Review

A review of cuttlefish camouflage and object recognition and evidence for depth perception

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Summary

Cuttlefishes of the genus *Sepia* produce adaptive camouflage by regulating the expression of visual features such as spots and lines, and textures including stipples and stripes. They produce the appropriate pattern for a given environment by co-ordinated expression of about 40 of these 'chromatic components'. This behaviour has great flexibility, allowing the animals to produce a very large number of patterns, and hence gives unique access to cuttlefish visual perception. We have, for instance, tested their sensitivity to image parameters including spatial frequency, orientation and spatial phase. One can also ask what features in the visual environment elicit a given coloration pattern; here most work has been on the disruptive body pattern, which includes well-defined light and dark features. On 2-D backgrounds, isolated pale objects of a specific size, that have well-defined edges, elicit the disruptive pattern. Here we show that visual depth is also relevant. Naturally, cuttlefish probably use the disruptive pattern amongst discrete objects, such as pebbles. We suggest that they use several visual cues to 'identify' this type of background (including: edges, contrast, size, and real and pictorial depth). To conclude we argue that the visual strategy cuttlefish use to select camouflage is fundamentally similar to human object recognition.

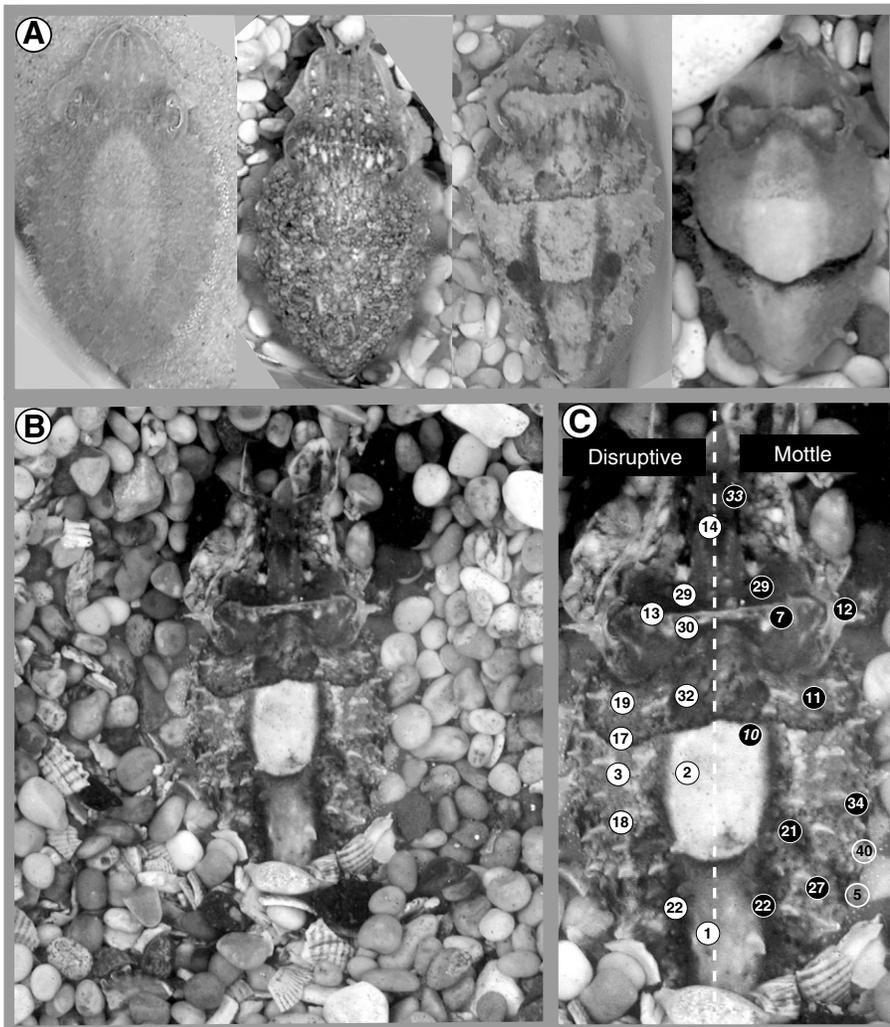Key words: cephalopod, cuttlefish, vision, camouflage, behaviour.

Background

Humans use a variety of different cues to segregate the 2-D retinal image into coherent 3-D objects and to determine their spatial locations (Gregory, 1980; Marr, 1982). These include, amongst others, local edge signals, physical depth (e.g. stereo and motion parallax) and pictorial depth (i.e. depth effects that can be applied to a flat picture). Optical illusions draw attention to the ambiguities that are inherent in images, and suggest how the brain interprets pictorial information. Non-human species probably have similar visual strategies (Cavoto and Cook, 2006; Aust and Huber, 2006). For example, the evidence that animals, ranging from bees to primates, see illusory contours in Kanizsa figures implies that they use similar processes to identify objects when they are partially occluded (van Hateren et al., 1990; Aust and Huber, 2006) (but see Fujita and Ushitani, 2005).

This article describes recent work on the vision of cuttlefish (mainly *Sepia officinalis* but also *S. pharaonis*), which is based on their remarkable powers of camouflage. We first outline how cuttlefish vary their coloration patterns, and then review how cuttlefish use 2-D and 3-D information in the visual image to control their appearance. To conclude we compare cuttlefish camouflage behaviour to human object recognition, and suggest that these animals use a two-stage visual process to select camouflage. The cuttlefish first sense multiple separate low-level cues in the retinal image, including the presence of edges, object size and depth. The cuttlefish then use these low-level cues to identify the 3-D environment, and hence to select the appropriate coloration pattern.

Cuttlefish body patterns

Coleoid cephalopods – octopus, squid and cuttlefish – are the most protean of all animals (Hanlon and Messenger, 1996). They change their appearance with great speed and versatility *via* skin chromatophores, which are under direct neuromuscular control (Messenger, 2001). Coleoids can also vary the physical texture of their skin from smooth to papillate (Fig. 1), and alter their body shape (especially in octopuses). In a key study, Hanlon and Messenger (Hanlon and Messenger, 1988) identified some 50 'behavioural components' that juvenile European cuttlefish (*S. officinalis*) use to control their appearance (Figs 1 and 2). These behavioural components are of four kinds: (i) chromatic components, which define the coloration pattern (Fig. 1); (ii) textural components, which define the skin texture; (iii) postural components; and (iv) locomotor components.

Cephalopod behavioural components can be compared to human facial signals, such as a smile or a frown, which are co-ordinated to produce basic expressions of happiness, fear, surprise and so forth (Ekman et al., 2002). Hanlon and Messenger (Hanlon and Messenger, 1988) proposed that cuttlefish can similarly co-ordinate their behavioural components to give 13 basic body patterns. Just as we can combine surprise with fear or happiness, the cuttlefish mix their body patterns, and also modulate the strengths of the behavioural components separately. This flexibility allows a vast range of patterns, and means that the classification of the principal body patterns is somewhat subjective. Nonetheless, when Crook and co-workers (Crook et al., 2002) used cluster analysis to investigate the expression of behavioural components in some 800

Fig. 1. Cuttlefish coloration patterns and their components. (A) Examples of four camouflage patterns from juvenile cuttlefish (mantle length 50 mm). From left to right the animals illustrate: a pale uniform pattern; a stipple with some mottle; a mottle with weak disruptive elements; and a high contrast pattern (but not typically disruptive). The animals also illustrate a range of skin textures. (B) A juvenile cuttlefish (*Sepia officinalis*) settled amongst pebbles, which is displaying components that are characteristic of both the disruptive and mottle body patterns. Increasing pebble size would cause the animal to emphasise components associated with the disruptive pattern, and decreasing pebble size would favour the mottle. The level of visual contrast within the image (e.g. between pebbles) appears to affect the overall contrast in the body pattern rather than the relative strengths of disruptive and mottle patterns (see Fig. 3A for further body patterns) (Mäthger et al., 2006; Kelman et al., 2007). (C) Some of these components numbered according to the scheme proposed by Hanlon and Messenger (Hanlon and Messenger, 1988) (see Fig. 2). In our principal components analysis (PCA) of cuttlefish, body pattern principal components (PCs) often approximate body patterns identified by Hanlon and his co-workers (Hanlon and Messenger, 1988; Mäthger et al., 2006). Here, features labelled on the left are often positively weighted in PCs that resemble the disruptive body pattern, and those on the right in PCs that resemble the mottle pattern (Figs 2–4). Features 5 and 40 are not clearly associated with either type of pattern.

Behavioural components

1. White posterior triangle	12. White major lateral papillae	22. Median mantle stripe
2. White square	13. White head bar	27. Mottle
3. White mantle bar	14. White arm triangle (not visible)	29. Anterior head bar
5. White fin spots	17. Anterior transverse mantle line	30. Posterior head bar
7. White neck spots	18. Posterior transverse mantle line	33. Dark arm stripes
10. White spots in the white square	19. Anterior mantle bar	40. Major lateral papillae
11. White splotches	21. Posterior paired mantle spots	

images of juvenile cuttlefish taken in diverse behavioural contexts (from a laboratory aquarium) they found the same number of clusters (13), several of which corresponded to the body patterns recognised by Hanlon and Messenger (Hanlon and Messenger, 1988). The fact that some clusters found by Crook and co-workers did not correspond to recognised body patterns emphasises the difficulty inherent in classifying such high-dimensional image data by eye.

Hanlon and Messenger (Hanlon and Messenger, 1988) distinguished 'acute' body patterns that are expressed transiently and are mostly used as communication signals, from 'chronic' patterns, that are expressed stably. Of the chronic patterns, Hanlon and Messenger recognised five main types, namely: uniform, stipple, light mottle, dark mottle and disruptive (Fig. 1). A sixth chronic pattern, which is called the 'weak zebra stripe', is primarily a sexual display. Hanlon (Hanlon, 2007) has proposed that visual camouflage across the animal kingdom falls into three main types, which by analogy with the cuttlefish body patterns he calls: uniform,

mottle and disruptive. However, cuttlefish often mix the different types of pattern (e.g. mottle and disruptive in Fig. 1B,C), and it is unclear whether they represent discrete behavioural states, or are parts of a continuum.

Given their remarkable control over camouflage, it is *a priori* likely that both cephalopods and their predators can discriminate many different types of visual background or habitat – otherwise the camouflage system would be partly redundant, and could not have evolved. In contrast to learning experiments, which test a single type of difference at a time, one can test how the cephalopods map high-dimensional natural signals into a complex response (Crook et al., 2002; Hanlon, 2007; Kelman et al., 2007), with a visuo-motor system that is likely to be evolutionarily optimised for classifying natural images. While cuttlefish camouflage behaviour gives a unique opportunity to study visual perception, exploiting its potential poses a challenge.

The task of analysing cephalopod coloration patterns would be reasonably straightforward if the animals expressed a small set

of well-defined patterns (e.g. disruptive, mottle and stipple) with varying strengths. This is the case in flatfish (Pleuronectiformes), which mix one to three basic body patterns, so that one can score the level of expression of each pattern directly from photographs (Kelman et al., 2006). Cephalopods have far greater control over their appearance than any fish (Figs 1 and 2) (Hanlon and Messenger, 1988; Crook et al., 2002; Hanlon, 2007; Kelman et al., 2007). To describe such a system one can estimate how many degrees of freedom (i.e. dimensions of variation) are required by a linear model that accounts for the gamut of patterns that are expressed (Ramachandaran et al., 1996). The dimensionality can be estimated by principal components analysis [PCA; Anderson et al. (Anderson et al. 2003) discuss PCA and compare this technique to the potentially more powerful method of independent components analysis (ICA)] of body patterns that cuttlefish express in a given range of conditions – for example over various natural substrates (Figs 1–4). The number of degrees of freedom that are observed may reflect one (or both) of two main types of constraint on the behaviour: either mechanistic constraints in the sensorimotor system – for example each body pattern might correspond to a single 'motor centre' (Hanlon and

Messenger, 1988) – or the nature of variation in the animal's context (e.g. the visual backgrounds used in a given set of experiments). It is therefore possible that the range of coloration patterns that are observed, even on natural backgrounds, may represent the classification of these backgrounds by a sophisticated pattern-recognition system – namely the cuttlefish – rather than the limitations of the animal's perceptual or motor systems.

In practice, our analysis of images of cuttlefish recorded on a wide range of natural backgrounds shows that this range of coloration patterns is described by six principal components (Fig. 2 and E.J.K., D.O. and R.J.B., in preparation, who used a scree plot to determine the number of meaningful principal components, PCs). Interestingly, the appearance of visual textures to humans can be described by a model with six degrees of freedom (Portilla and Simoncelli, 2000), which suggests that cuttlefishes' ability to classify visual patterns is comparable to that of humans – and presumably is matched by their natural predators and prey, such as teleost fish. By comparison, different species of flatfish, which have a similar ecology to cuttlefish, mix between one and three basic patterns (Kelman et al., 2006).
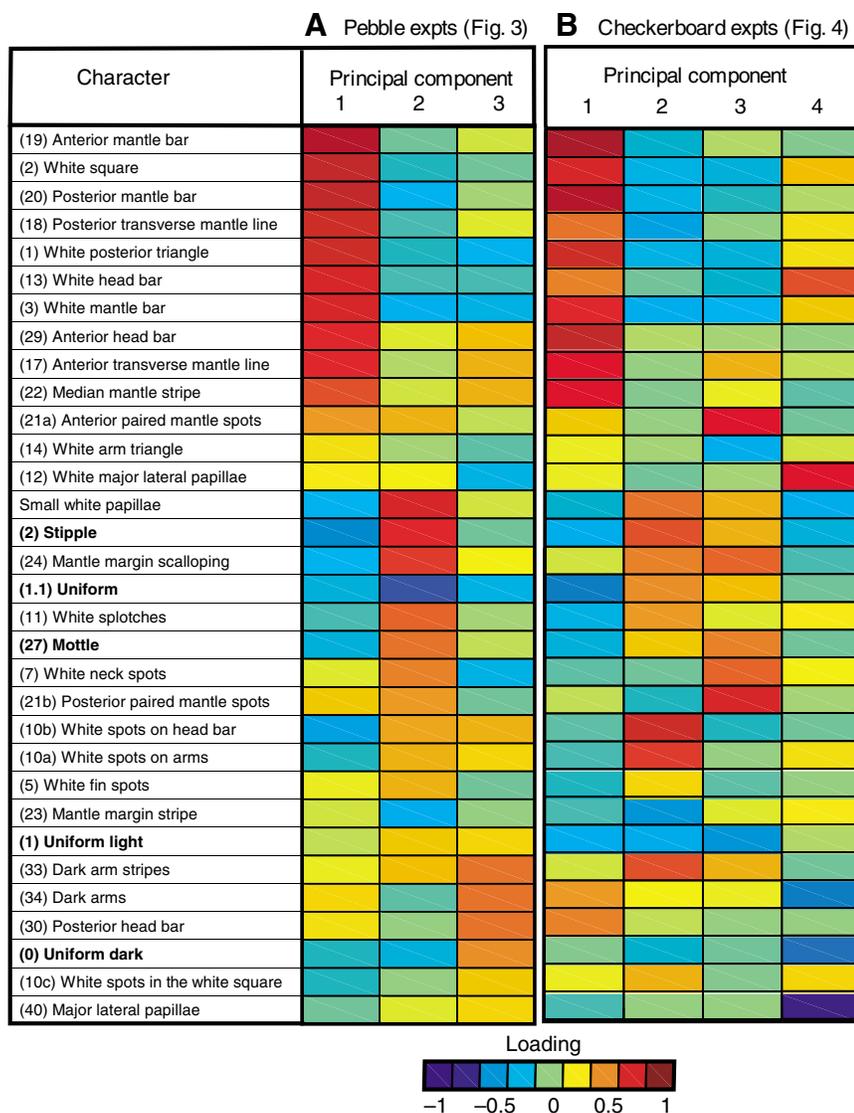

Fig. 2. PCs derived after Varimax rotation (SPSS version 11.5) (Kelman et al., 2007) from scores of the expression of 32 chromatic and textural components (see Fig. 1) (Hanlon and Messenger, 1988) of 20 juvenile cuttlefish (mantle length 50–70 mm) placed in a 300 mm diameter arena (area 0.07 m^2) on different backgrounds. Kelman and co-workers (Kelman et al., 2007) give further details of methods used for photographing the animals, scoring and PCA. Bold fonts indicate behavioural components that Hanlon and Messenger (Hanlon and Messenger, 1988) classified as body patterns. (A) PCs for pebble backgrounds of real pebbles under 5 mm Perspex, photographs of these pebbles at three contrast levels (see Fig. 3A,B) or photographs with 10 real pebbles (see Fig. 3C). For the 140 images that were graded (one per animal on each of seven backgrounds), three components (PC1–3) accounted for 47% of the total variance in the expression of the 32 behavioural components scored. A scree plot indicated that fitting further PCs was not meaningful. (B) PCs for checkerboard backgrounds (see Fig. 4). For the 60 body patterns that were graded, four PCs account for 59% of the total variance in the expression of 32 behavioural components. Fitting greater than four PCs was not meaningful. Positive values of three of the PCs correspond to body patterns identified by Hanlon and Messenger (Hanlon and Messenger, 1988): PC1 to the disruptive pattern; PC2 to the uniform stipple; and PC3 to the mottle pattern. PC4 involves two white components: white major lateral papillae (12) and white head bar (13).

Perception and selection of camouflage

It would be satisfying to have a model of cuttlefish vision that allows us to predict what coloration pattern a cuttlefish will express on any background (Fig. 5). In practice there are two complementary ways to approach this objective: (i) to test whether the animal is sensitive to a specified image parameter or visual feature (Marshall and Messenger, 1996; Shohet et al., 2006; Shohet et al., 2007; Kelman et al., 2007), or (ii) to identify the characteristics of an image that elicit a particular body pattern (Chiao et al., 2007).

Efforts to identify the image parameters cuttlefish can sense are inspired by psychophysical findings that mammals (mainly humans, monkeys and cats) have low-level mechanisms that represent colour, spatial frequency, orientation, spatial phase (e.g. edges and lines), directional motion and binocular disparity (Marr, 1982; Heeger et al., 1996). It is logical to compare cuttlefish vision to the better-known mammalian system. For instance, cuttlefish have a single spectral receptor with a peak sensitivity close to 500 nm and are colour-blind (Marshall and Messenger, 1996; Mäthger et al., 2006), but unlike mammals they can sense the polarisation plane of light (Shashar et al., 1996). Cuttlefish are sensitive to the mean reflectance of the background (Chiao et al., 2007) (E.J.K., unpublished observations). In spatial vision, we have found that although cuttlefish can sense orientation because they tend to orient themselves perpendicular to background stripes (Shohet et al., 2006), the body pattern is unaffected by the animal's orientation relative to a striped background. The coloration pattern is, however, sensitive to spatial frequency (Shohet et al., 2006; Shohet et al., 2007), and to the relative phase of separate spatial frequency components in the image (Kelman et al., 2007). This phase sensitivity suggests that these animals have specialised (non-linear) edge detectors (Morrone and Burr, 1988). Lastly, cuttlefish can estimate the distance of prey, possibly by stereopsis (Messenger, 1968), and this article gives new evidence that their choice of camouflage is sensitive to visual depth (Figs 3–5).

Expression of the disruptive pattern on 2-D backgrounds

As indicated above, an alternative to investigating the animals' sensitivity to low-level image parameters is to identify the features in the substrate that cause the cuttlefish to select a particular coloration pattern. This is comparable to asking when a human observer sees a specific object or pattern. Studies of this kind focus on the disruptive body pattern, which has a bold appearance with well-defined light and dark components (Figs 1–3) (Chiao and Hanlon, 2001a; Chiao and Hanlon, 2001b; Chiao et al., 2005; Barbosa et al., 2007; Chiao et al., 2007; Hanlon, 2007; Shohet
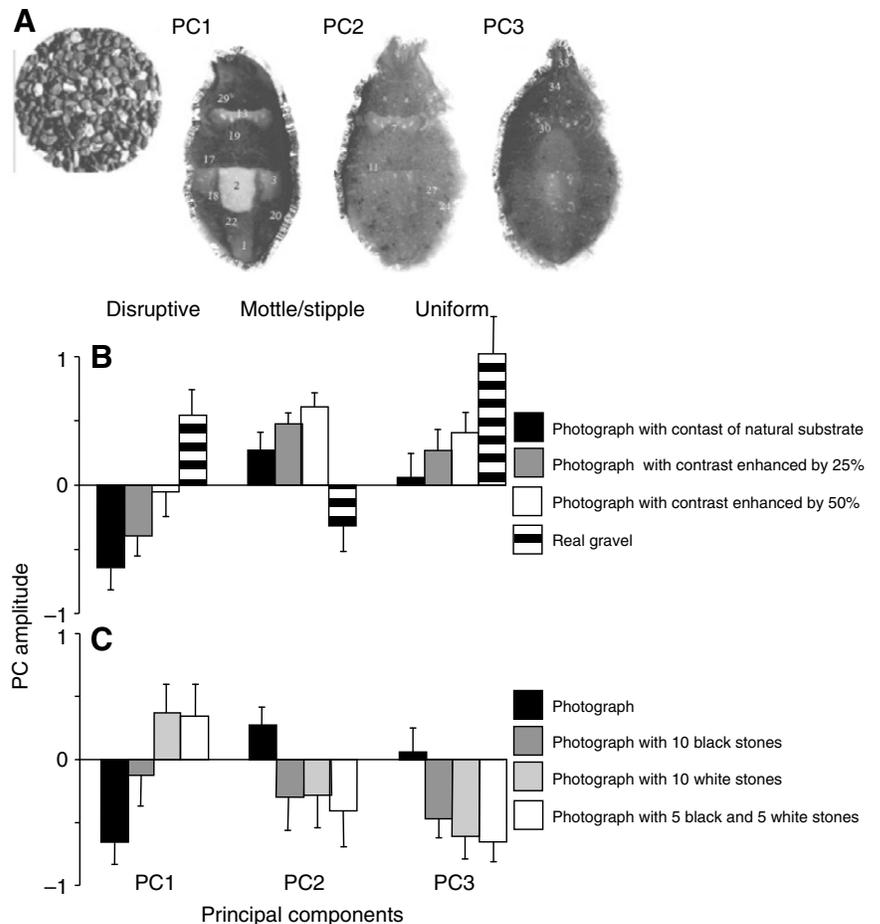

Fig. 3. A comparison of body patterns displayed by 20 juvenile cuttlefish (A) in response to pebbles under 5 mm Perspex, with responses to photographic images of these pebbles, suggests that they are sensitive to real visual depth in pebble backgrounds (B). Placing 10 real pebbles on the photograph (C) suggests that a small number of light, but not dark, 3-D objects give a similar response to a natural substrate. (A) A photograph of the pebble background, and illustrations of body patterns that typify the three PCs identified in this study (see Fig. 2A). Positively weighted behavioural components for each PC are numbered as in Figs 1 and 2. (B) Mean weights (+s.e.m.) of PCs 1–3 for real pebbles under Perspex or photographs of the pebbles at three contrast levels. The photographic backgrounds were presented at three contrast levels: (i) to match the natural pebbles; (ii) enhanced by 25% in Adobe Photoshop; or (iii) enhanced by 50% in Adobe Photoshop. Weights of all three PCs increase with image contrast in the photographs, whereas real pebbles give the strongest weights of PC1 (disruptive pattern, Fig. 2) and negative weights of PC2 (mottle/stipple). This indicates that no level of image contrast in a photograph could produce a response matching that to real pebbles. A repeated measures ANOVA showed a significant effect of the background and amplitude of PCs 1–3 between the natural pebbles and all three photographic backgrounds (PC1, $F_{3,57}$=19.61, P<0.05; PC2, $F_{3,57}$=8.556, P<0.05; and PC3, $F_{3,57}$=6.614, P<0.05). The ANOVA also revealed an interaction of background type (3-D vs 2-D) and the expression of PC1 and PC2 ($F_{1,19}$=27.95, P<0.05). (C) Evidence that placing 10 pebbles at arbitrary locations on the 2-D background (area 0.07 m^2) affects the body pattern. The presence of 10 light stones on the 2-D background enhances the expression of PC1 (disruptive; Student's t-test: t_{19}=−3.547, P<0.05) and suppresses PC2 (mottle/stipple). With 10 dark stones there is no significant effect on PC1 (Student's t-test: t_{19}=−1.811, P>0.05) but a suggestion that the expression of PC2 is suppressed. A mixture of five light and five dark stones gives similar responses to 10 light stones.

et al., 2007; Kelman et al., 2007; Mäthger et al., 2007). Given that cuttlefish vary the expression of the separate behavioural components independently, a convenient measure of the overall strength of the disruptive pattern is to score the level of expression of its 11 behavioural constituent components (Mäthger et al., 2006; Barbosa et al., 2007; Chiao et al., 2007). Scores are made on a four-

A

B

Disruptive Uniform/stipple Mottle

Flat checkerboard
Light upper check surface
Dark upper check surface

PC amplitude (y-axis, 0.5 to −0.5)
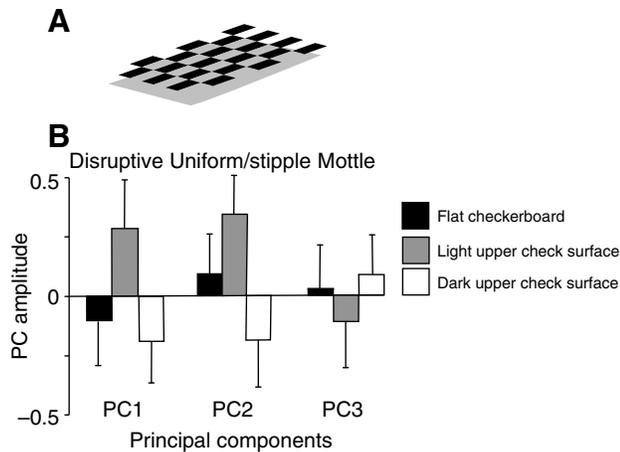
PC1   PC2   PC3

Principal components

Fig. 4. Evidence that cuttlefish discriminate depth in checkerboard patterns. This study used the same 20 juvenile cuttlefish as in the pebble study (Fig. 3), and again we analysed the response of each animal to each of the three experimental backgrounds, giving a total of 60 images (Fig. 2B). (A) The cuttlefish were settled on a Perspex floor above a checkerboard in which the dark and light squares were either in the same depth plane (flat) or in different depth planes separated by 10 mm. (B) Light squares above dark were most effective in eliciting the disruptive body pattern (PC1; Figs 1 and 2). The expression of PC1 (disruptive) was stronger when the light check pattern was in the upper plane (Student's t-test, $t_{19}=-2.635$, $P<0.05$). Similarly an ANOVA showed a significant interaction of the backgrounds (flat and depth with light checks on the upper surface) with the expression of PC1 and 2 ($F_{1,19}=0.5711$, $P<0.05$). There is no apparent effect of the experimental treatments on PC3 and PC4 (not illustrated).

point scale (0–3; i.e. absent to strongly expressed), so the summed scores give a single measure of disruptive expression ranging from 0 to 33.

Cuttlefish have been tested on printed patterns, and on natural substrates (Barbosa et al., 2007; Chiao et al., 2007; Hanlon, 2007; Mäthger et al., 2007). Given that the disruptive pattern includes well-defined visual features, it is not surprising that it is expressed on backgrounds with clearly defined regions, such as checkerboards (Chiao and Hanlon, 2001a; Chiao and Hanlon, 2001b). The area of the checks needs to be approximately equal to that of the white square on the mantle (Fig. 1) (Chiao and Hanlon 2001a; Chiao and Hanlon, 2001b; Barbosa et al., 2007). Recent work has investigated how modifications to a standard checkerboard pattern affect the strength of the disruptive pattern; this has shown that light features

are especially effective in eliciting the disruptive pattern, but their precise shape, spatial distribution and density is relatively unimportant (Chiao and Hanlon, 2001b; Chiao et al., 2007). Well-defined edges are also significant, because blurring (i.e. low-pass filtering) the pattern reduces the strength of the disruptive pattern (Chiao et al., 2005), as does disruption of spatial phase in images with a fixed spatial-frequency power spectrum (Kelman et al., 2007).

Their responses to 2-D backgrounds show that cuttlefish do not simply respond to image contrast, but express the disruptive pattern in the presence of definite pale regions or objects (Chiao et al., 2007). An interesting possibility, which needs further investigation, is that the level of contrast in the disruptive pattern is modulated to approximately match the contrast of the background (Chiao and Hanlon, 2001a; Mäthger et al., 2006; Kelman et al., 2007). Overall, it seems that the disruptive pattern is displayed to match the background in contrast, image polarity and the areas of prominent features. Whereas matching is consistent with the disruptive pattern being used as cryptic camouflage, it is not necessarily expected for 'disruptive camouflage', as the term is customarily used in the literature on animal coloration – because this states that disruptive camouflage should have a higher contrast than randomly selected elements from the visual background (Endler, 1978; Ruxton et al., 2004; Cuthill et al., 2005; Stevens et al., 2006).

Expression of the disruptive pattern on 3-D backgrounds and perception of visual depth and visual objects by cuttlefish

Published work suggests that the cuttlefish mainly use 2-D image data to control their camouflage. For example, responses to planar images of gravel are reportedly similar to those to real gravel (Chiao et al., 2005), and the responses to backgrounds that include real pale pebbles are consistent with those to printed backgrounds (Chiao et al., 2007). However, the seafloor is not 2-D; there may be sand ripples or objects such as pebbles, which create shadows and similar visual effects that are absent from 2-D surfaces. We now turn to the question of how cuttlefish sense and respond to visual depth.

The importance of shadowing in cuttlefish camouflage is suggested by the observation that the white square is often asymmetrically shaded, which gives a 3-D effect (Anderson et al., 2003; Langridge, 2006). It seems plausible that the shading accentuates the similarity of the white square to a (convex) pebble, and hence 'disrupts' the perceived planar surface of the mantle. More generally, the design of the disruptive pattern, with relatively large light regions and narrower dark lines and patches, is reminiscent of the pattern of highlights and shadow seen when pebbles are illuminated from above (see Fig. 1).

Visual input   Image parameter   Local feature   Components/ body pattern   Output (behaviour)

Spatial freq.   Edges
Retina → Spatial phase   Area
                Light regions   Background type   W1 →
Luminance   Visual depth   W2 →
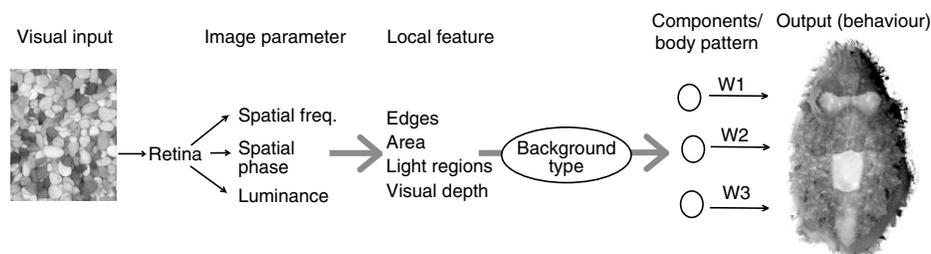   W3 →

Fig. 5. A summary of how visual information controls cuttlefish camouflage. The animal detects local visual features, which include edge and depth information, and from these relatively low levels then classifies the background. For example, on the basis of whether it is a continuous surface, or made of discrete objects such as pebbles, and on the spatial scale of the pattern/objects. This classification determines the primary weightings (W1–3) of the components of the coloration pattern. Image contrast (and perhaps other low-level measures) then modulate the strength of the pattern. It is unlikely that the classification of 'background type' is categorical, in the sense that an image has to be of one type or another, and this is why the animal is able to vary the relative levels of expression of the 40 or so chromatic components independently.

To test the effects of depth and shading on cuttlefish camouflage we compared responses to 2-D and 3-D pebble and checkerboard backgrounds (Figs 2–4). The coloration patterns were characterised by PCA of the expression of 32 chromatic components in the body pattern (Kelman et al., 2007). The levels of expression of the chromatic components were scored on a four-point scale (by an observer blind to the experimental treatment), and then subject to PCA with axes rotated to maximise variance of the loadings [the so called vari-max rotation (Kaiser, 1960)]. Technically, PCA followed by rotation to maximise variance yields a set of orthogonal factors that are not PCs because PC1 is no longer the axis that accounts for the greatest possible amount of the total variation. Nonetheless, for simplicity we refer to the rotated axes as PCs. After this rotation, the resulting axes (i.e. factors) often correspond to the main body patterns that were identified by Hanlon and Messenger (Hanlon and Messenger, 1988), especially the disruptive and mottle patterns (Figs 1–4) (Kelman et al., 2007). The reason for this correspondence is beyond the scope of this article, but it allows us to simplify discussion to refer to these PCs by the names of the body patterns.

We photographed six juvenile *Sepia officinalis* (mantle length 80 mm) that had settled for at least 10 min (Kelman et al., 2007) on each of three types of background: (i) ordinary pebbles; (ii) pebbles beneath a clear 5 mm Perspex sheet; and (iii) a laminated photograph of the same pebbles. In addition, the photograph was presented at three levels of contrast: 'normal', which matched the original (as confirmed by photometric measurement), and with contrast enhanced by 25% and 50% (performed using Adobe Photoshop). This gave a total of five experimental conditions. PCA followed by rotation to maximise variance (see above) yielded three meaningful components (Fig. 2 and Fig. 3A), the first principal component (PC1) corresponded well to the disruptive body pattern, and the second component (PC2) to the mottle pattern. Note that the 80 mm long cuttlefish was able to settle at any location of its choosing on the 700 mm diameter arena floor. This means that the cuttlefish are effectively taking multiple samples of the backgrounds, as they settle in different locations.

These new experiments show that cuttlefish are sensitive to visual depth (cf. Chiao et al., 2005; Chiao et al., 2007). Compared with a 2-D image of pebbles, responses to the real (i.e. 3-D) background elicit stronger expression of PC1 (the disruptive pattern), but suppresses PC2 (mottle/stipple; Fig. 3B gives further details and statistics). By comparison, the effect of increasing contrast of the 2-D patterns is to increase the weights of both mottle and disruptive components, which is consistent with the suggestion that contrast in the body patterns is correlated with contrast in the background (see above). These observations imply that the cuttlefish sees the 3-D substrate as qualitatively different from any 2-D image. The fact that animals viewed the substrate through a sheet of Perspex appears to be unimportant, as responses when the animal settled directly on the real pebbles were indistinguishable from those when the pebbles were seen through Perspex. This implies that the animals use visual rather than tactile cues to distinguish real objects from a photographic image.

It should be noted that neither the Perspex that covered the real gravel nor the laminate on the photographs acted as a Polaroid filter. Thus it is most unlikely that artefactual polarisation cues affected the experimental observations (Fig. 3). Equally we found (E.J.K., D.O. and R.J.B., unpublished observations) that the cuttlefishes' coloration patterns in response to real gravel were essentially identical (and certainly not statistically different) when the animals sat directly on the substrate or on a Perspex sheet, implying that there was no effect either of direct tactile contact with the gravel or visually of the Perspex.

Overall, the findings reported in Fig. 3 imply that real (as opposed to pictorial) visual depth drives expression of the disruptive pattern but, as with 2-D backgrounds, pale objects appear to be most effective in eliciting this body pattern (Barbosa et al., 2007; Chiao et al., 2007; Mäthger et al., 2007). If 5–10 pebbles are placed on a 0.07 m^2 photographic background of similar pebbles, the cuttlefish increase expression of PC1 to almost the same level as on the real substrate. In contrast, dark pebbles have no significant effect (Fig. 3B).

Further evidence that cuttlefish control the expression of the disruptive pattern by detecting pale 'objects' and real (physical) depth is seen when they settle on checkerboard backgrounds. We compared responses to conventional 2-D checkerboards with those to 3-D patterns where the light and dark squares lay in separate depth planes, 10 mm apart (Fig. 4A). The responses of six juvenile cuttlefish (the same individuals as in the previous study) were analysed using a separate PCA (Fig. 2), but again PC1 corresponded quite closely to the disruptive pattern, and another PC3 to the mottle. This study confirmed that cuttlefish are sensitive to visual depth, in that when the light squares are above the dark squares the disruptive pattern is expressed significantly more strongly than to a conventional 2-D checkerboard, whereas the mottle is suppressed. Intriguingly, when the dark squares lie above the light, expression of the disruptive pattern is not at all enhanced compared with a 2-D checkerboard (Fig. 4B; the legend to Fig. 4B gives statistics). The next section looks at the implications of these observations for our understanding of cuttlefish vision.

Visual information and selection camouflage patterns

Cephalopods' virtuosity in controlling their appearance is well documented (Hanlon and Messenger, 1988; Hanlon and Messenger, 1996), but it is only recently that we have exploited the potential of camouflage behaviour as a unique and powerful way to study visual perception. This approach is self-evidently different from more conventional methods of testing spatial vision and object recognition, which normally rely on the animal learning to associate a stimulus with a food reward (Wehner, 1981; van Hateren et al., 1990; Cook, 1992; Cavoto and Cook, 2006).

We have been struck by the similarity of the cuttlefishes' camouflage behaviour to human object recognition. Cuttlefish need to produce the correct pattern for a given visual environment, and intuitively it seems reasonable that this basically involves matching their coloration pattern to the background. However, the findings reviewed here emphasise the point made by Chiao and co-workers (Chiao et al., 2007) that many different image variables interact to control the camouflage pattern, showing that expression of the disruptive pattern is sensitive to diverse cues that can be present in a wide range of images. These include: well-defined edges (Chiao et al., 2005; Kelman et al., 2007), light objects, object area and visual depth (Fig. 3).

One interpretation of these findings is that, in nature, cuttlefish express the disruptive pattern (and its variants) on backgrounds that are composed of discrete objects (e.g. pebbles), whereas mottles and stipples are used on patterned surfaces (e.g. coarse sand). Discriminating between discrete objects and a patterned surface appears to be rather simple (and given that the body patterns are often mixed, we must be simplifying), but we know that in natural images three main factors affect the intensity of any given point in an image: (i) reflectance from that point; (ii) 3-D effects of surface

curvature and local shadowing of objects; and (iii) the illumination, which can vary because of shadows caused by light passing through the water surface or vegetation. Cuttlefish may then use several separate types of visual information to distinguish between these contexts – just as we do for image segregation. These include the presence of pale regions or 'highlights' (Chiao et al., 2007), well-defined edges (Chiao et al., 2005; Kelman et al., 2007) and visual depth.

It follows that when the animal sees an image with pale and dark regions, it need not 'see' a background composed of differentially pigmented materials, but instead patterns of light and shadow falling amongst small 3-D objects such as pebbles. A well-known pictorial depth effect for humans is created by the fact that pale highlights are normally found in front of shadows. The findings reported in Fig. 4 suggest that cuttlefish sense pictorial depth in similar way. When pale regions are in front of dark ones, then real and pictorial depth cues are in accordance and strongly consistent with the background being formed of discrete objects. This promotes expression of the disruptive pattern. By comparison, when dark regions are physically above pale areas, these cues are contradictory. In this case the disruptive pattern is not expressed.

We therefore propose a two-stage model of cuttlefish vision (Fig. 5), in which the animal first assesses low-level cues, and then uses these to classify its visual environment. Once the background has been classified – for example, either as being composed of discrete objects or as a continuous surface, the level of contrast in the image then determines the contrast in the body pattern (Fig. 3) (Chiao and Hanlon, 2001a; Mäthger et al., 2006; Mäthger et al., 2007; Kelman et al., 2007). This could depend on the variation in pebble colour and other relevant low-level cues.

This interpretation of how the cuttlefish selects camouflage immediately raises questions about how different types of evidence are combined (Dayan et al., 1996). For example, that the presence of a few real (light-coloured) pebbles on a 2-D image of pebbles strongly favours expression of the disruptive pattern over the mottle (Fig. 3B). Pictorial images that create ambiguous or impossible 3-D effects for humans are well known – as in the work of M. C. Escher (Gregory, 1980), and here we see (Fig. 4) that a 'counterfactual' scene with dark regions in front of a pale ground produces a different response from the more natural situation where light surfaces are in front.

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