Vision Research 83 (2013) 40–47

Contents lists available at SciVerse ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

How visual edge features influence cuttlefish camouflage patterning

Chuan-Chin Chiao [a,b,*], Kimberly M. Ulmer [a], Liese A. Siemann [a], Kendra C. Buresch [a], Charles Chubb [a,c], Roger T. Hanlon [a]

[a] Program in Sensory Physiology & Behavior, Marine Biological Laboratory, Woods Hole, MA, USA
[b] Department of Life Science, National Tsing Hua University, Hsinchu, Taiwan
[c] Department of Cognitive Sciences & Institute for Mathematical Behavioral Sciences, University of California at Irvine, USA

ARTICLE INFO

Article history:
Received 9 November 2012
Received in revised form 30 January 2013
Available online 13 March 2013

Keywords:
Edge perception
Spatial frequency
Line terminator
Disruptive body pattern
Sepia officinalis

ABSTRACT

Rapid adaptive camouflage is the primary defense of soft-bodied cuttlefish. Previous studies have shown that cuttlefish body patterns are strongly influenced by visual edges in the substrate. The aim of the present study was to examine how cuttlefish body patterning is differentially controlled by various aspects of edges, including contrast polarity, contrast strength, and the presence or absence of "line terminators" introduced into a pattern when continuous edges are fragmented. Spatially high- and low-pass filtered white or black disks, as well as isolated, continuous and fragmented edges varying in contrast, were used to assess activation of cuttlefish skin components. Although disks of both contrast polarities evoked relatively weak disruptive body patterns, black disks activated different skin components than white disks, and high-frequency information alone sufficed to drive the responses to white disks whereas high- and low-frequency information were both required to drive responses to black disks. Strikingly, high-contrast edge fragments evoked substantially stronger body pattern responses than low-contrast edge fragments, whereas the body pattern responses evoked by high-contrast continuous edges were no stronger than those produced by low-contrast edges. This suggests that line terminators vs. continuous edges influence expression of disruptive body pattern components via different mechanisms that are controlled by contrast in different ways.

1. Introduction

Cephalopod camouflage is the fastest changing and most versatile in the animal kingdom. These visually driven behaviors enable cuttlefish and octopuses to move throughout complex habitats such as coral reefs, kelp forests, and temperate rock reefs with relative impunity from detection or recognition by their numerous visual predators (Hanlon, 2007; Hanlon et al., 2011).

The cuttlefish disruptive body pattern may break up the animal's body outline as well as providing some degree of background matching that reduces detection (Cott, 1940). Most of the camouflage principles involved in disruptive body patterning emphasize contrast/edges of animal and background (Stevens & Merilaita, 2009). The edge of an object is an abrupt change in spatial properties between object and background, and it is known that the visual systems of many animals are highly sensitive to edges (Troscianko et al., 2009). However, complete edges of objects are rare in cluttered visual environments. Instead, edge segments (lines and corners) are more abundant in complex backgrounds; thus visual sensing of salient edges/lines in the background provides cuttlefish with rich information that can be potentially used for disruptive body pattern expression (Chiao, Kelman, & Hanlon, 2005; Zylinski, Osorio, & Shohet, 2009b).

The expression of camouflage body patterns in cuttlefish is a visually driven behavior (Hanlon & Messenger, 1988; Holmes, 1940; Marshall & Messenger, 1996), and previous studies have shown that several low-level visual cues (intensity, contrast, area, edges, visual depth, etc.) are important in eliciting disruptive body patterns (Barbosa et al., 2008; Chiao, Chubb, & Hanlon, 2007; Kelman, Osorio, & Baddeley, 2008; Zylinski, Osorio, & Shohet, 2009a). In a recent study, Zylinski, Osorio, and Shohet (2009b) conducted the first experiment exploring how edges alone affect the expression of disruptive body patterns. They showed that substrates comprising randomly arranged, high-pass spatial filtered disks (similar to the substrate S5 tested in the present study; see Fig. 1) evoked moderately disruptive body pattern responses from *Sepia officinalis* (similar in strength to those evoked by unfiltered, homogeneous white disks). Zylinski, Osorio, and Shohet (2009b) also observed that substrates derived by discarding all but 1/4 of each filtered disk (similar to the substrate S6 tested in the present study; see Fig. 1) continued to evoke disruptive body pattern responses nearly as strong as those evoked by the substrates populated by whole filtered disks.

* Corresponding author. Address: Department of Life Science, National Tsing Hua University, 101, Sec. 2, Kuang-Fu Road, Hsinchu 30013, Taiwan. Fax: +886 3 571 5934.
E-mail address: ccchiao@life.nthu.edu.tw (C.-C. Chiao).

0042-6989/$ - see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.visres.2013.03.001

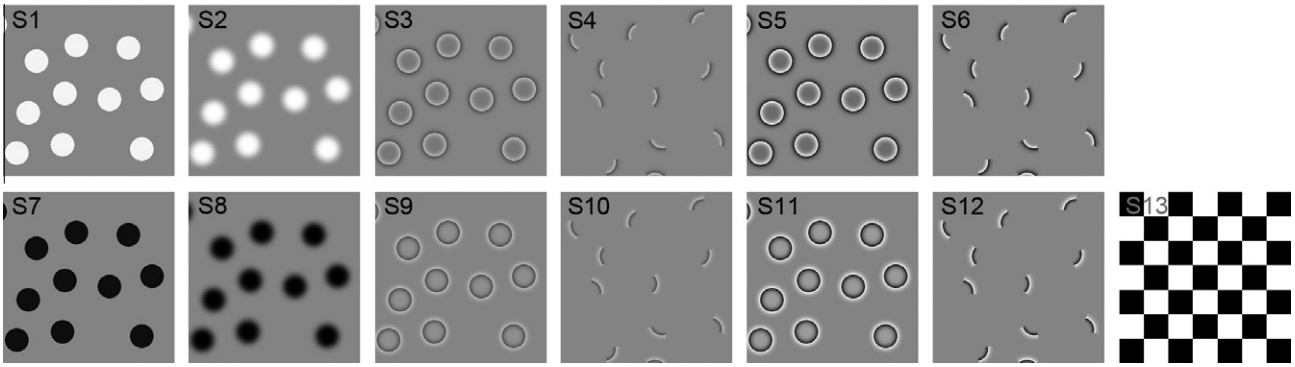

Fig. 1. Thirteen substrates used in the present study. A gray field populated with randomly placed white disks (S1) or black disks (S7) was filtered into low and high spatial frequency bands to produce blurred disks (S2 and S8) and low-contrast full-edge-rings (S3 and S9). Low-contrast, quarter-edge-rings (S4 and S10) were produced by erasing a random 270 deg arc from each low-contrast full-edge-ring. High-contrast versions of these edge substrates were generated by maximizing the overall contrast (S5–S6 and S11–S12). Substrates S1–S6 are positive contrast polarity, S7–S12 are negative polarity, and S13 is black-white checkerboard.

Much of the motivation for the present study was to pursue the interesting leads in Zylinski, Osorio, and Shohet (2009b), partly because we noted the importance of edges in our previous work (Chiao, Kelman, & Hanlon, 2005). Here we broadened the scope of the study to include additional substrate combinations and image analysis methods that allow us to quantify the activation of individual skin components. Specifically, we tested three hypotheses in the present study: (1) Cuttlefish respond to positive and negative contrast of objects (white and black disks on gray backgrounds, respectively) differently; (2) Contrast of edges is important for cuttlefish to modulate their disruptive body pattern response; and (3) Cuttlefish's sensitivity to lines and corners is different from continuous edges. By testing animals on carefully designed substrates (Fig. 1) and analyzing their corresponding responses, these experiments provide further insights into the mechanisms by which edges, edge-fragments, contrast energy, and contrast polarity control disruptive body patterns in cuttlefish.

2. Materials and methods

2.1. Animals and experimental setup

European cuttlefish (*S. officinalis*) were hatched, reared and maintained in the MBL Marine Resources Center (Woods Hole, MA, USA). Ten cuttlefish (mean ML = 5.57 cm) were used in this study. To provide a stable visual environment and minimize stress to the animals, the experimental trials were conducted inside a tent made of black plastic sheeting. Each animal was placed inside a 25 cm arena within a circular tank (50 cm diameter, 15 cm height) equipped with flow-through seawater, where various computer-generated artificial substrates (laminated to be waterproof) were presented on both the floor and wall. A circular 40 W fluorescent light source (Phillips CoolWhite, Andover, MA, USA) was placed directly above the arena to reduce the presence of shadows. Once the animal had acclimated (i.e. ceased swimming and hovering movements, and expressed a stable body pattern), a still image was taken remotely using a digital camera (Nikon Coolpix 5400, Melville, NY, USA) mounted 60 cm above the arena and connected to an LCD monitor located outside of the tent area so that the animal's movements could be observed without disturbing it.

2.2. Substrates

Thirteen artificial substrates were designed to examine the interactions of several key visual features of background objects (contrast polarity, contrast energy, edges, and edge-fragments) on disruptive body pattern expression (Fig. 1). A mid-gray uniform background with randomly placed white disks (S1) was filtered into low and high spatial frequency bands to produce blurred white disks (S2) and low-contrast full-edge-rings (S3). Note that the amplitudes of S2 and S3 have been adjusted so that their sum is precisely equal to S1; in addition, the filtering used to produce S2 and S3 ensures that the summed contrast energy of S2 and S3 is equal to the contrast energy of S1 itself. Low-contrast, quarter-edge-rings (S4) were produced by erasing a random 270 deg arc from each low-contrast full-edge-ring in S3. Substrates S5 and S6 were high-contrast versions of substrates S3 and S4. Substrates S7–S12 (negative contrast polarity) were analogous to substrates S1–S6 (positive contrast polarity) except that the initial disks in S7 were black instead of white. Substrate S13 was a high-contrast black–white checkerboard and served as a control as it has in many of our past experiments. Both the disk- and check-sizes on these substrates were selected to be approximately equal in area to the average area of our animals' white square skin component.

2.3. Quantification of the strength of disruptive body patterns

We have developed an automated method to quantify the activation of five light and five dark skin components (Chiao et al., 2009) used to generate disruptive body patterns described previously in *S. officinalis* (Hanlon & Messenger, 1988). In addition, we also derived a new set of statistics reflecting the activation of dark skin components on the head/arm of cuttlefish that have not been characterized previously. These statistics are "dark head," "dark arm tip," and the "third paired mantle spots" (see Fig. 2 for details). In brief, to perform this component analysis, each animal image was first cut out from the background on which it appeared and warped to conform in size and shape to a standard cuttlefish template. Then five intensity traces (one medial and four transverse traces) were extracted from the image. The fluctuation in image intensity along these traces was used to estimate the activation strengths of all light and dark components. The summary statistic (or, the disruptive score) was derived by adding the activations of five light and five dark disruptive components previously described in *S. officinalis* (Hanlon & Messenger, 1988).

3. Results

A glance at Fig. 3 reveals first that the skin components most strongly activated by experimental substrates S1 through S12 are the white square and the white head bar. However, those responses are variable, and few if any of them are maximal in

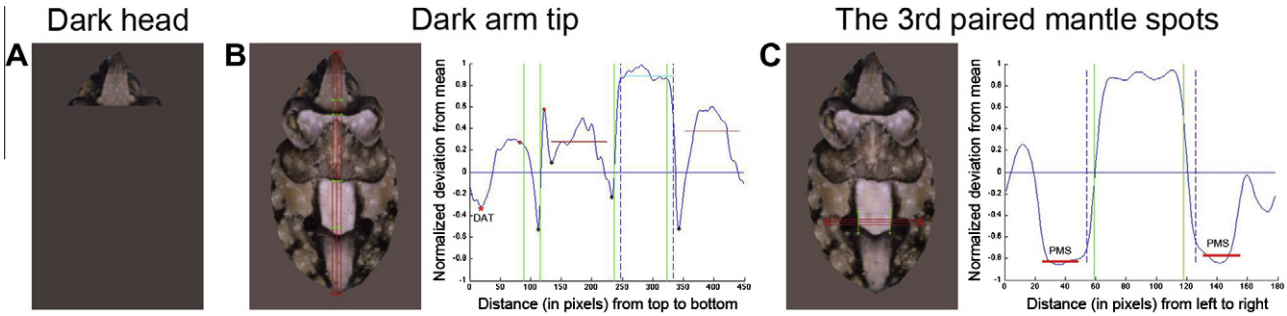

Fig. 2. Activation of 3 dark skin components on the head/arm of cuttlefish (Dark Head, Dark Arm Tip, and the 3rd Paired Mantle Spots) that have not been quantified previously (Chiao et al., 2009). (A) Dark Head (DH) is the mean intensity of the head/arm region. (B) Dark Arm Tip (DAT) is derived from the intensity trace of the medial line. We sample image intensities along the three red lines and take the average of the three traces. (C) The 3rd Paired Mantle Spots (PMS) is calculated by averaging activations derived from the intensity trace of a line that runs horizontally across the region of the 3rd paired mantle spots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

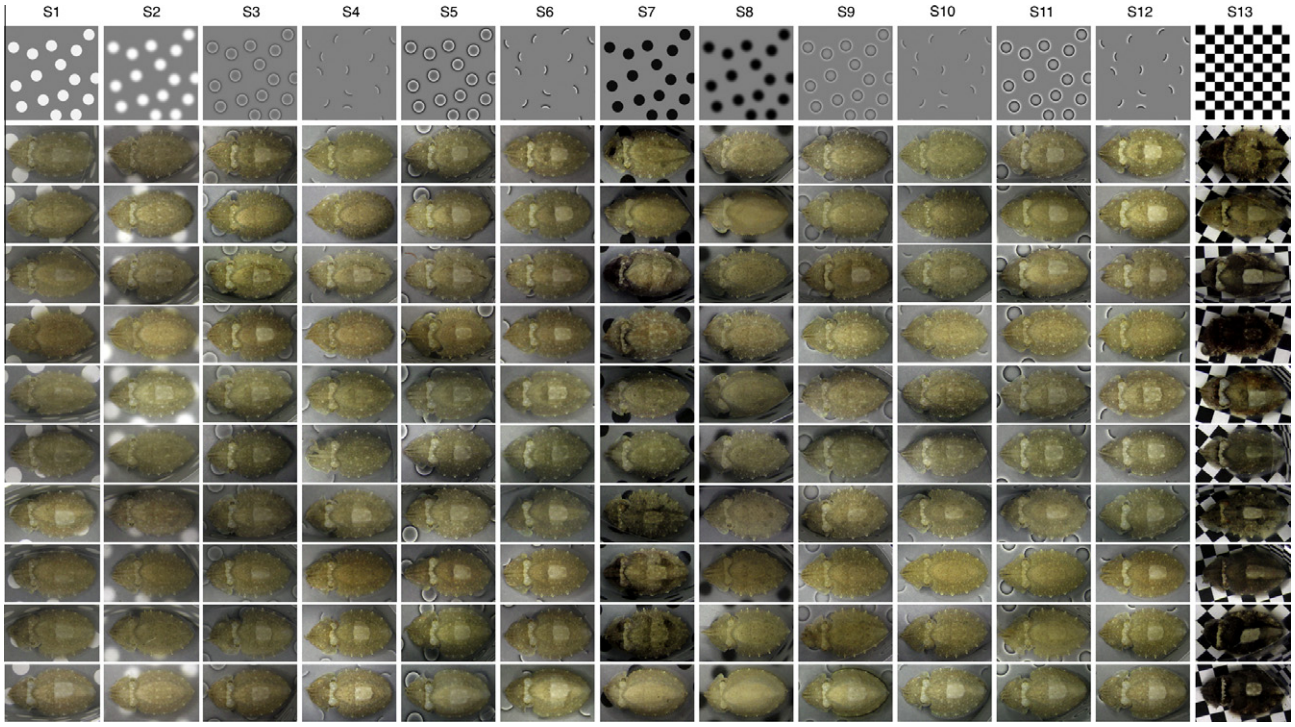

Fig. 3. Cuttlefish responses to 13 substrates (S1–S13 in Fig. 1) in the present study. Body patterns of all 10 animals were recorded immediately after a long acclimation time.

strength (to see this, note that the activations of these two skin components evoked by the control checkerboard substrate S13 tend to be substantially stronger than those evoked by the experimental substrates). Our overall strategy was to analyze how the variations in activation strength of these two skin components are controlled by the features of experimental substrates S1–S12. We observe in passing that our results (Fig. 4) seem to depart from earlier findings of Zylinski, Osorio, and Shohet (2009b) who reported that cuttlefish skin component activations evoked by substrates similar to S1 and S5 were much stronger.

3.1. Positive and negative contrast polarities activate different disruptive skin components

Although it has been known that light objects on dark backgrounds are effective in evoking disruptive body patterns in cuttlefish (Chiao & Hanlon, 2001a, 2001b), whether dark objects on light backgrounds are also effective in modulating body patterning is less studied (Mäthger et al., 2007). While overall disruptive body pattern expression and major light/dark skin component activations of cuttlefish on S1 and S7 were both weak (Fig. 4A), close examination of all animal responses revealed that animals showed more dark components on S7 than on S1, particularly in the head/arm region and the third paired mantle spots (Fig. 3). To quantify these responses, we developed a new set of statistics to capture these differences (Fig. 2): the "dark head", "dark arm tip", and "third paired mantle spots" statistics. Cuttlefish tend to express stronger dark head, dark arm tip, and third paired mantle spots on S7 than on S1 (Fig. 5). However, paired samples *t*-tests only partially confirm these observations. Dark head activation was higher on S7 than on S1, but not significantly so ($t = 2.248$, $df = 9$, $p = 0.051$, two-tailed); however, note that because activations are quantified based on deviations from the mean intensity of the animal, dark components on a dark animal have much lower activation strengths than a similarly dark head on a light animal. Dark arm tip activation was significantly higher on S7 than on S1 ($t = 2.568$, $df = 9$, $p = 0.030$, two-tailed). Finally, the third paired mantle spots activation was also higher on S7 than on S1, but this

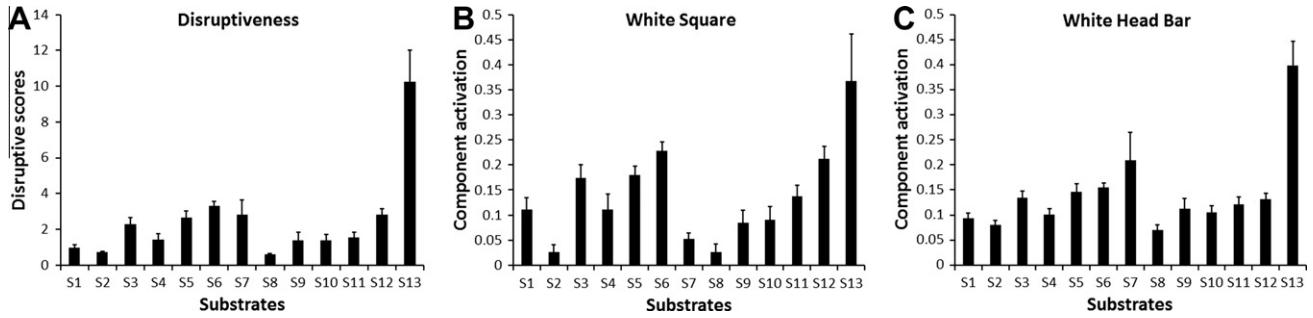

Fig. 4. Average total disruptive scores and individual disruptive skin component activations of 10 cuttlefish in response to 13 substrates. Disks of both contrast polarities evoked moderately disruptive patterns, but high-frequency information alone drove responding to white disks whereas high- and low-frequency information were both required to drive responding to black disks. Strikingly, high-contrast quarter-edge-rings evoked much more strongly disruptive responses than low-contrast quarter-edge-rings; by comparison, high- and low-contrast full-edge-rings evoked similar responses. WS, white square; WHB, white head bar. Error bars are SEM.

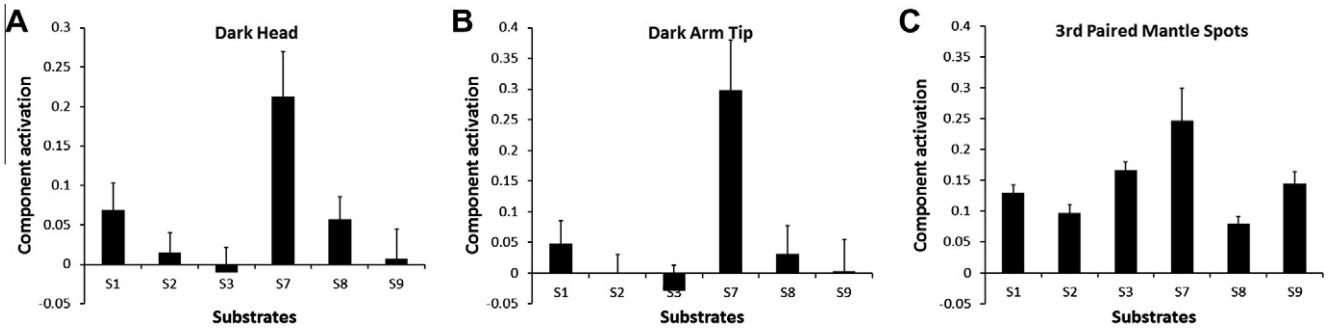

Fig. 5. Average dark skin component activations of 10 cuttlefish in response to substrates of different contrast polarity (S1–S3 vs. S7–S9). Cuttlefish pattern responses to white vs. black disks (S1 vs. S7) used different skin components. DH, dark head; DAT, dark arm tip; PMS, 3rd paired mantle spots. Error bars are SEM.

difference did not reach statistical significance ($t = 2.144$, $df = 9$, $p = 0.061$, two-tailed). On the other hand, cuttlefish showed more light components on S1 than on S7 (Fig. 3). In particular, white square activation was significantly higher on S1 than on S7 ($t = 2.531$, $df = 9$, $p = 0.032$, two-tailed); white head bar activation was also higher on S1 than on S7 but not significantly so ($t = 2.104$, $df = 9$, $p = 0.065$, two-tailed). Taken together, these results suggest that different skin components are activated by a substrate populated by mostly dark vs. light objects.

Note that substrate patterns S1 and S7 are photographic negatives of each other and therefore have identical Fourier energy spectra (excluding the 0-frequency "dc" Fourier component that reflects the mean reflectance of the substrate). Thus, the fact that cuttlefish produced significantly different patterns in response to white- vs. black-disk substrates underscores an observation made previously by Kelman et al. (2007) that patterning responses are sensitive not merely to the energy spectrum of the substrate, but also to the phase spectrum. A more surprising difference along these same lines is seen by comparing the white square activation evoked by the high-pass filtered white disks (S3) vs. the high-pass filtered black disks (S9). These two substrates are also photographic negatives of each other, and they have equal mean reflectance. They thus have identical Fourier energy spectra. It appears that the high-pass filtered white disks (S3) evoke stronger white square activation than the high-pass filtered black disks (S9) (Fig. 4B); however, this difference fails to achieve statistical significance ($t = 2.171$, $df = 9$, $p = 0.058$, two-tailed).

Considering the Fourier energy spectra of these substrates, the energy of S1 is the sum of those of S2 and S3. Thus, if Fourier energy were the critical factor in determining response strength, S1 should always produce activation at least as strong as either S2 or S3. However, significantly stronger overall pattern expression was evoked by S3 than S1 ($t = 2.815$, $df = 9$, $p = 0.020$, two-tailed); in addition, significantly stronger white head bar activation was evoked by S3 than S1 ($t = 2.877$, $df = 9$, $p = 0.018$, two-tailed). Although white square activation was also generally stronger on S3 than on S1, this difference was not statistically significant ($t = 1.621$, $df = 9$, $p = 0.139$, two-tailed). This confirms previous findings that edge information alone is sufficient to elicit disruptive body patterns in cuttlefish (Zylinski, Osorio, & Shohet, 2009b) and shows moreover that decreasing the amplitudes of the low-frequency Fourier components in the substrate actually increases the activation strength of both the overall disruptiveness and the white head bar.

The trend is different when we consider the negative polarities. Note that S7 is literally the sum of S8 and S9, and S7 produced significantly higher overall pattern expression than S8 by itself ($t = 2.908$, $df = 9$, $p = 0.017$, two-tailed), though not S9 by itself ($t = 1.942$, $df = 9$, $p = 0.084$, two-tailed). This is seen most clearly in Fig. 5, which shows that the dark heads, dark arm tips, and third paired mantle spots of the cuttlefish were significantly more strongly activated on S7 than on S8 (DH: $t = 2.640$, $df = 9$, $p = 0.027$, two-tailed; DAT: $t = 2.928$, $df = 9$, $p = 0.017$, two-tailed; PMS: $t = 3.234$, $df = 9$, $p = 0.010$, two-tailed) or on S9 (DH: $t = 2.976$, $df = 9$, $p = 0.016$, two-tailed; DAT: $t = 2.830$, $df = 9$, $p = 0.020$, two-tailed) except for the PMS ($t = 1.740$, $df = 9$, $p = 0.116$, two-tailed).Thus, in comparison to the case of the positive polarity disks, the high- and low-frequency information in S8 and S9 combine (in S7) to increase responding above that produced by either substrate alone.

Taken together, these results show that variations in positive vs. negative contrast play markedly different roles in determining activations of skin components for disruptive pattern response. Apparently, negative polarities tend to activate dark skin components whereas positive polarities tend to activate light skin components. Moreover, in substrate elements of positive contrast

polarity, high spatial frequencies operate strongly to activate light skin components while low spatial frequencies suppress such activation. By contrast, in substrate elements of negative contrast polarity, both high and low spatial frequencies seem to promote the activation of dark skin components.

3.2. Full high-pass filtered rings evoke different responses than ring segments

To provide insight into the processes by which continuous edges vs. fragmented edges control disruptive body pattern response, in substrates S3, S4, S5, S6, S9, S10, S11, and S12 the factors of polarity (positive vs. negative), contrast (low vs. high), and ring-state (full vs. quarter) were fully crossed. The results of a three factor ANOVA with repeated measures investigating how these three factors interact to control white square activation are given in Table 1. This table reveals a significant main effect of contrast, and a significant interaction between contrast and ring-state.

To better understand the nature of the interaction between contrast and ring-state, it is useful to consider the raw image data that enter into this analysis, displayed in Fig. 3. Each row of this figure shows the responses of a single cuttlefish to each of our 13 substrates. Note first that the white squares of all ten animals were activated by S6 (high contrast, positive polarity, quarter-rings) whereas the white square activations were generally much weaker in response to S4 (low contrast, positive polarity, quarter-rings). By comparison, white square activation appears to be of similar strength in response to S5 (high contrast, positive polarity, full-rings) and S3 (low contrast, positive polarity, full-rings). A similar trend of results is observed when we consider the negative polarity versions of these substrates, S9, S10, S11, and S12. White square activation appears much stronger for S12 than for S10; however, white square activation appears less different for S9 and S11.

Fig. 6A plots the marginal mean white square activations for low vs. high contrast full-ring (solid line) vs. quarter-ring (dashed line) substrates, where means pool across activations evoked by positive- and negative-polarity substrates. This plot distills the effects we noted in Fig. 3. In particular, increasing the contrast of the full-ring substrate had little effect on white square activation; however, increasing the contrast of the quarter-ring substrate produced a large increase in white square activation.

To gain deeper insight into the interaction between ring-state and contrast, we analyzed the effects of ring-state and polarity on white square activation within just the low-contrast substrates S3, S4, S9, and S10 and also just within the high-contrast substrates S5, S6, S11, and S12. We focus first on the low-contrast substrates (S3, S4, S9, and S10). Although the white square activations evoked by the positive polarity substrates S3 and S4 seem to be higher than those evoked by the negative polarity substrates S9 and S10, this effect fails to achieve statistical significance (the main effect of polarity in the two factor ANOVA of Table 2 yields $p = 0.065$). A completely different trend of results emerges when we focus on just the high-contrast full- and quarter-ring substrates S5, S6, S11, and S12. Even though the high-contrast, quarter-ring substrates S6 and S12 have only one quarter the total contrast energy of the corresponding high-contrast, full-ring substrates S5 and S11, the quarter-ring substrates evoked stronger white-square activation than the full-ring substrates. A two factor ANOVA (Table 3) analyzing the effects of ring-state and polarity within just the high contrast substrates S5, S6, S11, and S12 confirms that this effect of ring-state was highly significant.

For the white head bar, we performed an analysis parallel to that reported above for the white square. That is, for this skin component, we also conducted a three factor ANOVA with repeated measures (focused on substrates S3, S4, S5, S6, S9, S10, S11, and S12) investigating how the factors of polarity, contrast, and ring-state interact to control activation. The results for the white head bar are given in Table 4. As we found for the white square, there was a significant main effect of contrast as well as a significant interaction between contrast and ring-state for the white head bar. As shown in Fig. 6, the basic pattern of this interaction was the same for both the white square and the white head bar. In this case, increasing substrate contrast boosts skin-component activation more for quarter-ring substrates than it does for full-ring substrates. To further explore the nature of the contrast and ring-state interaction (as we did for the white square), we performed separate two factor polarity by ring-state ANOVAs within each of the two contrast levels. For the white head bar, both the low-contrast and the high-contrast polarity by ring-state ANOVA (Tables 5 and 6) yielded no significant effects.

To summarize: ring-state interacts strongly with contrast in controlling skin component activation. This is especially clear for the white square, but the white head bar also shows a similar pattern. In particular, high- (S5, S11) and low-contrast (S3, S9) full-ring substrates tend to evoke skin component activations of similar

Table 1
Result of a three factor ANOVA with repeated measures for activation of the *white square* of cuttlefish on Substrates 3–6 and 9–12.

	df	MS	*F*	*p*
Polarity (positive vs. negative)	1	0.036	4.057	0.075
Contrast (low vs. high)	1	0.110	11.880	0.007*
Ring-state (full vs. quarter)	1	0.005	1.386	0.269
Polarity × Contrast	1	0.003	1.302	0.283
Polarity × Ring-state	1	0.011	1.898	0.202
Contrast × Ring-state	1	0.040	8.255	0.018*
Polarity × Contrast × Ring-state	1	0.002	0.572	0.469

* $p < 0.05$ is statistically significant.

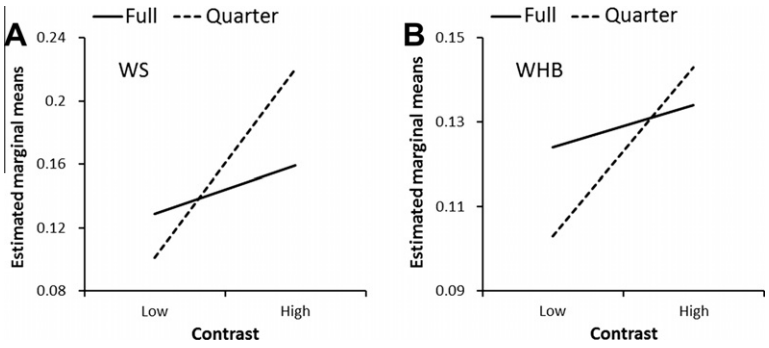

Fig. 6. Interactions between contrast (low vs. high) and edge ring (full vs. quarter) in three factor ANOVA with repeated measures for activations of the WS (white square) and WHB (white head bar). See Tables 1 and 2 for statistical results. These interactions suggest that line terminators and edges influence disruptive patterning via different mechanisms that are controlled by contrast in different ways. The *Y*-axis is scaled based on the standard errors of the dependent variables.

Table 2
Result of the two factor ANOVA with repeated measures for activation of the *white square* of cuttlefish on Substrates 3–4 and 9–10 (low contrast).

	df	MS	*F*	*p*
Polarity (positive vs. negative)	1	0.031	4.418	0.065
Ring-state (full vs. quarter)	1	0.008	1.130	0.315
Polarity × Ring-state	1	0.012	2.337	0.161

Table 3
Result of the two factor ANOVA with repeated measures for activation of the *white square* of cuttlefish on Substrates 5–6 and 11–12 (high contrast).

	df	MS	*F*	*p*
Polarity (positive vs. negative)	1	0.009	1.930	0.198
Ring-state (full vs. quarter)	1	0.037	26.185	0.001*
Polarity × Ring-state	1	0.002	0.373	0.556

* $p < 0.05$ is statistically significant.

Table 4
Result of a three factor ANOVA with repeated measures for activation of the *white head bar* of cuttlefish on Substrates 3–6 and 9–12.

	df	MS	*F*	*p*
Polarity (positive vs. negative)	1	0.006	1.122	0.317
Contrast (low vs. high)	1	0.012	7.896	0.020*
Ring (full vs. quarter)	1	0.001	0.274	0.613
Polarity × Contrast	1	0.001	3.355	0.100
Polarity × Ring-state	1	0.001	0.499	0.498
Contrast × Ring-state	1	0.005	8.157	0.019*
Polarity × Contrast × Ring-state	1	0.001	0.918	0.363

* $p < 0.05$ is statistically significant.

Table 5
Result of the two factor ANOVA with repeated measures for activation of the *white head bar* of cuttlefish on Substrates 3–4 and 9–10 (low contrast).

	df	MS	*F*	*p*
Polarity (positive vs. negative)	1	0.001	0.305	0.594
Ring-state (full vs. quarter)	1	0.004	2.175	0.174
Polarity × Ring-state	1	0.002	1.918	0.199

Table 6
Result of the two factor ANOVA with repeated measures for activation of the *white head bar* of cuttlefish on Substrates 5–6 and 11–12 (high contrast).

	df	MS	*F*	*p*
Polarity (positive vs. negative)	1	0.006	2.450	0.152
Ring-state (full vs. quarter)	1	0.001	1.006	0.342
Polarity × Ring-state	1	0.000	0.011	0.919

strength; by stark comparison, low-contrast quarter-ring substrates (S4, S10) tend to evoke activations that are lower than those evoked by the full-ring substrates (both low and high contrast) whereas high-contrast quarter-ring substrates (S6, S12) tend to evoke activations that are substantially higher than those evoked by the full-ring substrates despite the fact that the high-contrast quarter-ring substrates have only a quarter of the contrast energy present in the high-contrast full-ring substrates.

4. Discussion

These experiments afford several new insights into how disruptive body patterns in cuttlefish are controlled by various image features and statistics of the visual background. Although the substrates used in the current study evoked only weak disruptive body patterns (meaning that only 3 or 4 of the possible 11 components were expressed), the importance of edges and edge segments was evident. Disruptive coloration relies partly on false edges that break up the body outline (Cott, 1940; Stevens & Merilaita, 2009), and in cluttered visual environments where such body patterns appear effective, edge segments are abundant and may provide salient visual cues for evoking disruptive body patterns.

4.1. Termination points in quarter-ring substrates (i.e. line terminators) are important cues for driving disruptive pattern responses

Previous studies have shown that substrate contrast is important in evoking disruptive body patterns in cuttlefish (Barbosa et al., 2008; Chiao & Hanlon, 2001a; Chiao, Chubb, & Hanlon, 2007; Zylinski, Osorio, & Shohet, 2009a). The present study suggests further that continuous edges (of the sorts present in substrates S3, S5, S9, and S11) and line terminators (of the sorts present in substrates S4, S6, S10, and S12) influence disruptive body pattern expression via different mechanisms. The most obvious indication of this is that even though the high-contrast, quarter-ring substrates (S6 and S12) contain only 1/4th the contrast energy of the high-contrast full-ring substrates (S5 and S11), the high-contrast quarter-ring substrates nonetheless produced substantially higher white square component activation than did the high-contrast full-ring substrates (S5 vs. S6, $t = 2.478$, $df = 9$, $p = 0.035$, two-tailed; S11 vs. S12, $t = 2.535$, $df = 9$, $p = 0.032$, two-tailed). We conclude that cuttlefish are highly responsive to some features in the quarter-ring substrates that are absent from the full-ring substrates. The most likely candidate features are the end-points of the quarter-ring segments.

Why might one expect the end-points of the quarter-ring segments to be especially effective in driving disruptive body pattern expression? One reason is that these end-points have important statistical properties not present in the full-ring substrates. An image region that cannot be well-approximated by some pattern of straight, parallel grayscale striations is called "intrinsically two-dimensional." Although any small segment of one of the rings in a full-ring substrate is quite low in intrinsic two-dimensionality (since such a segment can, in fact, be well-approximated by a pattern of striations), the end-points of the segments present in the quarter-ring substrates have very high intrinsic two-dimensionality (since they cannot be well-approximated by patches of straight, parallel, gray-scale striations). Points of high intrinsic two-dimensionality are likely to be useful for identifying and localizing targets in a cluttered scene as well as for unambiguously identifying the direction of movement of a target. It has been proposed that flying insects that face the challenge of intercepting flying targets in cluttered environments are highly sensitive to points of high intrinsic two-dimensionality in the visual input (Nordström & O'Carroll, 2009). It has also been proposed that human vision is pre-attentively sensitive to intrinsically two-dimensional image features (Barth, Zetzsche, & Rentschler, 1998).

There are good reasons to suppose that the end-points in the quarter-ring substrates activate a population of visual neurons other than those activated by the continuous edges in the full-ring substrates. The continuous rings present in both the full- and quarter-ring substrates will drive simple and complex cells (assuming neurons of these sorts are present in cuttlefish); however, only the quarter-ring substrates (S6 and S12) will effectively drive hypercomplex (end-stopped) neurons (DeAngelis, Freeman, & Ohzawa, 1994; Gilbert, 1977; Hubel & Wiesel, 1968; Kato, Bishop, & Orban, 1978; Orban, Kato, & Bishop, 1979a, 1979b; Yamane, Maske, & Bishop, 1985). Hypercomplex neurons are selective not merely for bars of a particular orientation and spatial frequency but also require the bars to be truncated; they do not respond to continuous

elongated patterns. We therefore speculate that the activation of the white square and the white head bar evoked so much more effectively by the quarter-ring than the full-ring substrates, is mediated by neurons sensitive specifically to the end-points of the quarter-rings. These neurons may be hypercomplex cells. Alternatively, they may be selective not specifically for truncated bar patterns (as one would expect of hypercomplex cells) but for some other image statistic such as intrinsic two-dimensionality. A recent study showing that cuttlefish responded to fragmented circles and scattered circle fragments differently (Zylinski, Darmaillacq, & Shashar, 2012) suggests that cuttlefish responses to fragments may also depend on the orientation of neighboring objects.

The current results suggest that the neurons selectively activated by ring-segment end-points are much more sensitive to variations in contrast than the neurons activated by the full-ring. As shown clearly in Fig. 6, for each of the white square and the white head bar, skin component activation differs only slightly between the low- vs. high-contrast full-ring substrates (pooling over positive and negative polarities); by comparison, activation (in both of these skin components) is dramatically higher on the high-contrast vs. the low-contrast quarter-ring substrate.

It is also possible that cuttlefish are sensitive not only to the end-points of the quarter-ring segments, but also to the overall contrast of the substrate. The finding that S4 (the lowest in contrast energy among S3, S4, S5, and S6) evoked much weaker disruptive component activations than did S3, S5, and S6 (Fig. 3B and C) could be due to a nonlinear process in which substrates with energy less than some threshold are equivalent to uniform gray in terms of their influence on skin component activations. Perhaps the cuttlefish does some global computation of contrast energy, and if this net energy is less than some threshold, it automatically suppresses its response, irrespective of the properties of these substrates. However, this explanation cannot fully account for the finding that the high-contrast quarter-ring substrate produced higher activation than did the high-contrast full-ring substrate.

4.2. The failure of the Fourier amplitude principle: implications

Many perceptual processes obey the Fourier amplitude principle, which proposes that the salience of a stimulus and hence its effectiveness in controlling behavior is a non-decreasing function of the amplitude in the stimulus of any given Fourier component. This principle has been invoked in standard theories to explain (1) the detection and appearance for human observers of very low contrast patterns (Blakemore & Campbell, 1969; Campbell & Robson, 1968; Robson, 1966), and (2) motion perception (Chubb & Sperling, 1988; Watson, Ahumada, & Farrell, 1986).

In particular, Julesz (1962, 1975) famously conjectured that two visual textures will be preattentively discriminable only if they have different Fourier amplitude spectra. Although counterexamples to this conjecture were eventually discovered (e.g., Diaconis & Freedman, 1981; Julesz, Gilbert, & Victor, 1978), the amplitude spectrum principle proved remarkably successful in accounting for most instances of preattentive texture segregation (Bergen & Adelson, 1988; Sutter, Beck, & Graham, 1989).

Given, especially, its effectiveness in handling most cases of human preattentive texture segregation, one might wonder whether the Fourier amplitude principle holds for the processes by which visual substrates control skin component activation in cuttlefish. That this might be true is suggested by the observation that high-contrast substrates (i.e., substrates in which the amplitudes of Fourier components are predominantly high) tend to evoke pattern responses in which skin components are more strongly activated than do low contrast substrates (Barbosa et al., 2008).

Note, however, that if the Fourier amplitude principle holds for the processes through which skin component activations are controlled by the substrate, then lowering the amplitude of any given Fourier component in a substrate can never increase the strength with which any given disruptive skin component is activated. Under this principle, S1 should always produce activation at least as strong as either S2 or S3. However, we found that the overall disruptiveness and the white head bar were significantly more strongly activated on S3 than on S1 despite the fact that S3 is a high-pass filtered version of S1 (i.e., S3 is identical to S1 except that the amplitudes of many low spatial frequency Fourier components in S3 have been strongly attenuated).

This finding rules out a class of rudimentary models of disruptive pattern responding. Specifically, we must reject any model proposing that the activation of a given skin component is controlled by a weighted sum of the responses of visual neurons, each of which produces a response whose magnitude is a non-decreasing function of the amplitude of any given Fourier component in the visual input.

It is not, however, difficult to imagine simple modifications to models of this sort that could account for the current results. For example, if the visual neurons controlling skin component activation are subject to divisive normalization (review in Carandini and Heeger, 2011), then the response strength of any given visual neuron controlling skin component activation is likely to depend on the *relative* amplitudes of different Fourier components. In this case, if a skin component such as the white head bar is more sensitive to high than to low spatial frequencies in the substrate, its activation may well increase as the ratio of high-to-low spatial frequency energy in the substrate is increased. This is precisely what occurs in substrate S3 vs. S1: the ratio of high spatial frequency to low spatial frequency energy is much higher in S3 than it is in S1.

It should be noted that Zylinski, Osorio, and Shohet (2009b) did not observe a significant difference between the patterning responses on S1 and S3, nor did they observe a significant difference between the responses on S5 and S6. Although we do not know the exact cause of the discrepancy between their results and ours, different quantification methods (manual grading with principal component analysis vs. objective assessment of individual component activation) may lead to slightly different results. More importantly, they tested fewer animals; their study therefore had less statistical power to observe the effects we have documented here.

In any case, the present study provides new perspectives on the visual processing of edge information in controlling camouflage body patterning in cuttlefish. Specifically, we suggest that end-stopped neurons may be involved in detecting lines and corners, which are distinctly different from the continuous edges, and visual neurons that control skin component activation could use divisive normalization to assess various features of objects in the scene.

5. Conclusion

The current experiments have revealed a number of ways in which the features of visual edges in the substrate act to control the body pattern deployed by cuttlefish. First, the patterning response is quite sensitive to the contrast polarity of the substrate; that is, the skin components activated by the substrate comprising black disks on a gray background tend to be dark, whereas those activated by white disks on a gray background tend to be light. Although this sounds like a naturally expected result, it has not been suggested or reported in the past.

Second, high-pass filtering a substrate comprising white disks on a gray background (S1) yields a substrate (S3) with heightened power to activate the white square. This result rules out models in which skin component activation is a non-decreasing function of the amplitude of any given Fourier component. An alternative

model that could explain this finding proposes that activation is controlled by the ratio of high-to-low-frequency amplitudes in the substrate.

Third, the line terminators introduced into a substrate (e.g., S4, S6, S10, S12) when continuous rings are fragmented emerge as important features that operate differently from continuous edges (as in substrates S3, S5, S9, S11) to influence patterning. In particular, the effectiveness of line terminators in activating both the white square and the white head bar increases as substrate contrast is increased; by comparison, the effectiveness of continuous rings in activating these skin components changes little if at all with a corresponding increase in contrast. This suggests that line terminators control skin component activation via a different neural pathway (perhaps involving hypercomplex, or end-stopped, neurons) than the pathway used by continuous rings.

We begin to see, then, what it takes to achieve effective camouflage. The impact exerted by a visual edge on the patterning response of a cuttlefish depends in subtle and complicated ways on the features of the edge: its spatial frequency content; its contrast; whether or not it is continuous or fragmented; and various interactions among these features. The present study thus provides insights into visual perception and concealment strategy in animals (Troscianko et al., 2009). Both background matching and disruptive coloration tactics of camouflage rely on animals extracting edge features from scenes. In turn, activation of skin components is differentially sensitive to interactions of these features. This results in adaptive camouflage body patterns, which help animals to defeat the visual mechanisms of edge detection and object recognition of predators.

Acknowledgments

We thank Lydia Mäthger and Justine Allen for assisting with this experiment. This work was supported in part by NSC-98-2628-B-007-001-MY3 to Dr. Chiao, NSF BCS-0843897 to Dr. Chubb, and a Sholley Foundation gift to Dr. Hanlon. We would like to dedicate this work to Dr. Tom Troscianko.

References

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.

Barth, E., Zetzsche, C., & Rentschler, I. (1998). Intrinsic two-dimensional features as textons. *Journal of the Optical Society of America A, 15*, 1723–1732.

Bergen, J. R., & Adelson, E. H. (1988). Visual texture segmentation based on energy measures. *Journal of the Optical Society of America A, 3*, 98–101.

Blakemore, C., & Campbell, F. W. (1969). On the existence of neurons in the human visual system selectively responsive to the orientation and size of retinal images. *Journal of Physiology, 203*, 237–260.

Campbell, F. W., & Robson, J. G. (1968). Application of Fourier analysis to the visibility of gratings. *Journal of Physiology, 197*, 551–566.

Carandini, M., & Heeger, D. J. (2011). Normalization as a canonical neural computation. *Nature Review Neuroscience, 13*, 51–62.

Chiao, C.-C., Chubb, C., Buresch, K., Siemann, L., & Hanlon, R. T. (2009). The scaling effects of substrate texture on camouflage patterning in cuttlefish. *Vision Research, 49*, 1647–1656.

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.

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 in 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 patterning of cuttlefish (*Sepia officinalis*) requires visual information regarding edges and contrast of objects in natural substrate backgrounds. *Biological Bulletin, 208*, 7–11.

Chubb, C., & Sperling, G. (1988). Drift-balanced random stimuli: A general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A, 5*, 1986–2007.

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

DeAngelis, G. C., Freeman, R. D., & Ohzawa, I. (1994). Length and width tuning of neurons in the cat's primary visual cortex. *Journal of Neurophysiology, 71*, 347–374.

Diaconis, P., & Freedman, D. (1981). On the statistics of vision: The Julesz conjecture. *Journal of Mathematical Psychology, 24*, 112–138.

Gilbert, C. D. (1977). Laminar differences in receptive field properties of cells in cat primary visual cortex. *Journal of Physiology, 268*, 391–421.

Hanlon, R. H. (2007). Cephalopod dynamic camouflage. *Current Biology, 17*, R400–404.

Hanlon, R. T., Chiao, C.-C., Mäthger, L. M., Buresch, K. C., Barbosa, A., Allen, J. J., et al. (2011). Rapid adaptive camouflage in cephalopods. In M. Stevens & S. Merilaita (Eds.), *Animal camouflage: Mechanisms and functions*. Cambridge, U.K.: Cambridge University Press.

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.

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

Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology, 195*, 215–243.

Julesz, B. (1962). Visual pattern discrimination. *IRE Transactions on Information Theory, IT-8*, 84–92.

Julesz, B. (1975). Experiments in the visual perception of texture. *Scientific American, 4*, 34–43.

Julesz, B., Gilbert, E. N., & Victor, J. D. (1978). Visual discrimination of textures with identical third-order statistics. *Biological Cybernetics, 31*, 137–140.

Kato, H., Bishop, P. O., & Orban, G. A. (1978). Hypercomplex and simple/complex cell classifications in cat striate cortex. *Journal of Neurophysiology, 41*, 1071–1095.

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 Biological Sciences, 274*, 1369–1375.

Kelman, E. J., Osorio, D., & Baddeley, R. J. (2008). A review of cuttlefish camouflage and object recognition and evidence for depth perception. *Journal of Experimental Biology, 211*, 1757–1763.

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.

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

Nordström, K., & O'Carroll, D. C. (2009). Feature detection and the hypercomplex property in insects. *Trends in Neuroscience, 32*(7), 383–391.

Orban, G. A., Kato, H., & Bishop, P. O. (1979a). Dimensions and properties of end-zone inhibitory areas in receptive fields of hypercomplex cells in cat striate cortex. *Journal of Neurophysiology, 42*, 833–849.

Orban, G. A., Kato, H., & Bishop, P. O. (1979b). End-zone region in receptive fields of hypercomplex and other striate neurons in the cat. *Journal of Neurophysiology, 42*, 818–832.

Robson, J. G. (1966). Spatial and temporal contrast sensitivity function of the visual system. *Journal of the Optical Society of America, 56*, 1141–1142.

Stevens, M., & Merilaita, S. (2009). Defining disruptive coloration and distinguishing its functions. *Philosophical Transactions of the Royal Society of London B, 364*, 481–488.

Sutter, A., Beck, J., & Graham, N. (1989). Contrast and spatial variables in texture segregation: testing a simple spatial-frequency channels model. *Perception & Psychophysics, 46*, 312–332.

Troscianko, T., Benton, C. P., Lovell, P. G., Tolhurst, D. J., & Pizlo, Z. (2009). Camouflage and visual perception. *Philosophical Transactions of the Royal Society of London B, 364*, 449–461.

Watson, A. B., Ahumada, A. J. J., & Farrell, J. E. (1986). Window of visibility: A psychophysical theory of fidelity in time-sampled visual motion displays. *Journal of the Optical Society of America A, 3*, 300–307.

Yamane, S., Maske, R., & Bishop, P. O. (1985). Properties of end-zone inhibition of hypercomplex cells in cat striate cortex. *Experimental Brain Research, 60*, 200–203.

Zylinski, S., Darmaillacq, A. S., & Shashar, N. (2012). Visual interpolation for contour completion by the European cuttlefish (*Sepia officinalis*) and its use in dynamic camouflage. *Proceedings of the Biological Sciences, 279*, 2386–2390.

Zylinski, S., Osorio, D., & Shohet, A. J. (2009a). Edge detection and texture classification by cuttlefish. *Journal of Vision, 9*, 1–10.

Zylinski, S., Osorio, D., & Shohet, A. J. (2009b). Perception of edges and visual texture in the camouflage of the common cuttlefish, *Sepia officinalis*. *Philosophical Transactions of the Royal Society of London B, 364*, 439–448.