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Dark scene elements strongly influence cuttlefish camouflage responses in visually cluttered environments

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ABSTRACT

This study investigated how cuttlefish (*Sepia officinalis*) camouflage patterns are influenced by the proportions of different gray-scales present in visually cluttered environments. All experimental substrates comprised spatially random arrays of texture elements (texels) of five gray-scales: *Black*, *Dark gray*, *Gray*, *Light gray*, and *White*. The substrates in Experiment 1 were densely packed arrays of square texels that varied over 4 sizes in different conditions. Experiment 2 used substrates in which texels were disks separated on a homogeneous background that was *Black*, *Gray* or *White* in different conditions. In a given condition, the histogram of texel gray-scales was varied across different substrates. For each of 16 cuttlefish pattern response statistics c, the resulting data were used to determine the strength with which variations in the proportions of different gray-scales influenced c. The main finding is that darker-than-average texels (i.e., texels of negative contrast polarity) predominate in controlling cuttlefish pattern responses in the context of cluttered substrates. In Experiment 1, for example, substrates of all four texel-sizes, activation of the cuttlefish “white square” and “white head bar” (two highly salient skin components) is strongly influenced by variations in the proportions of *Black* and *Dark gray* (but not *Gray*, *Light gray*, or *White*) texels. It is hypothesized that in the context of high-variance visual input characteristic of cluttered substrates in the cuttlefish natural habitat, elements of negative contrast polarity reliably signal the presence of edges produced by overlapping objects, in the presence of which disruptive pattern responses are likely to achieve effective camouflage.

1. Introduction

Cuttlefish are masters of rapid adaptive camouflage. In milliseconds, a cuttlefish can alter its body pattern to elude detection across a wide range of habitat variations (Hanlon & Messenger, 1988, 1996; Messenger, 2001). It is well documented that the pattern produced by a cuttlefish is controlled predominantly by the visual input it receives from its surroundings (Hanlon & Messenger, 1988; Holmes, 1940; Marshall & Messenger, 1996), and substantial research has sought to understand the algorithm that takes environmental image data as input and produces a camouflage skin pattern as output (Allen, Mäthger, Barbosa, & Hanlon, 2009; Allen et al., 2010, 2003; Barbosa, Litman, & Hanlon, 2008a, 2008b; Barbosa et al., 2007, Barbosa, Allen, Mäthger, & Hanlon, 2012; Barbosa et al., 2007; Buresch et al., 2011; Chiao, Chubb, Buresch, Siemann, & Hanlon, 2009; Chiao & Hanlon, 2001a, 2001b; Chiao, Chubb, & Hanlon, 2007; Chiao, Kelman, & Hanlon, 2005; Chiao et al., 2010, 2013; Hanlon, 2007; Hanlon, Chiao, Mathger, & Marshall, 2013; Hanlon et al., 2009, 2011; Kelman, Baddeley, Shohet, & Osorio, 2007; Kelman, Osorio, & Baddeley, 2008; Marshall & Messenger, 1996; Mäthger, Barbosa, Miner, & Hanlon, 2006; Mäthger et al., 2007; Shohet, Baddeley, Anderson, Kelman, & Osorio, 2006; Shohet, Baddeley, Anderson, & Osorio, 2007; Shohet et al., 2007; Tublitz, Gaston, & Loi, 2006; Zylinski & Osorio, 2011; Hanlon, 2007; Zylinski, Osorio, & Shohet, 2009a, 2009b; Zylinski, Darmaillacq, & Shashar, 2012).

1.1. *The three main types of cuttlefish patterns*

The patterns produced by cuttlefish fall into three main classes: uniform, mottle, and disruptive. Uniform (or uniformly stippled) body patterns show minimal variation in color and contrast; such patterns are typically deployed by cuttlefish to achieve general resemblance to homogeneous backgrounds such as sand. Mottle patterns consist of relatively fine-grained, medium-contrast texture that covers the cuttlefish dorsum more or less homogeneously; such patterns are typically deployed to achieve general resemblance to substrates with fine-

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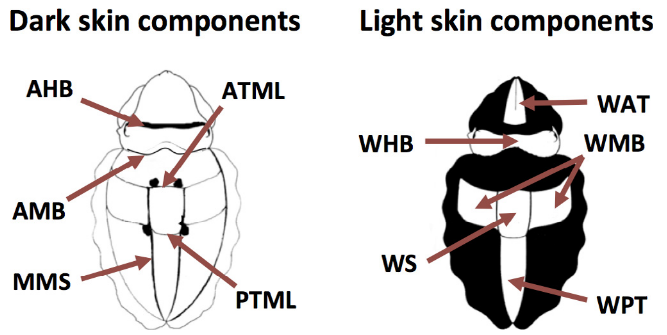

Fig. 1. Left: the five dark skin components that tend to be activated in disruptive coloration: AHB—anterior head bar, AMB—anterior mantle bar, ATML—anterior transverse mantle line, PTML—posterior transverse mantle line, and MMS—median mantle stripe. Right: the five light skin components that tend to be activated in disruptive coloration: WAT—white arm triangle, WHB—white head bar, WMB—white mantle bars, WS—white square, and WPT—white posterior triangle.

grained variations, e.g., regions composed of light and dark pebbles small in size relative to the cuttlefish (Chiao et al., 2010). Disruptive patterns are marked by highly salient, large, high-contrast skin components (as illustrated in Fig. 1) that are suppressed in uniform and mottle patterns. These elements tend to produce vivid edges, highly polarized in assigning one side to figure and the other to ground, that operate to fragment the cuttlefish into large chunks of visual "detritus"; such patterns are often deployed in visually cluttered environments comprising stones, shells, etc. whose sizes are comparable to the sizes of the large and differently oriented skin components that can be turned on and off selectively by the cuttlefish.

1.2. First-order image statistics and cuttlefish pattern responses

The current study aims to analyze how cuttlefish pattern responses are influenced by the first-order statistics (defined below) of the visual input in seven different cluttered contexts. All substrates used in this study are composed solely of different gray-scales. The current experiments ignore the possible influence of color because *Sepia officinalis* has only a single photopigment; thus, despite the surprisingly close color matches they sometimes achieve to substrates in their natural habitat, these animals seem to be colorblind (Marshall & Messenger, 1996; Mäthger et al., 2006; although see Stubbs A. L., 2015, for a theory of how they might sense color). In any case, even if *Sepia officinalis* is sensitive to color, substantial evidence suggests that variations in substrate intensity play a central role in controlling their pattern responses.

Experiment 1 analyzes four contexts composed of densely packed squares of different gray-scales; these contexts differ in spatial scale, i.e. in sizes of the square texture elements (texels) of which they are composed. Experiment 2 explores the influence of a basic aspect of context, the background gray-scale against which texels appear; in this experiment, circular texels are isolated against a background that is *Black*, *Gray*, or *White* in three different contexts.

A statistic extracted from an image is called a "first-order" statistic if its value is invariant with respect to spatial reordering of the elements composing the image. Thus, for example, (i) the mean gray-scale of an image is a first-order statistic because the value of the mean does not change no matter how one rearranges the pixels (or chunks) that make up an image. Other examples of first-order statistics are: (ii) the proportion of pixels in an image that have been assigned a given gray-scale, and (iii) the contrast of an image.

Because the statistical properties of cluttered scenes are largely invariant with respect to reordering of the homogenous chunks of which they are composed, one might expect first-order statistics to play an important role in controlling pattern responses in such contexts. To our knowledge, however, this issue has never before been investigated.

The specific purpose of the current experiments is to determine how each of 16 skin pattern statistics is influenced by different gray-scales in various cluttered contexts. Ten of these statistics are the activation levels of the 10 skin components illustrated in Fig. 1. We use statistics extracted automatically from the digitized image of the cuttlefish to estimate the activation of each of these 10 skin components in the pattern evoked by any given substrate. We also extract 6 additional image statistics; these "granularity spectrum coefficients" reflect the distribution of the image energy in the cuttlefish skin pattern across six different, isotropic spatial frequency bands.

1.3. The seven cluttered context substrates to be analyzed

The probability distribution that gives the proportions of the different gray-scales that make up a given, cluttered substrate S is called the histogram of S. We will write U for the uniform histogram that assigns equal probability to each of the five gray-scales g = *Black*, *Dark gray*, *Gray*, *Light gray*, *White*; that is, $U(g) = U(g) = \frac{1}{5}$.

The particular histogram U will play a central role in the experiments reported here. Specifically, each of the seven "context substrates" analyzed in this study comprises a spatially random array of texture elements (texels) with equal proportions of five gray-scales: *Black*, *Dark gray*, *Gray*, *Light gray*, and *White*. That is, the gray-scales of the texels in each of our 7 context substrates have histogram U. For example, one of the contexts that will be analyzed is the substrate $S_{1,\ 100\%}$ (Fig. 3) composed of a dense array of square texels equal in area to the WS of an average-sized cuttlefish subject; the gray-scales of the squares in $S_{1,100\%}$ have histogram U, and the spatial arrangement of gray-scales is random. In addition to $S_{1,100\%}$, we will analyze six other substrates. Like $S_{1,100\%}$, substrates $S_{1,50\%}$, $S_{1,30\%}$, and $S_{1,10\%}$ (Fig. 3), comprise densely packed, square texels; however, the texels in these substrates are smaller than the texels in $S_{1,100\%}$. Specifically, for K = 50, 30, 10, the area of a texel in $S_{1,K\%}$ is equal to $K\%$ of the area of the WS of a typical cuttlefish subject. The four context substrates $S_{1,100\%}$, $S_{1,50\%}$, $S_{1,30\%}$, and $S_{1,10\%}$ will be analyzed in Exp. 1. Three additional context substrates, $S_{1,Black}$, $S_{1,Gray}$ and $S_{1,White}$ will be analyzed in Exp. 2. In each of these substrates, texels are circular, equal in area to the WS of a typical cuttlefish subject, and separately individuated on a homogeneous background. In substrate $S_{1,Black}$ the gray-scale of this background will be *Black*; in substrate $S_{1,Gray}$ the gray-scale of this background will be *Gray*, and in substrate $S_{1,White}$ the gray-scale of this background will be *White*.

1.4. The strategy of the experiments

To analyze how pattern responses are influenced by different gray-scales in any given context $S_{1,X}$ for X = 100%, 50%, 30%, 10% (in Experiment 1) or *Black*, *Gray*, or *White* (in Experiment 2), we must test cuttlefish on substrates whose histograms deviate from U, the histogram of the context substrate $S_{1,X}$. Consider the context substrate, $S_{1,100\%}$, for example: testing cuttlefish on $S_{1,100\%}$ would enable us to measure the average pattern response evoked by $S_{1,100\%}$; however, this observation alone would not inform us of the relative influence of different gray-scales in evoking this response. To gain insight into this deeper issue, we must vary the proportions of different gray-scales in our test substrates and see how these variations affect the response pattern of the cuttlefish.

Examples of the different substrates used in both experiments are shown in Fig. 2. The bar graph associated with a row of substrates in Fig. 2 shows the texel gray-scale histogram of the substrates in that row. This set of histograms is sufficiently rich to enable us to fully characterize the differential effectiveness with which the different gray-scales *Black*, *Dark gray*, *Gray*, *Light gray*, and *White* influence any one of the 16 image statistics that we use to characterize the response pattern of a cuttlefish. The key property enabling full characterization is that the 9 histograms of these substrates span the space of all real-valued