CUTTLEFISH CAMOUFLAGE: VISUAL PERCEPTION OF SIZE, CONTRAST AND NUMBER OF WHITE SQUARES ON ARTIFICIAL CHECKERBOARD SUBSTRATA INITIATES DISRUPTIVE COLORATION

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Summary

We investigated some visual background features that influence young cuttlefish, *Sepia pharaonis*, to change their skin patterning from 'general resemblance' of the substratum to disruptive coloration that breaks up their body form. Using computer-generated black/white checkerboard patterns as substrata, we first found that the size of the white squares had to be within a certain narrow range (relative to the size of the cuttlefish 'white square') for the animal to exhibit disruptive skin patterning. Second, given the appropriate size of checker, cuttlefish regulated their disruptive skin patterns according to the contrast between white and black squares. Third, by manipulating the number of white squares on a black background, we found that as few as four white squares among 316 black squares (or 1.25 %) produced disruptive patterning, yet increasing the number of white squares to 20, 40 or 80 did not increase the frequency of appearance of the cuttlefish 'white square', but only its clarity of expression. These results demonstrate that the size, contrast and number of white objects in the surrounding substratum influence the production and expression of disruptive skin patterns in young cuttlefish.

Movies available on-line

Key words: camouflage, visual perception, sensory, colour patterns, disruptive coloration, cuttlefish, *Sepia pharaonis*.

Introduction

Cephalopod camouflage (or crypsis) is among the most sophisticated in the animal kingdom because the neurally controlled chromatophores permit a diverse repertoire of body patterning that can be changed instantly (e.g. Hanlon and Messenger, 1996). The extraordinary patterns in the skin are mainly under visual control (Hanlon and Messenger, 1988; Marshall and Messenger, 1996). While the body patterns of cuttlefish such as *Sepia officinalis* have been well characterized (Hanlon and Messenger, 1988), it is not yet understood how the cuttlefish brain controls this patterning (see Boycott, 1961; Packard, 1995). Since cephalopods change their body patterning almost entirely as a result of visual input, applying a defined visual stimulus and recording the corresponding body patterning (i.e. motor output) allows aspects of visual perception to be examined (Marshall and Messenger, 1996; see also Saidel, 1988; Ramachandran et al., 1996). Using a behavioral approach, we report here the kinds of potential visual information that young cuttlefish, *Sepia pharaonis*, use to control body patterning for camouflage on diverse backgrounds.

Cuttlefish use tens of skin patterns for camouflage on benthic substrata, yet the repertoire can be grouped into three general categories of pattern: uniformly stippled, mottled and disruptive (Hanlon and Messenger, 1988). We measured only the extremes of this continuum, looking particularly for visual features of the substratum that would produce a change from uniformly stippled to the disruptive body patterns that can be so effective for camouflage (Fig. 1). Cephalopod body patterns can be analyzed into their 'components', which may be postural, locomotor, textural or chromatic (Packard and Hochberg, 1977). The chromatic components, which result mostly from direct neural control of skin patterns, are discrete entities that can number 15–45 in different species. There are several chromatic components that are particularly well defined and are major contributors to the disruptive patterns; these are the components White square and White mantle bar on the mantle, and the transverse White head bar (outlined in Fig. 2). These chromatic components can be thought of not only as morphological units in the skin but also as physiological units in the brain (Packard, 1982). That is, expression of these morphological units is determined by the physiological units in the brain of cuttlefish that control the skin through the pathway: visual input → eyes → optical lobes → lateral basal lobes → chromatophore lobes → skin. Thus, the appearance of certain chromatic components against well-defined backgrounds may give us clues about the

Fig. 1. Disruptive body patterning by a young cuttlefish on a rocky substratum. Notice the strongly expressed 'White square' chromatic component on the mantle of the animal that resembles other randomly scattered white rocks amidst the substratum. Scale bar, 9 mm.

visual perception and neural processing of body patterning. Since the major chromatic components of the disruptive body patterns of *Sepia* spp. are white rectangles, splotches and bars, we decided to test various features of dark and light substrata whose features we could control with some precision. A similar approach has been applied in flatfish (Ramachandran et al., 1996) to examine basic components of the skin patterns. In the present study, black/white checkerboard patterns with various sizes (experiment 1) and contrasts (experiment 2) were used to determine which visual features cuttlefish use to select disruptive patterns in the skin. Then, in experiment 3, various numbers of regularly spaced white squares in the black background were used to examine more closely the effects of background features on the expression of disruptive body patterns.

Materials and methods

Six young cuttlefish, *Sepia pharaonis* (8–12 cm mantle length), were reared from eggs in the laboratory of the National

Research Center for Cephalopods (University of Texas Medical Branch, Galveston, TX, USA) and were maintained in the Marine Resources Center at the Marine Biological Laboratory. Cuttlefish were 10 weeks old at the beginning of the experiments and 20 weeks old at the end. Each animal was placed in a running seawater tank (25 cm×40 cm×10 cm) and was restricted by a four-wall divider to an area (20 cm×26 cm) where various computer-generated backgrounds (laminated to be waterproof) were presented as the substratum. A digital video camera was used to record the body patterning of *S. pharaonis* over a period of 30 min (i.e. to record for 2 s in every 1 min period; to give a total of 60 s recorded for each cuttlefish on each substratum). In nature, it has been observed that cuttlefish can match their body pattern to the background within a second or so (Hanlon and Messenger, 1988). However, cuttlefish cannot perfectly match backgrounds that are completely artificial (e.g. checkerboard patterns). Furthermore, it was imperative to wait until the cuttlefish were acclimated to the tank, and this could sometimes take several hours. Acclimation was gauged by the cessation of excessive swimming and hovering movements and by the chronic expression of a stable body pattern. Nevertheless, once acclimated, *S. pharaonis* showed various grades of disruptive patterns based on certain features of these well-defined backgrounds. Therefore, we sought to quantify the corresponding body patterns as functions of the known and controlled features of the checkerboard (i.e. the size and the contrast of each square and the number of white squares).

A simple grading scheme of patterning (Fig. 2) was used to determine the responses of the animals to different substrata. The assigned grades were: 1, uniformly stippled pattern; 2, indistinct pattern; 3, disruptive pattern. We graded '1' if the animal was uniformly stippled, '3' if it clearly and distinctively showed the White square or White mantle bar on its mantle, and '2' if it showed anything in between. For example, in grade 2, there were elements of both a uniform stipple and a partial disruptive pattern (see Fig. 3, Fig. 4, Fig. 5). Fig. 2B illustrates some details of grading the White square. Often only a part of the White square on the animal's mantle was expressed unilaterally (e.g. Fig. 3B) or the White square itself was not uniformly white (e.g. Fig. 2B, Fig. 3D). We did not grade the White head bar, nor did we assess features such as the dark contrast of skin on other parts of the mantle. Grading was conducted by playing the video tape back and assigning a grade (whole integer, 1–3) every 10 s. Thus, since all tapes lasted 60 s, six grades were determined for each animal on each substratum. The mean values (and overall standard deviation) of all animals combined were plotted in the figures.

For testing different checker sizes (experiment 1), we chose a variety of square sizes that ranged from slightly larger than the White square on the mantle to much smaller than the White square on the mantle (note that the White square is not truly square, but rectangular; see Fig. 1). To test contrast (experiment 2), we chose the checker size that gave the highest grade of disruptive pattern in experiment 1, and we varied only the percentage of contrast while keeping the mean intensity the

A

B

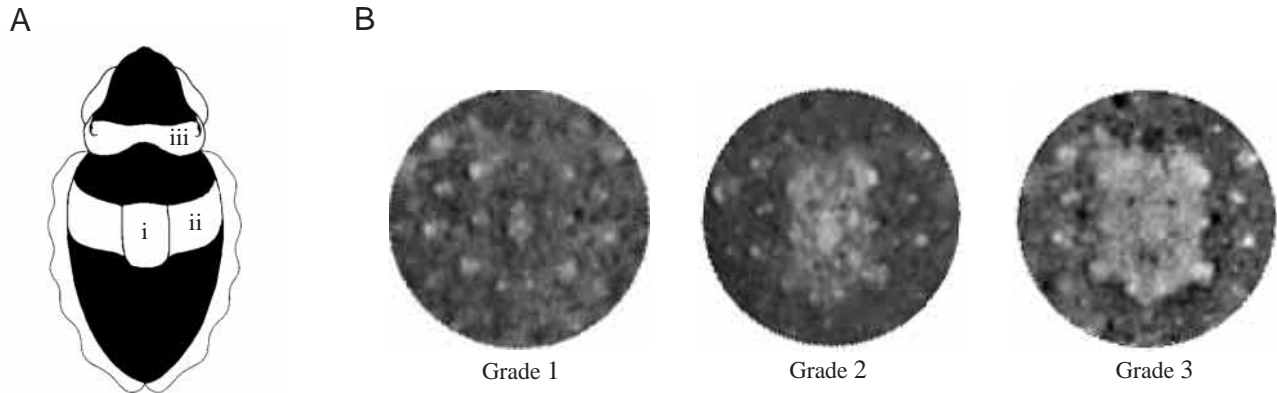Grade 1   Grade 2   Grade 3

Fig. 2. Grading criteria for judging disruptive coloration in young cuttlefish. (A) Cuttlefish outline showing (i) the White square, (ii) the White mantle bar (which includes the White square) and (iii) the White head bar. (B) Actual close-up images of the White square on the cuttlefish shown in Fig. 3 to illustrate different expressions that were used to assign grades 1, 2 and 3. Compare Figs 3–5. Images are life-size and exactly the same region of skin.

same for all checkerboards. The contrast here is defined as $(I_{white}-I_{black})/(I_{white}+I_{black})$, where I is the intensity value of black/white squares. For testing the number of white checker squares (experiment 3), we again chose the checker size that gave the highest grade of disruptive pattern in experiment 1, and varied only the number of white squares in the black background. Note that we distributed the white squares regularly (not randomly) across the space, so that there was a greater likelihood of both eyes of the cuttlefish seeing a similar number (or proportion) of them. To be consistent with the existing literature on cephalopod skin patterning (e.g. Hanlon and Messenger, 1988; Hanlon and Messenger, 1996; Packard, 1995), we capitalize the first word of the formal name of the chromatic components in the skin (e.g. White square).

Results

Thirteen trials were conducted over the course of 10 weeks: four cuttlefish were run through experiment 1, five through experiment 2 and four through experiment 3. Video examples are available on the Journal of Experimental Biology website to support the data and figures presented herein (http://www.biologists.com/JEB/movies/jeb3276.html).

In experiment 1, we tested substratum checker sizes of 2.6, 6.5, 13.0, 19.5 and 26.0 mm. The White square component on the dorsal mantle of the cuttlefish was approximately 18–22 mm (long dimension). Cuttlefish generally showed uniformly stippled body patterns when the checker size was 2.6 or 26.0 mm (Fig. 3A,E). Checker sizes of 6.5 and 19.5 mm produced mixtures of patterning in which the White square was partially expressed (e.g. Fig. 3B,D; see also Fig. 2B, grade 2). With a checker size of 13.0 mm, the cuttlefish almost always showed a consistent and clear expression of White square (Fig. 3C,F; see also Fig. 2B, grade 3). The white checkers were approximately half the size of the White square component (Fig. 3C). The same trend of expression was seen in the White head bar, which is not present in Fig. 3A,E, but is slightly expressed in Fig. 3B,D and most strongly in Fig. 3C with 13.0 mm squares.

In experiment 2, we altered the contrast between black and white squares by presenting checkerboards at different contrast values: 10, 20, 30, 50 and 100 % (note that no unit value can be assigned since this is a relative measurement). The White square was expressed occasionally at 10 % contrast (Fig. 4A), but its incidence and clarity of expression increased at 20 and 30 % contrast (Fig. 4B,C). The clearest responses occurred at 50 and 100 % contrast (Fig. 4D,E). There was no clear threshold at which visual contrast suddenly induced all of the cuttlefish to produce the White square (Fig. 4F). It is evident from Fig. 4B–D that White square could be shown in different gradations, particularly within the square. For example, Fig. 4B,C were scored as '2' because there are dark stipples within the square, whereas in Fig. 4D,E, a score of '3' was assigned because fewer or no stipples were present within the square, resulting in a whiter and thus stronger disruptive effect. Furthermore, note that the White head bar was not expressed at 10 % contrast, slightly expressed at 20 and 30 % contrast and expressed most strongly at 50 and 100 % contrast.

In experiment 3, we tested various numbers of regularly spaced white squares on a black background, all with 100 % contrast (note that our standard checkerboard pattern had 160 white squares and 160 black squares, each with 13.0 mm sides). First, on a completely black background (i.e. no white squares; Fig. 5A), no cuttlefish showed the White square component on its mantle. Second, when only four white squares were present (out of a total of 320 black and white squares, or 1.25 %), some cuttlefish showed partial White squares (Fig. 5B). Third, when 20 white squares (or 6.25 % of the 320) were present, the White square on the mantle was shown often, albeit in various forms with other chromatic components (Fig. 5C). Fourth, with increased numbers (i.e. proportions) of white squares, the frequency and clarity of expression of the White square chromatic component did not increase substantially (Fig. 5D,E), as indicated by the fairly large amount of variation (note the standard deviations in Fig. 5F). Note also that the White head bar was absent when no white squares were present, that it was expressed vaguely with four white squares, yet it was expressed strongly with 20 or more white squares on the substratum.
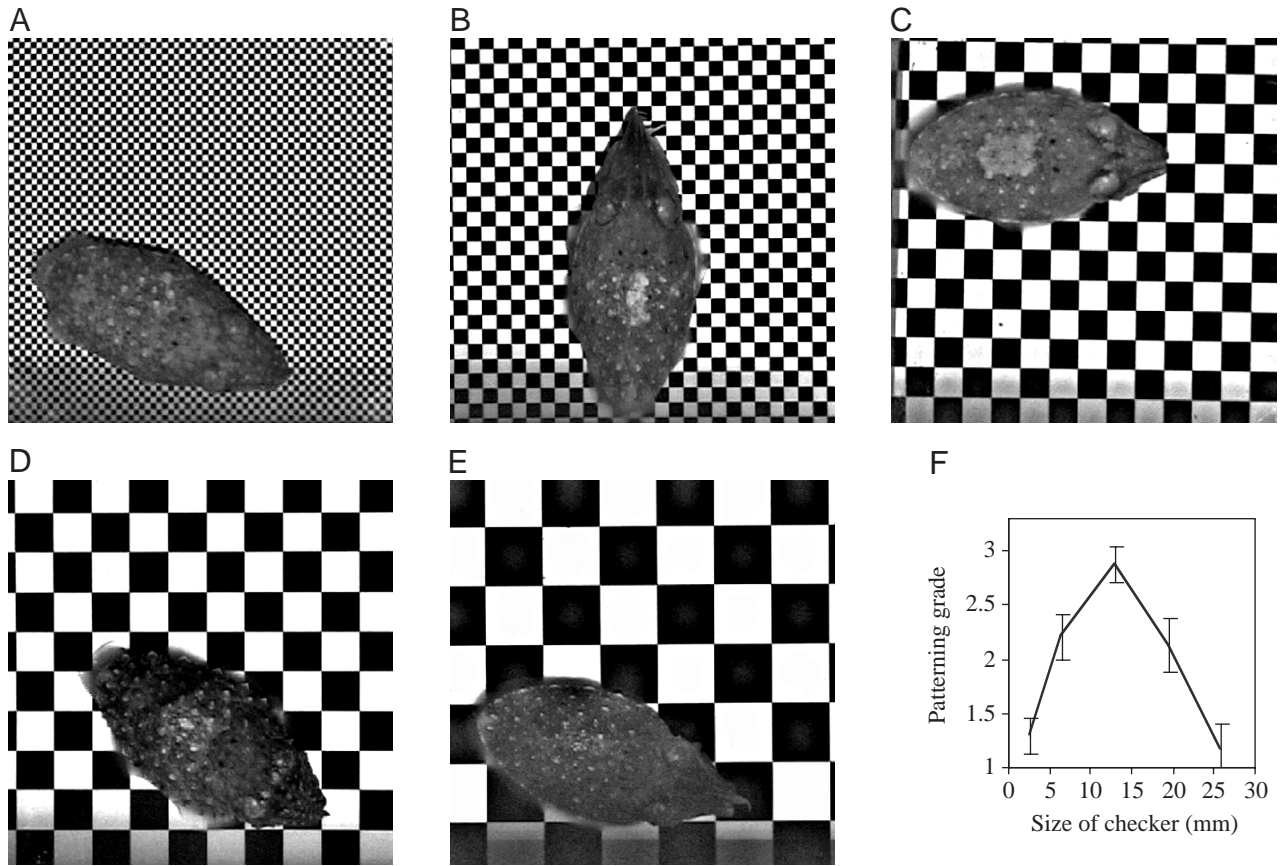
Fig. 3. (A–E) The same individual cuttlefish on substrata with checker sizes of 2.6, 6.5, 13.0, 19.5 and 26.0 mm. Assigned grades were '1' for A and E, '2' for B and D, and '3' for C. (F) Plot of the means (± S.D.) of the gradings of four cuttlefish for their patterning expression on the different square sizes; the peak response occurred at a checker size of 13.0 mm. See video at http://www.biologists.com/JEB/movies/jeb3276.html.

Discussion

One of the fascinating aspects of cephalopod camouflage is that shallow-water, benthic cephalopods such as octopus and cuttlefish can use different mechanisms to achieve crypsis because they have such adaptive skin that is under direct neural control. Unlike most animals that can use one or a few mechanisms of crypsis (Cott, 1940), cephalopods are known to have several and can switch easily from general resemblance to disruptive coloration, countershading, deceptive resemblance, mimicry and rarity through neurally controlled polyphenism and cryptic behavior (Hanlon and Messenger, 1996; Hanlon et al., 1999). However, rather little is known about the visual features of the substratum that are used to switch from one mechanism of crypsis (e.g. general resemblance) to another (e.g. disruptive coloration), despite knowledge of many aspects of cephalopod vision (see Messenger, 1991). Disruptive coloration is common in the animal kingdom (Cott, 1940), and cuttlefish use it frequently in their natural habitat (Hanlon and Messenger, 1988). Holmes (Holmes, 1940) was the first to detail some aspects of adaptive coloration in *Sepia officinalis*, and he demonstrated in outdoor tanks that cuttlefish would produce disruptive coloration when the substratum included a mixture of sand and large lightly colored shells. Hanlon and Messenger (Hanlon and Messenger, 1988) followed up this work with extensive laboratory and field observations of young cuttlefish on various substrata, and they were able to document the repertoire of body patterns used for a variety of behavioral functions, including crypsis by disruptive coloration (see Fig. 1 as an example). Marshall and Messenger (Marshall and Messenger, 1996) showed that cuttlefish do not respond to the spectral aspects of the substratum (they are almost certainly colorblind) but they perceive different intensities in the background. The higher the perceived contrast in the background, the bolder the pattern the animal shows.

Two complementary definitions of camouflage are appropriate for cephalopods and for interpreting this laboratory study. Edmunds (Edmunds, 1974) stated that 'animals which are camouflaged to resemble part of the environment are said to be cryptic', while Endler (Endler, 1991) stated that 'colour or pattern is cryptic if it resembles a random sample of the visual background as perceived by the predator at the time and place at which the prey is most vulnerable to predation'. The uniformly stippled patterns shown by cuttlefish in this study neatly fit the definition of Edmunds (Edmunds, 1974), while the disruptive patterns function in the manner described by
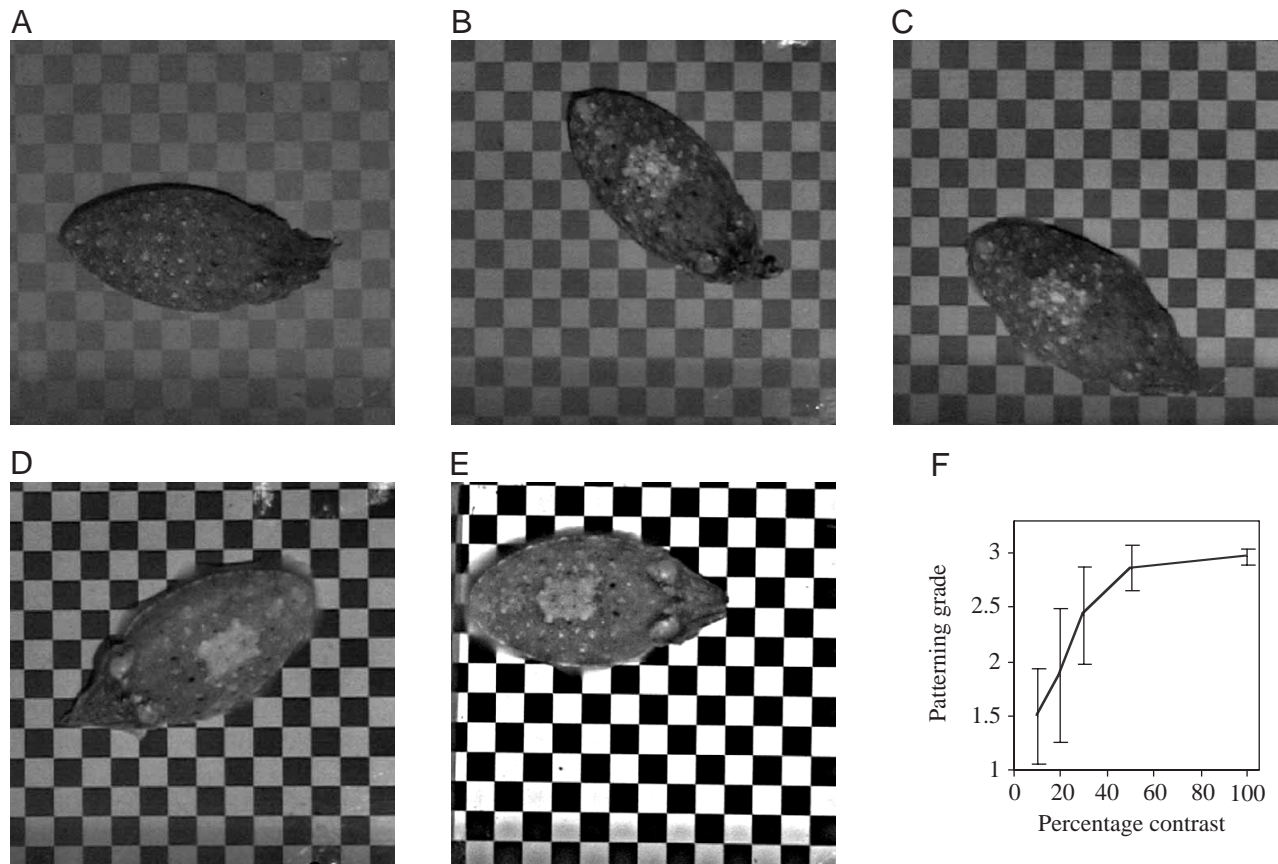
Fig. 4. (A–E) The same individual cuttlefish on different substrata in which the square size was constant (13.0 mm) but the black/white contrast was 10, 20, 30, 50 or 100 %. Assigned grades were '1' for A, '2' for B and C, and '3' for D and E. (F) Plot of the means (± S.D.) of the gradings of five cuttlefish for their patterning on all contrasts; responses plateaued at 50 % contrast or greater. See video at http://www.biologists.com/JEB/movies/jeb3276.html.

Table 1. *Summary of the results from the three sets of experiments*

	Experiment 1	Experiment 2	Experiment 3
Number of animals	4	5	4
Background patterns	Checkerboard with various checker sizes	Checkerboard with various contrasts	Varying numbers of white squares on black background
Results	Animals exhibit disruptive skin patterns only within a certain range of checker size	Animals regulate their disruptive skin patterns according to the contrast of the checkerboard	Animals produce disruptive skin patterns when there are as few as four white squares in the black background

Endler (1991). In particular, the brightness and conspicuousness of the White square are used by cuttlefish to represent a random sample of other white objects that are common in marine habitats (see Fig. 1 plus numerous illustrations in Hanlon and Messenger, 1988).

We developed a laboratory technique, not unlike that of Marshall and Messenger (Marshall and Messenger, 1996), whereby we manipulated the visual environment to elicit certain skin patterns in young cuttlefish. This direct relationship provides the opportunity to study aspects of visual perception in a non-invasive manner. This technique is similar to the method used by Ramachandran et al. (Ramachandran et

al., 1996), in which the rapid adaptive camouflage of tropical flatfish was examined. We concentrated on the ability of cuttlefishes to use other visual features to produce disruptive coloration. Our results indicate that the size, contrast and number of white squares in the black background are cues that the cuttlefish use to regulate the change from uniformly stippled skin patterns (general resemblance) to disruptive skin patterns (see Table 1 for a summary of the results).

The White square chromatic component on the mantle was most strongly expressed when the white checkerboard squares were slightly smaller than the White square of the animal. It might have been predicted that cuttlefish would respond well
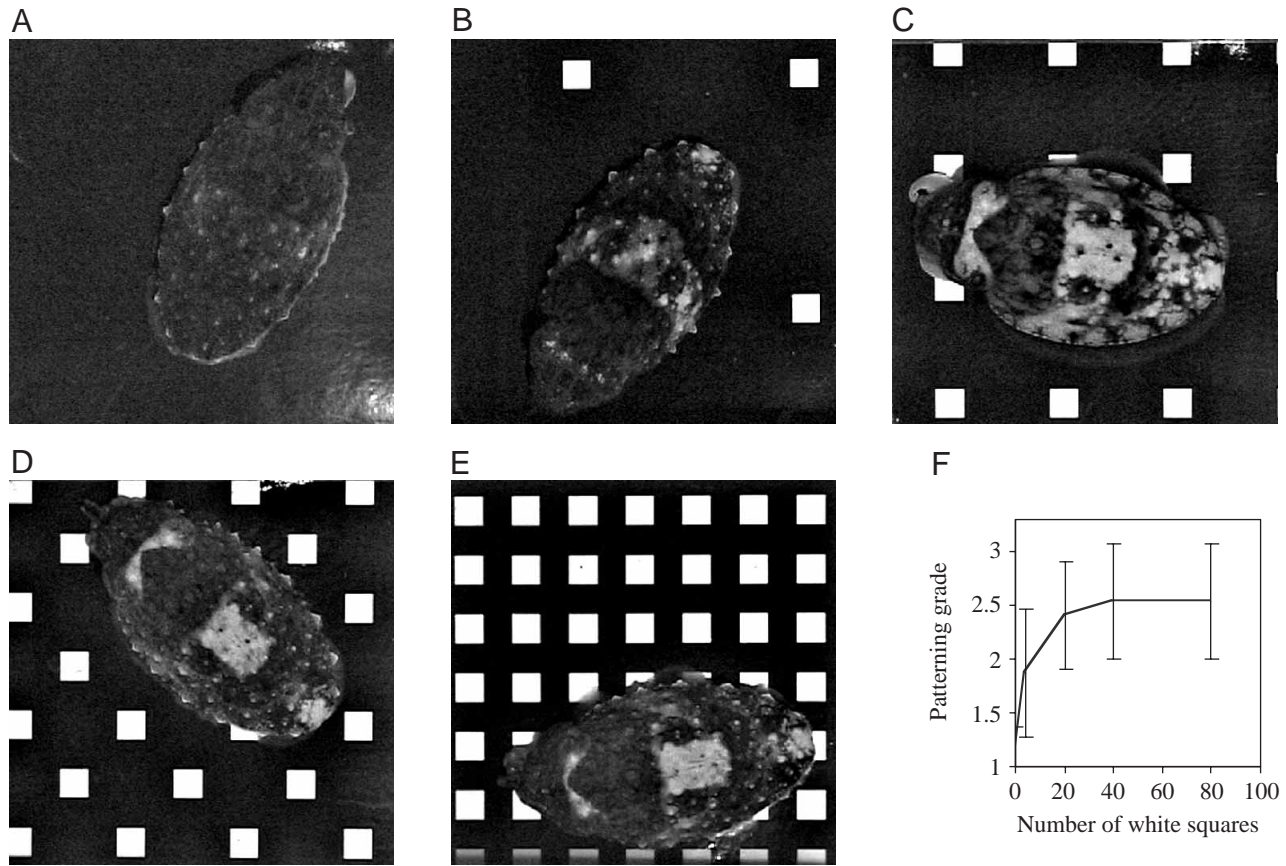
Fig. 5. (A–E) The same individual cuttlefish on different substrata in which the number of white squares (13.0 mm each side, 100 % contrast) was 0, 4, 20, 40 or 80. Assigned grades were '1' for A, '2' for B, and '3' for C–E. Note the two round dark spots on either side of the White square in B–E; this is a feature of mottle patterns. (F) Plot of the means (± S.D.) of the gradings of four cuttlefish. See video at http://www.biologists.com/JEB/movies/jeb3276.html.

(or even best) to white checkerboard squares equal in size to the White square, but they did not (Fig. 3D,E). One explanation may be that cuttlefish have only one large white chromatic component on their bodies, White square, but they have several other smaller white components (full listing in Hanlon and Messenger, 1988). Because some of the light chromatic components in the skin of cuttlefish are smaller than the White square, it is possible that cuttlefish cue on such small objects in nature. To achieve the disruptive effect (i.e. make chromatic components of their body appear as random samples of the substratum components; Endler, 1991), they might achieve best disruptive coloration by producing several (or numerous) components, thereby drawing attention away from their body outline. It has been noted previously that young cuttlefish have the ability to perceive substratum particle size relative to their own size and to change their body pattern dramatically during ontogeny while receiving the same visual input from unchanging particle size in the substratum (see figs 84–87 in Hanlon and Messenger, 1988).

Substratum contrast influenced disruptive patterning, although there was a good deal of variability in the results (Fig. 4F). When contrast was increased from 10 to 20 to 30 %, the disruptive effect increased, but the effects were more consistent above 50 % contrast (Fig. 4). This indicates that edge detection may play a role in assessing the pattern of the substratum. The transition from uniformly stippled to disruptive patterns also depended upon the number of regularly spaced white squares in the black background (Fig. 5), indicating that the number of light objects viewed on the dark substratum is a cue to producing disruptive patterns for camouflage. As with contrast, there were large variations (Fig. 5F) that may be due partly to each eye receiving different visual input depending upon its exact positioning at the time the pattern was graded. By using regularly spaced white checkerboards (rather than randomly generated and distributed ones, which we tried first), we minimized the variation that each eye was likely to receive.

Some marine flatfish are good at camouflaging themselves on substrata (e.g. Mast, 1916; Burton, 1981; Saidel, 1988) and one species, the tropical flatfish *Bothus lunatus*, has shown an impressive ability to match black and white substrata somewhat similar to those we used in our cuttlefish study (Ramachandran et al., 1996). The flatfish *B. lunatus* and our cuttlefish *Sepia pharaonis* responded differently to small *versus* larger checkerboards. Both showed uniformly stippled patterns on small checkers, but flatfish showed a mottled pattern on large squares whereas cuttlefish showed either disruptive patterns or

stippled patterns depending on the checker size. Although cuttlefish possess a large repertoire of patterns, including mottled patterns, they did not use mottling because this does not camouflage as well on checkerboards as do disruptive patterns. In this respect, the more refined skin of cuttlefish (with its neural correlates) imparts a more flexible and adaptive system for camouflage than that of flatfishes. Nevertheless, both organisms provide behavioral assays (manifest through adaptive skin) that provide insights into visual perception.

From knowledge of the natural habitat of *Sepia* spp. (e.g. Boletzky, 1983; Hanlon and Messenger, 1988; Hanlon and Messenger, 1996), one would predict that checkerboard substrata would be extremely unnatural and challenging for cuttlefish to adapt to. Nevertheless, the cuttlefish did attempt to match these artificial substrata and respond to changes in their features. Our use of checkerboards as the substratum was appropriate only insofar as we were testing for the presence/absence of the White square component in cuttlefish.

Our results revealed two ideas worthy of future investigation. First, it is probably not the shape *per se* (i.e. square) that is most important to the cuttlefish for producing disruptive patterns, but the contrast and size of an object in the substratum background. Second, Fig. 5B–E (which shows some mottled skin patterns) provides clues about how to test for mottled patterns using various combinations of different sizes, contrasts and numbers of light objects against dark backgrounds. Further analyses of the spatial frequency components of the experimental substrata may also shed light on the mechanism of skin patterning (e.g. principal component analysis in flatfish, Ramachandran et al., 1996; independent component analysis in both flatfish and cuttlefish, J. C. Anderson, R. J. Baddeley, D. Osorio, N. Shashar, C. W. Tyler, V. S. Ramachadran, A. C. Crook and R. T. Hanlon, in preparation). *Sepia* spp. may provide a particularly good model of visual perception because the rigid mantle (due to the presence of the cuttlebone) presents an immovable and non-flexible body part that relies on fine-tuned skin patterning to achieve a wide range of optical illusions. As pointed out previously (Hanlon and Messenger, 1988), the wide range of disruptive patterns shown by *Sepia* spp. are carried out with five light chromatic and six dark chromatic components of patterning; we concentrated on only two of these: the White square and White head bar. Perhaps most useful for future studies is the fact that several optical principles of disruption (first mentioned by Cott, 1940) are found in *Sepia* spp. and are illustrated in Fig. 1. These include first the principle of differential blending, achieved when some chromatic components blend with the substratum while others contrast sharply with it, thus allowing some body parts to stand out and others to fade away. In addition, the principle of maximum disruptive contrast operates when adjacent components of the pattern have great tonal contrast and, thus, provide a strong disruptive function. In another principle, that of adjacent contrast, a broken visual pattern made up of sudden transitions of color, sharply contrasted passages of tone and of irregular shapes of all kinds results in an image of multiple objects rather than parts of one form. Finally, gradations of tone within individual components such as the White square can also produce the visual illusion of relief to a human observer, giving the impression that the square is elevated or depressed, making it seem even more separate from the body. Thus, it is clear that aspects of grading the resultant skin patterning can be refined and correlated with increasingly sophisticated substrata, both of which could be quantified in a manner not attempted in this initial experiment.

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