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Color blindness and contrast perception in cuttlefish (*Sepia officinalis*) determined by a visual sensorimotor assay

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Abstract

We tested color perception based upon a robust behavioral response in which cuttlefish (*Sepia officinalis*) respond to visual stimuli (a black and white checkerboard) with a quantifiable, neurally controlled motor response (a body pattern). In the first experiment, we created 16 checkerboard substrates in which 16 grey shades (from white to black) were paired with one green shade (matched to the maximum absorption wavelength of *S. officinalis*' sole visual pigment, 492 nm), assuming that one of the grey shades would give a similar achromatic signal to the tested green. In the second experiment, we created a checkerboard using one blue and one yellow shade whose intensities were matched to the cuttlefish's visual system. In both assays it was tested whether cuttlefish would show disruptive coloration on these checkerboards, indicating their ability to distinguish checkers based solely on wavelength (i.e., color). Here, we show clearly that cuttlefish must be color blind, as they showed non-disruptive coloration on the checkerboards whose color intensities were matched to the *Sepia* visual system, suggesting that the substrates appeared to their eyes as uniform backgrounds. Furthermore, we show that cuttlefish are able to perceive objects in their background that differ in contrast by approximately 15%. This study adds support to previous reports that *S. officinalis* is color blind, yet the question of how cuttlefish achieve "color-blind camouflage" in chromatically rich environments still remains.

Keywords: Disruptive coloration; Body patterning; Camouflage; Contrast sensitivity; Behavior

1. Introduction

Cephalopods, such as the cuttlefish *Sepia officinalis*, are masters of disguise in the animal kingdom. Unlike most animals that can use one or a few mechanisms of camouflage (Cott, 1940), cuttlefish are known to have a diverse range of body patterns and they can switch between them almost instantaneously, using their neurally controlled chromatophore system (Hanlon & Messenger, 1988, 1996; Messenger, 2001). It has been shown that visual information in the immediate background is crucial for the expression of camouflage body patterns (Hanlon & Messenger, 1988, 1996; Holmes, 1940). Since body patterns in some fish (Ramachandran et al., 1996) and most cephalopods (e.g., Hanlon & Messenger, 1988) appear to change mainly as the result of visual input, it is possible to investigate the animals' visual capabilities by presenting them with controlled visual stimuli and observing the corresponding motor output expressed as a body pattern. A robust visual sensorimotor assay for cuttlefish has been developed based on this system (Chiao & Hanlon, 2001a, 2001b; Chiao, Kelman, & Hanlon, 2005).

Cuttlefish, like other cephalopods, are reported to be color blind. The evidence is twofold.

(1) *Visual pigment evidence.* By measuring spectral absorption of retinal extracts, Brown and Brown (1958) suggested that cuttlefish have only one visual pigment with a maximal absorption (λ_{max}) at 492 nm. As far as we are aware, this is the only study looking at the absorption of *S. officinalis* visual pigment; no modern techniques, such as microspectrophotometry, have

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been applied to the study of color vision in this species. Further evidence comes from studying the rhodopsin gene of the cuttlefish, which shows that only a single type of rhodopsin is expressed (Bellingham, Morris, & Hunt, 1998). Since the spectral sensitivity of visual pigments can be predicted from the amino acid composition of the opsin, Bellingham et al. (1998) were able to model the maximum absorption and they proposed a λ_{max} of 492 nm, which agrees with Brown and Brown (1958).

(2) *Behavioral evidence.* Marshall and Messenger (1996) took advantage of the fact that cuttlefish try to camouflage on any background they are placed. They presented cuttlefish with gravel substrates of varying colors: red, white, blue, and yellow. These authors suggest that while red and white gravel would appear as a strong contrast to the cuttlefish visual system, yellow and blue would not appear as different contrasting shades of color. They reported that cuttlefish produced a bold coarse mottled pattern when placed on red and white gravel, presumably in an attempt to "match" the coarse patterning of the gravel, whereas the animals showed an overall uniform pattern on blue and yellow gravel, suggesting that these shades did not appear as two contrasting colors but instead as a uniformly colored gravel background.

Cuttlefish are capable of showing dozens of body patterns for camouflage and these body patterns can be grouped into three categories: uniform/stipple, mottle, and disruptive (Hanlon & Messenger, 1988, 1996). To date, little is known about what visual background cues elicit a mottled coloration, which forms the basis of the study by Marshall and Messenger (1996). The visual background cues that elicit disruptive coloration are much better understood (Chiao & Hanlon, 2001a, 2001b; Chiao et al., 2005).

In nature, cuttlefish show a disruptive pattern when, for example, settled on a mixture of light and dark gravel. In disruptive coloration the patterns break up the actual outline of the animal by creating "false" lines and edges (Cott, 1940) and it is remarkable how difficult it is to spot a cuttlefish that has camouflaged itself this way (e.g., see Fig. 2A). The response is evoked best when the size of the light objects is comparable to the size of the animal's White Square component, which is frequently shown as part of the disruptive pattern. In the laboratory, the disruptive pattern can be evoked by presenting a cuttlefish with a black and white checkerboard, specifically when the white squares of the checkerboard are similar in size to the animal's White Square component (Chiao & Hanlon, 2001a). Although cuttlefish cannot perfectly match such an artificial background, within as little as a few seconds the animal will process the visual background information and translate it into the most appropriate camouflaged body pattern. This highly robust behavioral assay has since been used to show that cuttlefish cue visually on area, not the shape or aspect ratio, of light objects on a dark background (Chiao & Hanlon, 2001b).

Cuttlefish are very good at blending into colorful natural environments (at least in shallow depths of water), apparently being unable to see colors themselves (Marshall & Messenger, 1996). To us it would seem that color vision would be extremely useful for this type of task. Since the research of Marshall and Messenger (1996), a good deal has been learned about which visual stimuli evoke certain body patterns in cuttlefish (Chiao & Hanlon, 2001a, 2001b; Chiao et al., 2005). For this reason, we felt that the question of color vision should be re-tested using the new behavioral assay described by Chiao and Hanlon (2001a), which allows a quantitative approach.

2. Materials and methods

2.1. Animals and experimental set-up

Young *S. officinalis* that were hatched, reared, and maintained at the MBL Marine Resources Center (Woods Hole, MA) were used for these experiments. 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 in a tank ($55 \times 40 \times 15$ cm) with flowing seawater and restricted to a cylindrical arena (25 cm diameter and 11 cm height) in which the experimental substrate was presented on both the floor and wall. Once the animal had acclimated (i.e., cessation of excessive swimming and hovering movements and expression of a stable body pattern) a 30 min trial was recorded using a digital video camera (Sony VX-1000) mounted on a remotely controlled servo directly above the arena and connected to an external monitor so that the animal's movements could be followed from outside the chamber without disturbing it. The camera was set to record for 1 s every 30 s, thus yielding 60 s of footage per animal per substrate. From the resulting 60 s of footage, a still image was retained from every sixth 1 s clip of footage to yield 10 images; these 10 images were used to grade the animal's response (see below on grading method). During Experiment 1, we used two photographic light sources (Quartzline, 500 W, GE) arranged opposite each other to reduce the effects of shadow. A light meter (Extech EasyView EA30) was used to take readings around the perimeter and near the center of the arena (center 1.86–1.99 klux and perimeter 1.35–1.5 klux), showing that the arena was lit relatively evenly. During Experiment 2, we used one circular 40 W fluorescent light source (Phillips CoolWhite), which reduced the effect of shadow even more. Light levels where found to be 1.07 klux in the center and 1.03 klux at the perimeter. Ten cuttlefish (2.94–3.46 cm mantle length) were used in the first experiment and five (6.1–7.8 cm mantle length) in the second experiment.

2.2. Experimental design

2.2.1. Experiment 1

In this experiment, we created checkerboard substrates based on Frisch's (1914) "grey card" experiment in which bees were shown to be able to discriminate between a color and many shades of grey. In this type of experiment, it is assumed that at least one grey shade gives a similar achromatic signal to a color, so that a monochromat (color blind) individual would not be able to distinguish between the grey shade and the color. Dichromacy (the possession of two visual pigments) is the minimum requirement for an individual to discriminate between the grey shade and the color.

Sixteen green and grey checkerboards were made in Powerpoint and printed on a Hewlett Packard 5500 color laser printer. We chose a green with a reflectance spectrum resembling the absorption spectrum of the known visual pigment of 492 nm (Fig. 1A). Grey shades were chosen at

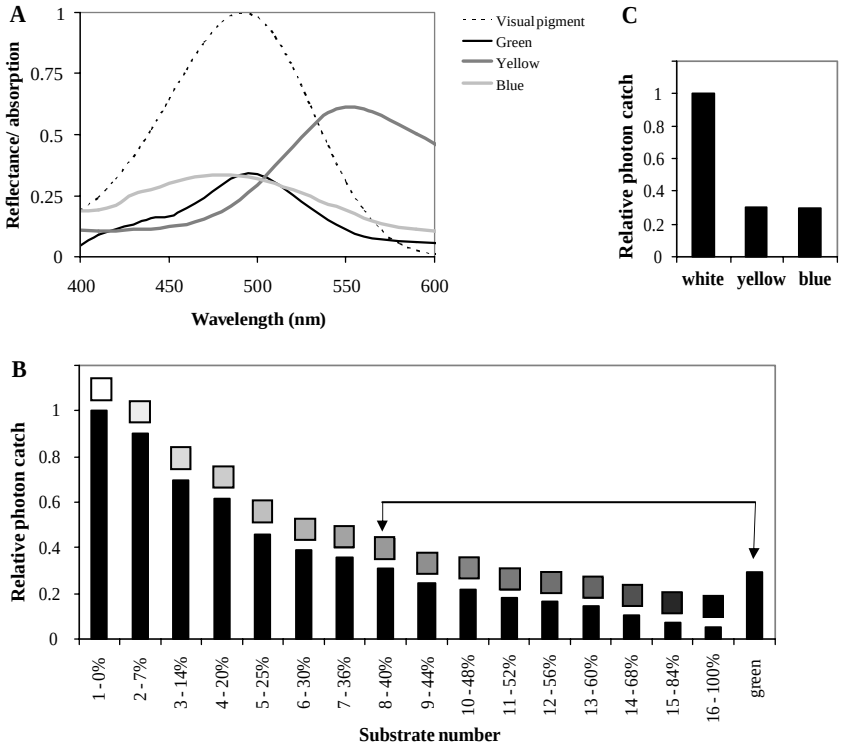

Fig. 1. (A) Reflective spectra of green (used for checkerboards of Experiment 1), blue and yellow (used in Experiment 2). Spectra are shown as percent reflectance relative to white diffuse reflectance standard. Also shown is spectral absorption (normalized) of *Sepia officinalis* visual pigment ($\lambda_{max} = 492$ nm), calculated using template from Stavenga et al., 1993. (B) Experiment 1, relative photon catch of green (λ_{max} approximately 490 nm) and 16 grey shades, showing that the green and grey of substrate 8 are matched in intensity to the peak sensitivity of the visual pigment of *S. officinalis*. Percentages refer to black ink coverage. (C) Experiment 2, relative photon catch of yellow and blue shades used for yellow and blue checkerboard. Both shades are matched in intensity.

small increments ranging from white to black. The green was the same on every checkerboard; only the grey shade was changed. In Fig. 1B, the "percentage black ink coverage" of each grey shade is shown along the *x*-axis. These were calculated from the RGB values, ranging from 255 (white—0% ink coverage) to 0 (black—100% ink coverage). The area of each checkerboard square was equal to the mean area of the ten *Sepia*'s "White Square" light disruptive components (0.774 cm^2). The substrates were cut to fit the experimental arena, and laminated so they were waterproof. Each animal was introduced onto the experimental substrates and to one black and white control substrate in random order, with no animal being subjected to a trial more than once per day.

If cuttlefish were able to discriminate color, we would predict them to show disruptive body patterning on all substrates. If cuttlefish were color blind, we would expect them show an overall uniform body pattern on the substrates whose green versus grey checker are indistinguishable to the cuttlefish visual system.

2.2.2. Experiment 2

In this experiment, we created a blue and yellow checkerboard (see Fig. 1A for reflectance spectra). The idea was based on the work by Marshall and Messenger (1996), who used blue and yellow gravel. Blue and yellow shades were created in Powerpoint and printed on a Hewlett Packard 990 Deskjet printer. The blue and yellow that were matched in intensity to an eye with one visual pigment at 492 nm were identified using the methods described below. The area of each checker was comparable to the mean area of all five animal's "White Square" component (3.03 cm^2). The animals were randomly exposed to four substrates: (1) blue and yellow checkerboard, (2) uniform blue, (3) uniform yellow, and (4) black and white checkerboard, the latter three substrates acting as controls.

If these animals are color blind, then the blue and yellow should appear to have the same overall intensity and thus we would expect the animals to show an overall uniform pattern on substrate 1, as well as on substrates 2 and 3.

To determine which checkers were matched in intensity, relative reflectance spectra of the laminated checkerboard colors (Experiments 1 and 2) were measured using a spectrometer (USB2000, Ocean Optics, FL, USA). Illumination was provided by the light sources used during the experimental trials (see above). A diffuse reflection standard (made of PTFE, Ocean Optics), which reflects more than 98% of light between 400 and 1500 nm, was used to standardize measurements. All measurements were made in a dark room to prevent the influence of stray light. The fiber optic cable (200 μm diameter) was held by a micromanipulator at an angle of approximately 45°. The light source and fiber optic cable were not moved between measurements, thus it was possible to obtain relative reflectance spectra of all substrate colors.

After the relative reflectance spectra of all checker colors were obtained, they were transformed into quantum units (divided by wavelength) and the number of photons (N) absorbed by a cuttlefish photoreceptor was calculated. This is given by

$$N = \int (1 - \exp(-kS(\lambda)l)) \times R(\lambda)\,d\lambda \quad (1)$$

(after Warrant, 2004) where $S(\lambda)$ is the spectral sensitivity of the visual pigment, $R(\lambda)$ is the spectral composition of the light reflected from the checker, l is the length of the rhabdom (400 μm; from Hanlon & Messenger, 1996) and k is the quantum efficiency of transduction (0.0067/μm; Warrant & Nilsson, 1998). The spectral sensitivity of the visual pigment was calculated using a template kindly provided by A. Kelber, Lund, Sweden (based on Stavenga, Smits, & Hoenders, 1993). Figs. 1B

and C shows relative photon catch of a cuttlefish photoreceptor. The green and grey checkers used in substrate 8 of Experiment 1 were matched in intensity by 95%, the blue and yellow checkers of Experiment 2 were matched by 99%.

From these data, it was possible to calculate the Michelson contrast (C) between the green and the various grey shades as perceived by the cuttlefish eye: $C = (B_{MAX} - B_{MIN})/(B_{MAX} + B_{MIN})$, where B_{MAX} is the greater of the quantum catches produced by the lights reflected from the two checkers and B_{MIN} is the lesser. Contrast thus ranges from 0 (0%) to 1 (100%) (data included in Fig. 4A).

3. Analysis

From the video recordings, we took 10 images per animal per substrate, yielding a total of 1700 images (grey card experiment) and 200 images (blue and yellow experiment) that were graded using the grading scheme described below (Fig. 2B). To ensure that the experimenters grading the images were not influenced by the background on which the animals were placed, an impartial person removed all backgrounds using Photoshop and renamed the images in a random fashion (Fig. 2C). The origin of the image was only re-established after grading had been completed. Grading was done by two people and each grade was averaged. Disruptive patterning in cuttlefish consists of up to 13 individual dark and light components, which are independent physiological units that can be shown singly or in combination with each other (Hanlon & Messenger, 1988). The components are produced by selective expansion (dark components) and retraction (light components) of chromatophores, which either expose or cover underlying white reflectors. When expressed, components can be shown with varying intensities. The most commonly shown 11 dark and light components were used for grading (Fig. 2B); each component was assigned a grade ranging from 0 (not expressed), 1 (weakly expressed), 2 (moderately expressed) to 3 (strongly expressed). The following components were graded: light chromatic components; 1—white posterior triangle; 2—white square; 3—white mantle bar; 13—white head bar; 14—white arm triangle. Dark chromatic components; 17—anterior transverse mantle line; 18—posterior transverse mantle line; 19—anterior mantle bar; 21—paired mantle spots; 22—median mantle stripe; 29—anterior head bar. These components were originally described and numbered by Hanlon and Messenger (1988). For consistency, we have listed these numbers here. Thus, using this grading scheme, an animal can be given a total grade ranging from 0 (no expression of any disruptive components) to 33 (maximum expression of all 11 disruptive components, resulting in a strongly disruptive body pattern) (see Fig. 2C for example of grading).

4. Results

4.1. Experiment 1: "Grey card" experiment

On the control substrate (black and white checkerboard, Fig. 3A, leftmost image), cuttlefish showed very strong disruptive body patterning. Fig. 3A shows how the disruptive patterning diminishes towards substrate 8. The disruptive patterning was strong on a green and white (e.g., substrate 1 in Fig. 3A) and a green and black checkerboard (e.g., substrate 16 in Fig. 3A). Importantly, the overall body pattern became non-disruptive on substrates 7–9 (Fig. 3A and Fig. 4A). The resultant non-disruptive body pattern shows clearly that these animals were not capable of distinguishing the grey from the green checkers. The average grades were: black and white checkerboard, 25.15 (SE = 1.38); substrate 1, 17.50 (SE = 1.20); substrate 16, 26.01 (SE = 1.94). The average grades for substrates 7–9 varied from 0.43 (SE = 0.21) to 1.16 (SE = 0.74) (Fig. 4A). This means that, on average, for substrates 7–9, the animals expressed weakly only one of 11 chromatic components, and this is barely visible and cannot be considered to contribute to disruptive coloration.

4.2. Experiment 2: Blue and yellow checkerboard

Cuttlefish failed to show disruptive coloration on a blue and yellow checkerboard whose photon catch was matched to the eye of *S. officinalis* (Fig. 1C); all five animals (e.g., Fig. 3B) produced uniform body patterns (average grade of zero). Uniform body patterning (average grade of zero) was also shown on the control substrates (uniform blue and uniform yellow) (Fig. 3B).

4.3. Contrast perception

There was a strong positive correlation between contrast of the green and grey checkers (Experiment 1) and average grade (Fig. 4B). Using the results of Experiment 1, we can make inferences regarding the contrast sensitivity of cuttlefish. Although somewhat arbitrary, it was decided that a total grade of three (i.e., one component fully expressed, or two or three components expressed weakly or partially) indicates that the animal's visual system has detected enough information to switch to the weakest expression of disruptive coloration. Any component grading less than three is barely perceivable to us and cannot be considered to contribute to disruptive coloration. In Fig. 4B it can be seen that the disruptive patterning expressed on substrates 10 and 6, whose checkers differ in contrast by 15%, scored an average disruptive grade of three. This implies that cuttlefish are able to detect contrast differences of 15% or less. It may well be, however, that the cuttlefish contrast detection threshold is substantially lower than the threshold obtained here for eliciting disruptive coloration.

5. Discussion

5.1. Color vision

A previous behavioral paper concluded that *S. officinalis* was color blind (Marshall & Messenger, 1996). In our present communication, we approached the problem

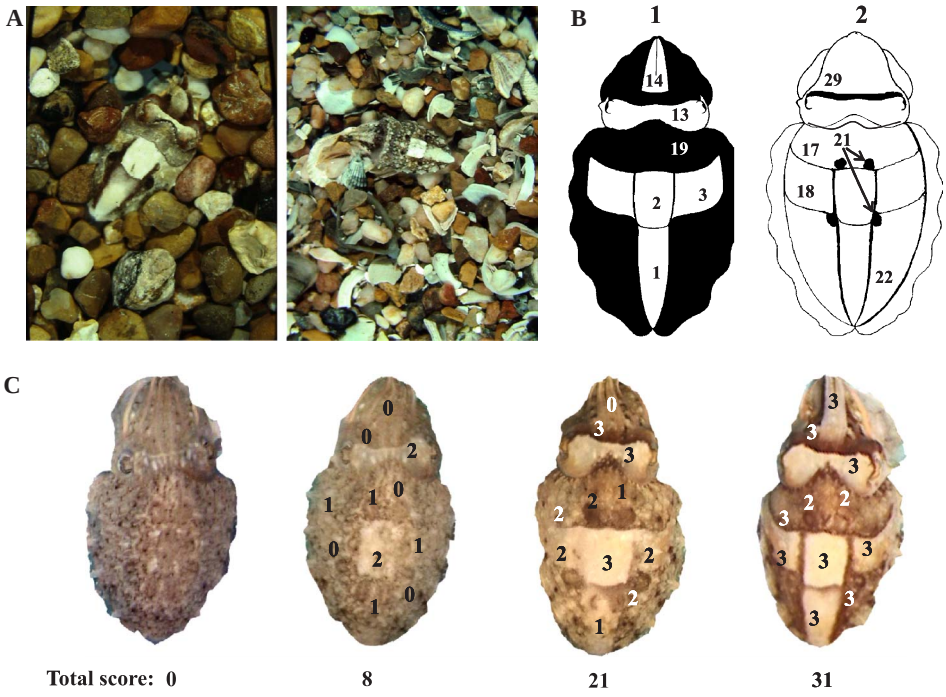

Fig. 2. (A) Images of cuttlefish on natural backgrounds showing disruptive coloration. Despite color blindness animals show superb ability to match background colors. (B) The chromatic components of disruptive body patterning that were graded. **1**, light chromatic components; **2**, dark chromatic components (see Section 3 for details). Components were graded from 0 (not expressed), 1 (weakly expressed), 2 (moderately expressed) to 3 (strongly expressed). Total grade can range from 0 (no expression of any components) to 33 (strongly disruptive body patterning). (C) Cuttlefish images for which the background has been removed for grading, showing variations in disruptive patterning and example of how chromatic components were graded.

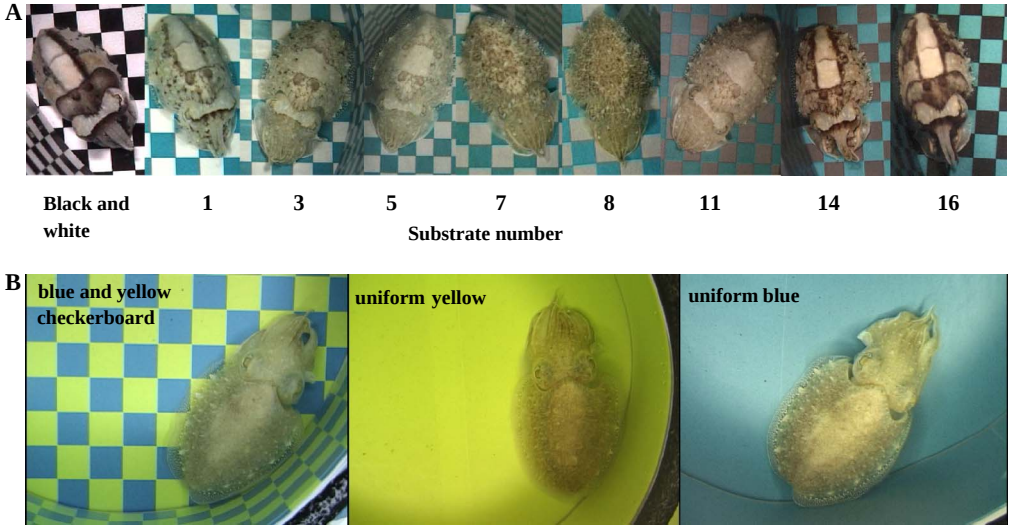

Fig. 3. (A) Images of cuttlefish on a selection of checkerboards, showing that disruptive patterning is elicited by green and white, green and light grey, green and dark grey as well as green and black checkerboards. Intermediate grey shades (approximately 40%) did not elicit disruptive body patterning. (B) Cuttlefish on blue and yellow checkerboard (matched in intensity) as well as uniformly blue and yellow substrates; no disruptive was elicited. These show that cuttlefish are color blind.

in more depth and with three additional experimental designs. First, we took advantage of recent research that provided a large database describing which visual background stimuli elicit disruptive coloration; this forms the basis of a robust sensorimotor bioassay (Chiao & Hanlon, 2001a, 2001b; Chiao et al., 2005; unpublished data). Second, we developed a detailed grading scheme for disruptive body patterns in cuttlefish, so that we could quantitatively grade the responses of 11 chromatic components of body patterns to visual stimuli. Third, in addition to presenting checkerboards of different color but identical brightness, we performed a more refined test of color vision based on assessing the animal's capability of discriminating between a single color and various

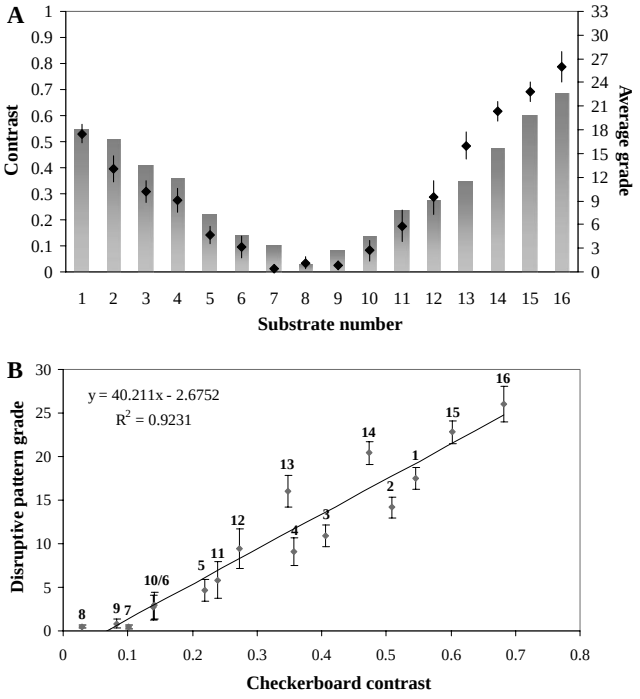

Fig. 4. (A) Average grade ($n = 10$) of cuttlefish disruptive body patterning shown on the 16 checkerboards (Experiment 1). Bars show Michelson contrast values of grey and green checkers of each checkerboard. Lowest grading score was recorded for substrate 8 (low contrast checkers). As contrast increased towards substrates 1 and 16, the average disruptive grading score increased. Error bars are ±SE. (B) Average grade of cuttlefish disruptive body pattern as a function of contrast (from 0 to 1), showing that grade increased with an increase in contrast of green and grey checker. Substrate numbers (1–16) are shown above each data point. Note that the disruptive patterning expressed on substrates 10 and 6 (0.15% or 15% contrast between checker shades) scored an average of three (see Section 4 for details). Trendline is exponential regression; R^2 value shown.

shades of grey. Both of these tests are convincing ways of testing for color vision (Kelber, Vorobyev, & Osorio, 2003). In the former type of test, in which stimuli of different wavelengths are used, we took advantage of the fact that it is possible to adjust the intensities of two spectral stimuli to yield identical photoreceptor responses in a monochromatic animal. Thus, the stimuli are only distinguishable on the basis of wavelength. This type of test has been used to show color vision in a variety of animals, such as hummingbirds (Goldsmith, Collins, & Perlman, 1981) and butterflies (Kelber & Pfaff, 1999); for review and more references see Kelber et al. (2003). In the latter type of test, a single color and various shades of grey are tested, assuming that one shade of grey gives a similar achromatic signal to the tested color. Only an animal capable of color vision would be able to distinguish between that grey and the color. Adaptations of this test have demonstrated color vision both in invertebrates (spiders, crustaceans, and insects) and vertebrates (fish, amphibians, birds, and mammals); for extensive list of references, see Table 2 in review by Kelber et al. (2003).

Our results provide a comprehensive complement to those of Marshall and Messenger (1996) and provide strong evidence for color blindness in *S. officinalis*. The results met our predictions very closely. Cuttlefish showed non-disruptive patterning when placed on a green and grey, as well as a blue and yellow checkerboard, for which the intensities were matched to an eye with one visual pigment ($\lambda_{max} = 492$ nm). This suggests that the cuttlefish eye perceives these substrates as uniform backgrounds, prompting the animal to show a uniform coloration.

The substrate colors were chosen carefully and the relative number of photons absorbed by a photoreceptor with a λ_{max} of 492 nm was calculated by the equation given in Section 2. Our results thus provide behavioral confirmation that the single visual pigment of cuttlefish does indeed have a λ_{max} value at or close to 492 nm, as previously described (Bellingham et al., 1998; Brown & Brown, 1958).

Cuttlefish are not the only cephalopods that have been reported to be color blind. The visual pigments of over twenty cephalopods have been studied, showing that with one exception all species have only one visual pigment (Matsui, Seidou, Horiuchi, Uchiyama, & Kito, 1988; Seidou et al., 1990). *Octopus vulgaris* and *Octopus apollyon* are almost certainly color blind, as has been established in a series of behavioral studies (Messenger, 1973; Messenger, 1977; Roffe, 1975), as well as electroretinogram (ERG) measurements, showing that there is no Purkinje shift (shift in ERG response to a change in wavelength of light stimulus with same intensity), which would be expected if there were receptors with different spectral sensitivities (Hamasaki, 1968). So far, the only cephalopod that appears to be able to see colors is the firefly squid *Watasenia scintillans*, whose retina contains three visual pigments (Michinomae, Masuda, Seidou, & Kito, 1994; Seidou et al., 1990).

5.2. Contrast sensitivity

The outcome of the present study gave us an insight into the contrast perception of these animals, which we suspected might be a crucial factor in uncovering what determines body patterning in cuttlefish. We found that there was a strong correlation between contrast and disruptive pattern grade—the higher the perceived contrast in the background the stronger the disruptive patterning (Fig. 4B). This result is not entirely surprising when considering that these color blind animals presumably rely on contrast cues in their environment (in addition to other visual cues, such as size of objects) when deciding on which particular body pattern to show. Our results imply that cuttlefish are able to detect contrast differences of 15%. However, it is possible—even probable—that cuttlefish can detect lower contrasts than those required to trigger deployment of disruptive coloration. We can also not rely on the motor output (i.e., body pattern) being a direct indication of contrast sensitivity, much less contrast threshold. Our findings thus provide

only a weak upper bound on the visual contrast threshold of *S. officinalis*.

We are not aware of any studies looking at the contrast threshold of cuttlefish. However, the contrast threshold of humans is 2% (Lythgoe, 1979, p. 244) and that of owls is 1% (Porciatti, Fontanesi, & Bagnoli, 1989). This suggests that the contrast threshold of *S. officinalis*, which is also a highly visual animal with very large and well developed eyes with high acuity (Groeger, Cotton, & Williamson, 2005; Messenger, 1981, 1991; Muntz, 1999), could be much lower than 15%.

In a study of color vision in *O. vulgaris*, Messenger (1973) reported that while octopus do not show a nystagmus response to rotating stripes of different wavelengths but same brightness (suggesting color blindness in these animals) they do show a nystagmus response to grey stripes that differ in brightness by 18%, yielding a Michelson contrast of 8%.

5.3. Color-blind camouflage

In shallow depths of water, broad-spectrum sunlight is available (Jerlov, 1976) and consequently colored object in the natural environment (such as sand, rocks, algae, coral, tunicates, sponges, etc.) will appear colorful (e.g., Hochberg and Atkinson, 2000; Hochberg, Atkinson, and Andréfouët, 2003, 2004; Marshall, Jennings, McFarland, Loew, and Losey, 2003; laboratory measurements of sand and rocks of natural habitats, Mäthger, unpublished data). At greater depths, the composition of daylight becomes increasingly restricted to the blue-green parts of the spectrum and the environment loses its colorful appearance. In this light environment, camouflage by intensity matching may be highly effective (Cott, 1940; Denton & Nicol, 1966; Lythgoe, 1979, p. 244). Certainly, cuttlefish have broadband light reflectors (leucophores) that reflect the ambient wavelengths of light and may thus aid intensity matching at least at a localized level (Froesch & Messenger, 1978; Hanlon & Messenger, 1988). However, the vexing question of how *S. officinalis* masters the task of camouflage in chromatically rich environments, such as those found at shallow depths of water, remains to be answered.

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