PCA

Ten cuttlefish were tested on checkerboard backgrounds of the seven different check sizes, each at five contrast levels, on a single occasion. Animals were also tested once on a Uniform gray background giving a total of 360 images. Images were each graded for levels of expression of 32 body pattern components, and these grading scores used in a PCA. Consistent with the two degrees of freedom in the stimuli (check size and contrast), the first two principal components (PCs) were retained using the Kaiser criterion (retaining PCs with a variance >1) and judged as relevant from assessing a scree plot of the variance subsumed by each PC (Figure 2a). PC1 and PC2 accounted for 30% and 26% of the variance in the data. The proportion of the variance represented rapidly dropped off after PC2, with PCs 3 and 4 each subsuming 5%. The remaining PCs (5–32) each accounted for $<3\%$ and tended to be represented by a single body pattern component.

There is a straightforward relationship between the cuttlefish body patterns identified by Hanlon and Messenger (1988) and the principal components we found. Body pattern components contributing positively to PC1 are associated with the Disruptive pattern (Hanlon & Messenger, 1988), such as white head bar, white square, and white posterior triangle (Figures 2b and 2c). Body pattern components contributing highly to PC2 are those associated with the Mottle or strong stipple patterns (Hanlon & Messenger, 1988), such as landmark spots, paired mantle spots, mantle margin scalloping, and coarse skin texture (Figures 2b and 2c). Of interest, yet with a variance of <1 and so not retained using the Kaiser criterion, PC3 coefficients correspond to a high contrast body pattern that may be classed as a distinctive type of Disruptive pattern. This “PC3” pattern was sometimes shown in response to larger check sizes at intermediate contrasts. It is primarily

characterized by a light overall color with a conspicuous posterior transverse mantle bar and is often expressed by cuttlefish on natural backgrounds (see Kelman et al., 2008; Figure 1a).

Animal responses

Figure 3a shows the responses of an *individual animal* to all stimuli and illustrates the overall results. There is a clear correlation between the body pattern responses expressed and mean PC1 and 2 amplitudes (Figure 3). High PC1 amplitudes are associated with large check sizes at high contrast. PC1 expression decreases with decreasing check size and/or contrast. PC2 amplitude (i.e., Mottle pattern) is largest at intermediate contrast values and check sizes (Figure 3b).

MANOVA of PC scores between treatments reveal significant interactions within PC1 and PC2 (Hotelling’s T-square, $F(70,644) 23, P \ll 0.001$). There are three main divisions, which are identified by statistical relationships by Mahalanobis distance on both PC1 and PC2 as groups with homogeneous responses (Figure 3a). Responses to stimuli between 4 and 10 mm at higher contrasts form a distinct group that is characterized by high PC1 scores (i.e., Disruptive pattern). The relationships within this group are dependent on both spatial scale and contrast, with the contrast threshold increasing with decreasing check size (Figure 4). The center group includes responses characterized by a high PC2 (i.e., strong Mottle patterns). This includes low-frequency patterns at intermediate contrasts and intermediate frequencies at high contrasts. A final group contains large check sizes (10 and 8 mm) at low contrast, small check sizes (1 mm) at all contrasts, and 2 mm checks at the lowest contrast (0.25); this shows that low contrasts in large-scale features gives a response more similar to a Uniform than either a Mottle or Disruptive body pattern.

Plotting the mean amplitudes \pm SE of PC1 and PC2 in response to each check size against contrast enables us to visualize the interaction between Mottle- and Disruptive-type components (Figure 4). It is clear that area is an important cue for the high expression of PC1 attributes (Barbosa, Mäthger, et al., 2008; Chiao et al., 2007; Chiao & Hanlon, 2001a, 2001b). Check sizes <4 mm consistently give a low PC1 score at all contrasts, while those of 4 mm and above score highly on PC1 at high contrasts. In other words, increasing check size above the threshold level of 4 mm (i.e., reducing pattern spatial frequency) increases the expression of PC1. For checks smaller than 4 mm, and Uniform gray, PC1 remains at a base-level value of 0.1 (K-W ANOVA, $p > 0.1$; Figure 3). The baseline score >0 is probably because PC1 is correlated with body components such as smooth skin that are also part of the Uniform pattern. Linear regression shows a strong positive correlation between PC1 attributes and contrast for size classes >4 mm (linear regression: 6, 8, and 10 mm: $r^2 =$

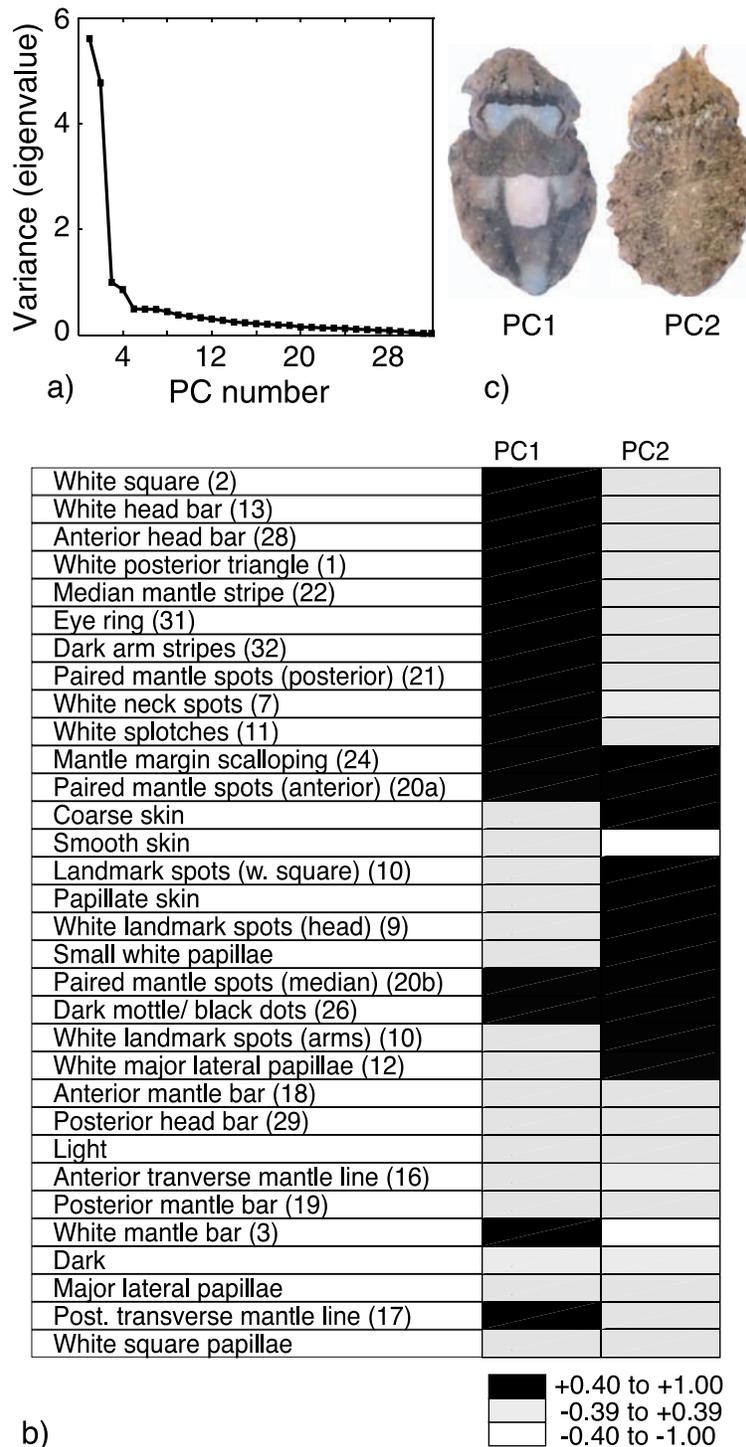


Figure 2. (a) Scree plot showing that PCs 1 and 2 account for a vast majority of the variance in the original data relative to the remaining PCs. (b) The contribution of 32 graded body pattern components (Hanlon & Messenger, 1988) to PC1 and PC2 (loadings are thresholded at 0.4 to allow components making a strong positive or negative contribution to be readily identified), showing that the two principal components generally account for very different characteristics. Numbers in brackets are the chromatic component numbers given by Hanlon and Messenger (1988) where appropriate. (c) Examples of body patterns typifying PC1 and PC2, respectively. PC1 is primarily characterized by Disruptive components and PC2 by Mottle components.

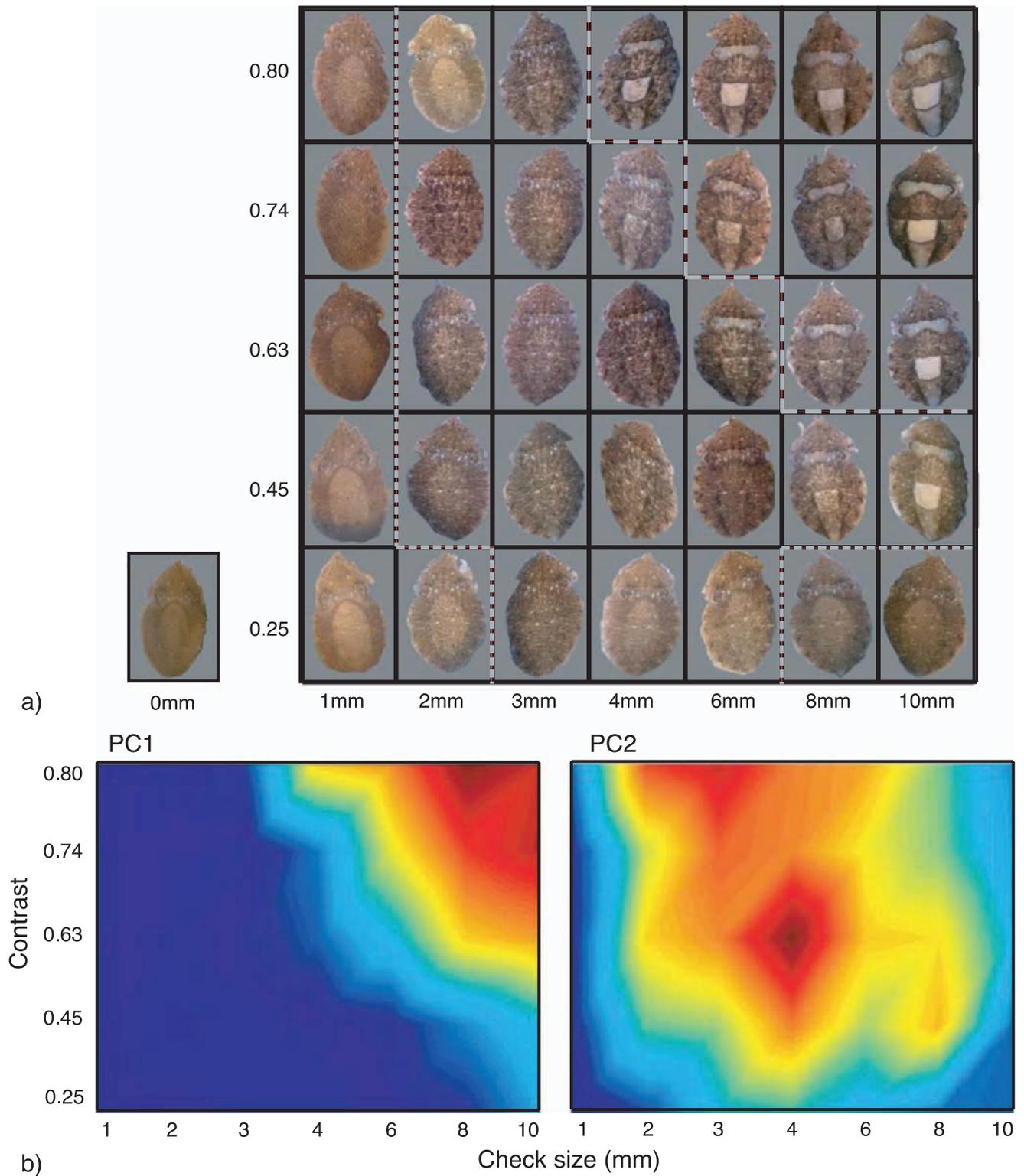
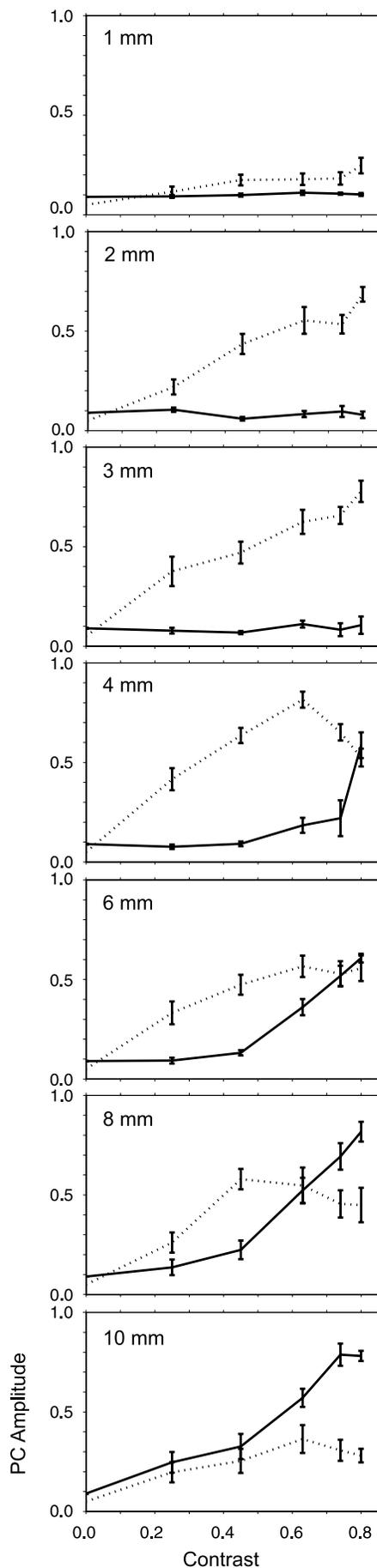


Figure 3. (a) The body patterns of a single animal expressed on all checkerboard sizes at all contrasts showing a typical set of observed responses. (b) Plots show the amplitude of mean PC coefficient scores for all animals as a color map for PC1 (left) and PC2 (right) across all checkerboard sizes and contrast. Red indicates a high (~1) coefficient; blue indicates a low (~0) coefficient.



0.73, 0.75, and 0.70, respectively; $p \ll 0.05$ for all; 4 mm: $r^2 = 0.44$, $p \ll 0.05$; 3, 2, and 1 mm: $r^2 < 0.05$, $p > 0.05$).

PC2 amplitudes have a very different trend with contrast modulation (Figure 4). PC2 amplitude peaks at intermediate contrasts for several check sizes (e.g., for 4 mm at a contrast of 0.63 the PC2 response is significantly higher than for contrasts of 0.45 or 0.74; K-W ANOVA, $p = 0.007$ and 0.023 , respectively). Animals did not exhibit high PC1 and PC2 characteristics simultaneously. Four-millimeter checks at contrast 0.80 elicit a high PC1 response that rapidly falls with reduction in contrast to be replaced by a high PC2 response. There is no clear linear relationship between contrast and PC2, although a weak correlation is apparent at 2 and 3 mm ($r^2 = 0.50$ and 0.39 , respectively; $p < 0.05$ in both cases). As with PC1, the lower contrast stimuli correspond to lower expression of PC2. However, even at the lowest contrast value (contrast 0.25) the PC2 response significantly exceeds that for Uniform gray stimulus at all check sizes above 1 mm (K-W ANOVA, $p < 0.005$ for 2–10 mm; $p = 0.25$ for 1 mm). In other words, animals respond to texture even at the lowest contrast value for small check sizes. Low amplitudes of PC1 and PC2, which correspond to stipple or Uniform body patterns, occur for both the smallest and the largest check sizes (1 and 10 mm) at the lowest contrast value (contrast 0.25) and for the Uniform gray control stimulus (Figures 3 and 4).

In summary our observations confirm that, on a high-contrast periodic stimulus, spatial scale (i.e., check size) determines whether the animals display Uniform, Mottle (high-PC2), or Disruptive (high-PC1) body patterns (Figures 1–4). At intermediate check sizes (4–8 mm), there are contrast-dependent interactions between PC1 and PC2 attributes.

Discussion

For a series of checkerboard patterns with varying spatial scale and contrast, much of the variation in the coloration patterns displayed by juvenile cuttlefish are described by two principal components, which (approximately) correspond to the Disruptive and Mottle body patterns (Hanlon & Messenger, 1988; Hanlon et al.,

Figure 4. Mean PC1 (solid line) and PC2 (dashed line) scores rescaled to a 0–1 range for all 10 animals across all contrast values for each checkerboard size \pm SEM. All origins are taken from the mean PC1 and PC2 response scores for the Uniform gray stimulus (0.09 and 0.05, respectively). ANOVA shows PC1 amplitude for 4 mm at a contrast of 0.8 to be significantly higher than at a contrast of 0.74 ($p = 0.003$). It also shows PC2 amplitude for 4 mm at a contrast of 0.63 to be significantly higher than that of a contrast of either 0.45 ($p = 0.007$) or 0.74 ($p = 0.023$). See text for further interpretation.

2007). We know that cuttlefish use multiple cues to select camouflage, including visual depth, spatial scale, and the presence of light objects and edges (Barbosa et al., 2007; Barbosa, Mähger, et al., 2008; Chiao & Hanlon, 2001a, 2001b; Chiao et al., 2007; Kelman et al., 2008). Contrast within the visual background also has a strong effect on the contrast of the pattern, as might be expected for cryptic camouflage. In particular, Barbosa, Mähger, et al. (2008) found that body patterning was check-size dependent at high contrast but not at low contrast and that small changes in contrast resulted in the “fine-tuning” of body pattern contrast and fine structure.

Here we account for the transitions between Uniform, Mottle, and Disruptive patterns by a simple model (Figures 1, 3, and 5). This proposes that when at least one spatial frequency (in a periodic pattern) is visible (i.e., passes the animal’s MTF), the stimulus is classed as non-Uniform, and when two spatial frequencies (e.g., fundamental and third harmonics in a square wave) are detectable, the animal can recognize edges. Specifically, on high-contrast checkerboard backgrounds, the Mottle (PC2) is expressed on check sizes of 1–3 mm and the Disruptive pattern (PC1) when the checks are larger (up to 10 mm; Figures 3 and 4). These values are consistent with behavioral/psychophysical MTF with a cut-off at about 0.35 cycles per millimeter. At intermediate check sizes, there are contrast-dependent interactions between PC1 and PC2 attributes. These interactions are consistent with a contrast

dependent cut-off—as expected for both optical and neural MTFs (Figure 5; Campbell & Robson, 1968). It is known that expression of the Disruptive pattern (and presumably edge detection) is sensitive to spatial phase (Kelman et al., 2007; Zylinski et al., 2009), and there is no evidence here that this phase sensitivity requires suprathreshold contrasts. Further corroboration of the model presented here might be provided by the response of *S. officinalis* to a two-dimensional plaid pattern. We would predict that animals would not express Disruptive (PC1) body patterns in response to such stimuli, irrespective of the plaid coarseness. However, we might expect to find certain Disruptive components expressed (potentially forming a separate PC), which might enable us to identify which body pattern components are expressed in response to edginess and which are expressed in response to large-scale high contrast patches.

These observations raise the question of what mechanism determines the cuttlefishes’ behavioral/psychophysical MTF. From an evolutionary point of view, camouflage may be influenced by two factors, first the animals’ own visual thresholds and second the choice of pattern that minimizes detection by potential predators such as fish (Langridge, Broom, & Osorio, 2007). Unfortunately the stimulus presentation, where animals are settled on a background, makes it impossible to specify the (angular) spatial frequency of the stimuli. Cephalopods are thought to have good visual acuity (Sweeney, Haddock,

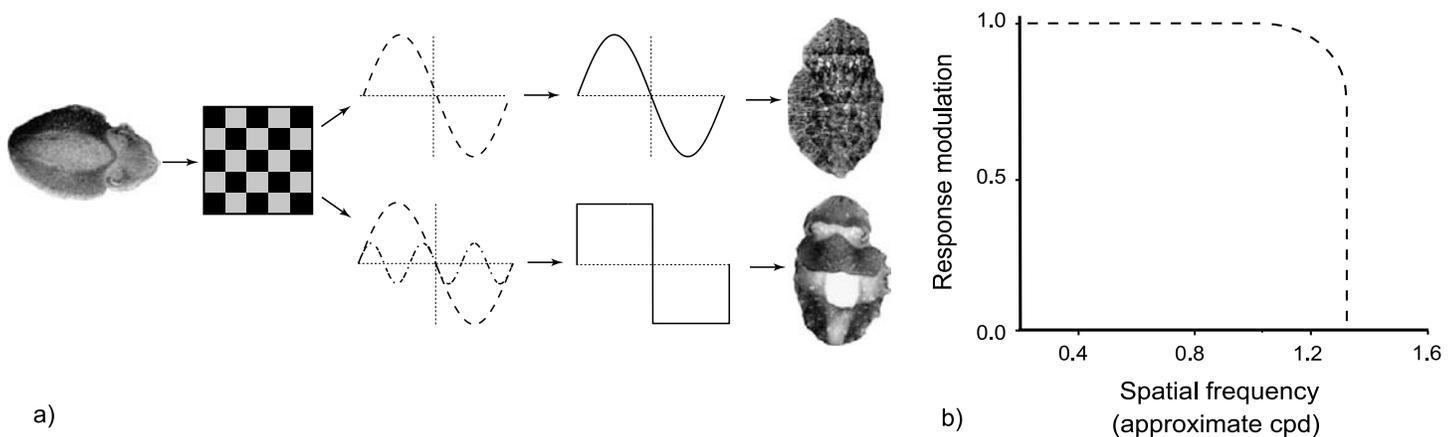


Figure 5. (a) A simple model of cuttlefish edge detection. When the animal views a visual environment containing structure it either detects the fundamental alone (e.g. other harmonics are lost in noise), leading to the interpretation of a non-edgy background and resulting in a Mottle-type response, or detects the fundamental wave and (at least) the third harmonic, leading to the perception of an edgy object and resulting in a Disruptive-type response. (b) Model modulation transfer function as determined from our results, showing estimated spatial frequency of checkerboard stimuli in cycles per degree (cpd) of visual angle. Visual angle (ν) for a cycle of check size (s) at a viewing distance (d) of 100 mm (taken as approximately the arena center-to-wall distance) determined by $\nu = 2 \arctan(s/2d)$. The highest spatial frequency to elicit a response lies in the region of 1.3 cpd (extrapolated for a check size of 1.3 mm). According to our model this will be where the fundamental frequency (f) alone is detectable, resulting in the use of Mottle body patterns. As the third harmonic is $3f$, we would predict from the behavioral MTF that Disruptive components will be used at a check size three times higher than the MTF, and indeed the threshold check size at which Disruptive components are used is 4 mm (0.44 cpd). Responses at 0.80 MC show that at the threshold check size of 4 mm, the main Disruptive components such as the white square and the white head bar are “switched on” (Figure 3). Reducing the stimulus to 0.74 MC “switches off” these components.

& Johnsen, 2007); thus, we tentatively favor the view that neural mechanisms rather than optical limits underlie the MTF (Figures 3 and 5).

Edge detection and camouflage in the aquatic environment

The great range of camouflage patterns used by cephalopods poses fascinating questions about their own vision, and that of potential predators—such as teleost fish—who have driven their evolution (Hanlon & Messenger, 1996; Langridge et al., 2007; Packard, 1972). Superficially, the choice of body pattern seems like a problem of texture matching (Julesz, 1981; Portilla & Simoncelli, 2000). A set of image parameters (e.g., power at specific spatial frequency bands; phase coherence) could characterize the visual environment and hence drive the choice of pattern. This would be a straightforward way to “match” the background. In practice, we know that the animal uses multiple signals to control the relative strengths of Disruptive and Mottle body patterns (PCs 1 and 2, respectively, here; Figures 2–4). We propose that these signals inform the animal whether the background is made of discrete objects or is a continuous surface (e.g., Barbosa et al., 2007; Chiao et al., 2007; Chiao, Kelman, & Hanlon, 2005; Kelman et al., 2008). These cues include visual depth, object size, and texture boundaries as well as edges (Zylinski et al., 2009). This strategy is reminiscent of the way in which humans use multiple cues for image segregation.

The use of multiple cues to classify the visual environment may be a consequence of the often turbid and visually complex shallow marine habitat where cuttlefish live (see Zylinski et al., 2009, and discussion below). We would expect the coloration system of cuttlefish (from visual input to body pattern output) to maximize the defensive qualities of the patterns expressed and hence be matched to the visual capabilities of predators within their environment (Portilla & Simoncelli, 2000; Shohet, Baddeley, Anderson, & Osorio, 2007; Stuart-Fox, Whiting, & Moussalli, 2006; Zeil & Hemmi, 2006).

Most natural scenes contain features that have complex intensity profiles (e.g., steps, roofs, and ramps) to which “traditional” edge detectors (e.g., the Sobel operator) are insensitive or give spurious responses (Kovesi, 2002; Perona & Malik, 1990), and this may be more true in underwater environments than on land. *S. officinalis* lives in fairly turbid coastal waters where contrast is rapidly degraded; light absorption by water and scatter by suspended materials attenuates the image forming light and decreases the difference between object and background radiance resulting in a low-frequency and low-contrast world (Douglas & Hawryshyn, 1990; Lythgoe, 1979). The low-level invariance of phase congruency to illumination, scale, and contrast (Kovesi, 1999, 2000) would make local energy a powerful means of detecting features in unstable optical environment where reliable

step edges might be rare (Zylinski et al., 2009). We speculate that, given the optical conditions typical of the aquatic environment, such an invariant means of edge detection may be of greater use in water than on land.

Conclusions

We know that multiple visual cues control the cuttlefishes choice of body patterns. Here we have demonstrated that edge detection in cuttlefish is consistent with a minimal model, whereby edginess is defined by fundamental and third harmonic detectability, which shows strong parallels with human visual processing. Edge detection is important for determining when Mottle and Disruptive chromatic components are used, and this simple mechanism may be especially well suited to the complex and capricious optical conditions of the aquatic environment, where an especially robust mechanism that is invariant to factors such as contrast and intensity would be favored.

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References

- Barbosa, A., Litman, L., & Hanlon, R. T. (2008). Changeable cuttlefish camouflage is influenced by the horizontal and vertical aspects of the visual background. *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, *194*, 405–413. [PubMed]
- Barbosa, A., Mäthger, L. M., Buresch, K. C., Kelly, J., Chubb, C., Chiao, C.-C., et al. (2008). Cuttlefish camouflage: The effects of substrate contrast and size in evoking Uniform, Mottle or Disruptive body patterns. *Vision Research*, *48*, 1242–1253. [PubMed]
- Barbosa, A., Mäthger, L. M., Chubb, C., Chiao, C.-C., Florio, 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*, 1139–1147. [PubMed] [Article]
- Campbell, F. W., & Robson, J. G. (1968). Application of Fourier analysis to the visibility of gratings. *The Journal of Physiology*, *197*, 551–566. [PubMed] [Article]
- 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*, 2223–2235. [PubMed]
- 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. [PubMed] [Article]
- Chiao, C.-C., & Hanlon, R. T. (2001b). Cuttlefish cue visually on area—not shape or aspect ratio—of light objects in the substrate to produce Disruptive body patterns for camouflage. *Biology Bulletin*, *201*, 269–270. [PubMed] [Article]
- Chiao, C.-C., Kelman, E. J., & Hanlon, R. T. (2005). Disruptive body patterning of cuttlefish (*Sepia officinalis*) requires visual information regarding edges and contrast of objects in natural substrate backgrounds. *Biology Bulletin*, *208*, 7–11. [PubMed] [Article]
- Douglas, R. H., & Hawryshyn, C. W. (1990). Behavioural studies of fish vision: An analysis of visual capabilities. In R. H. Douglas & M. B. A. Djamgoz (Eds.), *The visual system of fish*. London: Chapman & Hall.
- Georgeson, M. A., May, K. A., Freeman, T. C. A., & Hesse, G. S. (2007). From filters to features: Scale-space analysis of edge and blur coding in human vision. *Journal of Vision*, *7*(13):7, 1–21, <http://journalofvision.org/7/13/7/>, doi:10.1167/7.13.7. [PubMed] [Article]
- Hanlon, R. (2007). Cephalopod dynamic camouflage. *Current Biology*, *17*, 1–5. [PubMed]
- Hanlon, R. T., Chiao, C.-C., Mäthger, L. M., Barbosa, A., Buresch, K. C., & Chubb, C. (2009). Cephalopod dynamic camouflage: Bridging the continuum between background matching and Disruptive coloration. *Philosophical Transactions of the Royal Society of London B, Biological Sciences*, *364*, 429–437. [PubMed]
- 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, Biological Sciences*, *320*, 437–487.
- Hanlon, R. T., & Messenger, J. B. (1996). *Cephalopod behaviour*. Cambridge: Cambridge University Press.
- Hanlon, R. T., Naud, M.-J., Forsythe, J. W., Hall, K., Watson, A. C., & Mckechnie, J. (2007). Adaptive night camouflage by cuttlefish. *American Naturalist*, *169*, 543–551. [PubMed]
- Julesz, B. (1981). Textons, the elements of texture perception, and their interactions. *Nature*, *290*, 91–97. [PubMed]
- Kelman, E. J., Baddeley, R. J., Shohet, A. J., & Osorio, D. (2007). Perception of visual texture and the expression of Disruptive camouflage by the cuttlefish *Sepia officinalis*. *Proceedings of the Royal Society of London B, Biological Sciences*, *274*, 1369–1375. [PubMed] [Article]
- Kelman, E. J., Osorio, D., & Baddeley, R. (2008). Review on sensory neuroethology of Cuttlefish camouflage and visual object recognition. *Journal of Experimental Biology*, *211*, 1757–1763. [PubMed] [Article]
- 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*, 3288–3292. [PubMed] [Article]
- Kovesi, P. (2002). *Edges are not just steps*. The 5th Asian Conference on Computer Vision, Melbourne, Australia.
- Kovesi, P. D. (1999). Image features from phase congruency. *Journal of Computer Vision Research*, *1*, 2–26.
- Kovesi, P. D. (2000). Phase congruency: A low-level image invariant. *Psychological Research*, *64*, 136–148. [PubMed]
- Langridge, K., Broom, M., & Osorio, D. (2007). Selective signalling by cuttlefish to predators. *Current Biology*, *17*, R1044–R1045. [PubMed]
- Lythgoe, J. N. (1979). *The ecology of vision*. Oxford: Clarendon Press.
- Marr, D., & Hildreth, E. (1980). Theory of edge detection. *Proceedings of the Royal Society of London B, Biological Sciences*, *207*, 187–217. [PubMed]
- 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*, 2657–2666. [PubMed] [Article]
- Morrone, M. C., & Burr, D. C. (1988). Feature detection in human vision: A phase-dependent energy model. *Proceedings of the Royal Society of London B, Biological Sciences*, *235*, 221–245. [PubMed]
- Packard, A. (1972). Cephalopods and fish: The limits of convergence. *Biology Review*, *47*, 241–307.
- Perona, P., & Malik, J. (1990). Detecting and localizing edges composed of steps, peaks and roofs. In

Proceedings of the 3rd International Conference on Computer Vision.

- Portilla, J., & Simoncelli, E. P. (2000). A parametric texture model based on joint statistics of complex wavelet coefficients. *International Journal of Computer Vision*, 40, 49–71. [[Article](#)]
- 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. [[PubMed](#)]
- Shohet, A., Baddeley, R., Anderson, J. C., & Osorio, D. (2007). Cuttlefish camouflage: A quantitative study of patterning. *Biological Journal of the Linnean Society*, 92, 335–345.
- Stevens, M., & Cuthill, I. C. (2006). Disruptive coloration, crypsis and edge detection in early visual processing. *Proceedings of the Royal Society of London B, Biological Sciences*, 273, 2141–2147. [[PubMed](#)] [[Article](#)]
- Stuart-Fox, D., Whiting, M. J., & Moussalli, A. (2006). Camouflage and colour change: Antipredator responses to bird and snake predators across multiple populations in a dwarf chameleon. *Biological Journal of the Linnean Society*, 88, 437–446.
- Sweeney, A. M., Haddock, S. H. D., & Johnsen, S. (2007). Comparative visual acuity of coleoid cephalopods. *Integrative and Comparative Biology*, 47, 808–814. [[Article](#)]
- Torre, V., & Poggio, T. A. (1986). On edge detection. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 8, 147–163.
- Zeil, J., & Hemmi, J. M. (2006). The visual ecology of fiddler crabs. *Journal of Comparative Physiology A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 192, 1–25. [[PubMed](#)]
- Zylinski, S., Osorio, D., & Shohet, A. (2009). Perception of edges and visual texture in the camouflage of the common cuttlefish, *Sepia officinalis*. *Philosophical Transactions of the Royal Society of London B, Biological Sciences*, 364, 439–448. [[PubMed](#)]