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RESEARCH ARTICLE

Visual perception and camouflage response to 3D backgrounds and cast shadows in the European cuttlefish, *Sepia officinalis*

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ABSTRACT

To conceal themselves on the seafloor, European cuttlefish, *Sepia officinalis*, express a large repertoire of body patterns. Scenes with 3D relief are especially challenging because it is not possible either to directly recover visual depth from the 2D retinal image or for the cuttlefish to alter its body shape to resemble nearby objects. Here, we characterised cuttlefish camouflage responses to 3D relief, and to cast shadows, which are complementary depth cues. Animals were recorded in the presence of cylindrical objects of fixed (15 mm) diameter, but varying in height, greyscale and strength of cast shadows, and to corresponding 2D pictorial images. With the cylinders, the cuttlefish expressed a '3D' body pattern, which is distinct from previously described Uniform, Mottle and Disruptive camouflage patterns. This pattern was insensitive to variation in object height, contrast and cast shadow, except when shadows were most pronounced, in which case the body patterns resembled those used on the 2D backgrounds. This suggests that stationary cast shadows are not used as visual depth cues by cuttlefish, and that rather than directly matching the 2D retinal image, the camouflage response is a two-stage process whereby the animal first classifies the physical environment and then selects an appropriate pattern. Each type of pattern is triggered by specific cues that may compete, allowing the animal to select the most suitable camouflage, so the camouflage response is categorical rather than continuously variable. These findings give unique insight into how an invertebrate senses its visual environment to generate the body pattern response.

KEY WORDS: 3D camouflage, 3D visual perception, 3D body pattern, Camouflage threshold, Two-stage response

INTRODUCTION

Human vision allows us to assemble and interpret cues that distinguish objects from backgrounds (figure from ground), identify these objects and locate them in space (Marr, 1976). Camouflage and camouflage breaking offer a natural laboratory to test how non-human animals accomplish these tasks (Osorio and Cuthill, 2015). The third dimension presents special challenges for vision because of the problem of recovering 3D information from a 2D retinal image, and for camouflage because animals have a limited ability to alter their body shapes to match objects around them. Flatfish are well concealed on flat substrates, while stonefish resemble the structurally complex environments in which they live (Marshall and Johnsen, 2011). In general, however, animals have constraints on how much they can vary their body shape, which means that they cannot always match their 3D surroundings with their body shape. Instead, they evolve patterns that act as pictorial cues that deceive the visual depth perception of their adversaries, which would otherwise make them easily visible; for example, countershading (Osorio and Cuthill, 2015). The most protean of animals, the shallow-water benthic octopuses (Hanlon et al., 1999), are an exception in being able to change their shape for concealment. Like octopuses, cuttlefish are cephalopod molluscs that use rapid dynamic camouflage that is visually driven, but unlike octopuses they are constrained by their basic shape. European cuttlefish, *Sepia officinalis*, can vary the expression of about 50 components that make up their overall body pattern and texture (Hanlon and Messenger, 1988), and so have the potential to produce a vast number of composite patterns. These patterns have been placed into three main categories: Uniform (with negligible contrast), Mottle (small patches with small contrast) and Disruptive (larger components and shapes with contrasts between them) (Hanlon and Messenger, 1998; Hanlon et al., 2007).

Some aspects of cuttlefish camouflage seem straightforward; for example, they approximately match the mean intensity of uniform surfaces (Hanlon and Messenger, 1988) and can express components in their body patterns that resemble objects in the surroundings. Notably the 'white square' component at the centre of the mantle is used when the background contains high-contrast objects that approximately match the surface area of the white square (Barbosa et al., 2008). However, cuttlefish cannot match every type of background or object, and 3D objects smaller than their body pose a particular problem. In such cases, inconsistencies between their form and objects in the background will make them conspicuous. One solution would be to resemble the 2D image as seen either by the cuttlefish itself or by a predator passing overhead. Alternatively, the cuttlefish might sense the 3D form of the objects in their surroundings, and respond with a different type of body pattern, perhaps suited to defence against predators that can use depth perception to break camouflage.

The cuttlefish's dynamic camouflage gives the opportunity to explore both what it is visually perceiving from available cues and the more general cognitive strategy that underlies camouflage selection. One possibility is that the cuttlefish simply chooses a pattern that is a direct physical match to the 2D image on its retina. Alternatively, camouflage selection might be a two-stage process in which the cuttlefish first evaluates the physical composition of its surroundings and then chooses a suitable pattern (Kelman et al., 2008). When we classify objects – for example, as chairs or sofas – we make categorical decisions (Harnad, 1987), and there is evidence that cuttlefish camouflage operates in a similar way. Studies have shown that there are thresholds of visual stimuli that trigger certain responses; the sizes and aspect ratios of black and white contrasts needed to elicit a white square response (Chiao and Hanlon, 2001b), and the patch

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size on a uniform background needed to elicit a response in a moving cuttlefish (Josef et al., 2017). Cuttlefish are able to switch from background matching and being cryptic to masquerading as an inedible object. In such conditions, camouflaging as an average visual aspect of the scene would break the camouflage, as it would look neither like the background nor like another present object; hence, there could be thresholds between visual cues that trigger camouflage responses to switch directly from one to the other. As prey, it would be most adaptive to develop camouflage thresholds that are similarly sensitive to the visual cues that will be noticed by the eyes of the predators (Josef et al., 2017). An analogous phenomenon was noted when the cuttlefish was on a uniform background scene containing only one object about the size of its mantle, where a choice needed to be made between matching the background or resembling the object. Buresch et al. (2011) found that the cuttlefish resembled the object, and hence masqueraded instead of matching the background, only when the object was in high contrast to the background, again suggesting threshold triggers that could be engaging both primary visual attention and the camouflage response.

The recovery of visual depth from the 2D retinal image exemplifies the ability of the visual system to integrate multiple sources of information (Gregory, 2015; Marr, 1982). Humans combine direct measures of stereo-disparity and motion parallax with more subtle pictorial cues such as occlusion, shading, perspective and size (Gregory, 2015). Findings that non-human animals have similar abilities (Aust and Huber, 2006) pose questions about how far our visual perception is dependent on specific neural systems, especially the cerebral cortex. Comparisons are especially interesting for cephalopods, where advanced vision has evolved independently of that in vertebrates (Zylinski et al., 2012, 2009b).

Animals could potentially sense visual depth through direct measures including stereopsis, parallax and focus (for example with a W-shaped lens; Mäthger et al., 2013), and also by pictorial cues such as shading and perspective. It is clear that cuttlefish can sense depth; they use stereopsis for prey capture (Feord et al., 2020; Messenger, 1968), depth in backgrounds affects camouflage (Kelman et al., 2008), and they can use illumination and shading as depth cues (Zylinski et al., 2016). Kelman and co-workers (2008) found that cuttlefish could visually distinguish backgrounds that were composed of real 3D pebbles from photographs of the same pebbles and, interestingly, that the response to physical depth of this kind was abolished by a ‘counterfactual’ pictorial cue – where dark surfaces lay above light ones. It is, however, unknown how cuttlefish use depth information for camouflage in scenes with pronounced 3D relief, or whether cast attached shadows are perceived as a depth cue. Shading on objects is a cue that is distinct from actual shadows on surfaces that are caused by objects. Cast shadows are shadows that are formed because an object obstructs the light. These shadows can be attached to the object, beginning from the edge of the object, or they can be unattached; for example, when an object is raised from a surface.

Cuttlefish appear to use pictorial shading within objects as a cue to physical depth and surface curvature (Zylinski et al., 2016), as do other non-human animals including pigeons (Cook et al., 2012) and chimpanzees (Imura and Tomonaga, 2003). Human infants use virtual cast shadows as a depth cue from the age of 7 months (Yonas and Granrud, 2006). There are species differences; in a study presenting Pacman shapes occluding circles with or without virtual cast shadows, humans could see the Pacman shape, and hence depth, when it was accompanied by a cast shadow, while chimpanzees were unable to make this distinction (Tomonaga and Imura, 2010). They speculate that chimpanzees see shadows as separate from the objects that cast them, and not as a depth cue. However, macaques do appear to recognise real cast shadows – and depth information from the shadows – when the shadows are moving (Mizutani et al., 2015). It is therefore interesting to ask whether cuttlefish use real stationary cast shadows of 3D objects, as well as virtual cast shadows, as a depth cue or whether they visualise them as something else.

To investigate their visual perception of 3D stimuli and camouflage response, we tested how cuttlefish react to 3D form by assessing their camouflage body pattern responses to objects of different heights. The objects were of a diameter within the range predicted to elicit the expression of the Disruptive body pattern in the 2D form (40–120% of the white square) (Barbosa et al., 2008, 2007). We also tested the effects of cast shadows and of visual contrast between the objects and background, and compared responses to 2D patterns that correspond to the 3D backgrounds (with and without virtual representative cast shadows) when viewed from above.

MATERIALS AND METHODS

Cuttlefish

Twenty European cuttlefish, *Sepia officinalis* Linnaeus 1758, were reared from eggs laid on lobster pots by wild stocks off the coast of Sussex, UK, at the Brighton Sea Life Centre (see Kelman et al., 2007). The conditions were consistent with best practice for this species (Fiorito et al., 2015). This was a behavioural study that did not cause any harm or distress to the animals and was approved by the committee at the Sea Life Centre in Brighton (Merlin Entertainments) where the experiment was held.

Animals were held in continuous-flow, natural seawater holding tanks (100×50×75 cm) with dividers, each of which contained 10 individuals, and were fed live shrimp daily. The juvenile animals tested, 4–5 months post-hatching of unknown sex, had mantle lengths ranging from 47 to 81 mm. Experiments were conducted in a 900×750 mm tank containing 50 l of water. For each trial, individuals were introduced one at a time into a clear Perspex arena 25 cm in diameter and 15 cm deep that contained one of the 14 visual treatments, and then returned to a third divider in the holding tank after the period of observation. Seawater was refreshed in the arena for each individual and 10 cuttlefish were observed for each experimental treatment (on the rare occasions that they showed any signs of stress, they were returned to the holding tank, and could not be photographed). Each cuttlefish was given at least 1 day to rest between each observation. A minimum sample size of 8–10 was expected to show camouflage trends and establish statistically significant effects of the experimental treatment on the animals' camouflage behaviour.

Experimental backgrounds

Experimental backgrounds were designed to test responses to backgrounds containing 3D objects presenting high and minimal visual contrast with the (uniform) substrate, and with and without cast shadows, and to compare them with 2D patterns that were visually similar in plan-view.

2D shapes of a similar plan-view size to the white square of the cuttlefish induce the expression of the white square, so in order to test the visual sensitivity to 3D form and shadows, we used clay cylinders with a similar diameter (15 mm) to the white square of the experimental cuttlefish. These were either 15 or 30 mm in height. To test whether the degree of contrast affected responses, we used grey cylinders on a grey background (contrast 0.05) and white on grey (contrast 0.39) for the 15 mm height. Backgrounds comprised alternating grids, with a spacing of 60 mm between cylinders or circles, measuring a total of 300×420 mm, and extended beyond the walls of the Perspex arena. The arena was illuminated with an LED light that yielded approximately 20 lx (RS-105 light meter). To test the effects of cast shadows, the illumination angle was either directly overhead (0 deg to the vertical), giving minimal shadow, or from 60 deg to the vertical to cast prominent attached shadows of the same length between the grey and white cylinders and longer shadows from the taller 30 mm cylinders.

We further tested 2D treatments that replicated the plan view of each 3D treatment. These consisted of flat white spots of the same 15 mm diameter, and then the same white spots with added black illustrations of attached shadows with the average length measured of the real shadows (of both the 15 and the 30 mm cylinders). Plain grey backgrounds were used as controls and all treatments (including the 2D ones) were tested with light from above and also obliquely from the side, resulting in 14 treatments (Fig. 1) with 10 animals drawn randomly from the pool of 20 for each.

Analyses

The level of expression of 36 body pattern components was scored by eye, blind to the experimental treatment (by A.E.N.). Cuttlefish images were cropped from their backgrounds, and orientated to face left for consistency (Corel PaintShop Pro X6). Images were scored blind by assigning each image a random file number. The 36 body pattern components (Fig. 2; Hanlon and Messenger, 1988) were scored on a 4-point scale (0–3), where 3=fully expressed and 0=absent. We checked the consistency of the 4-point scale scores by re-scoring a randomly selected subset of 20% of the images. This check found an 80% match to the original scores.

Body pattern component scores were then subjected to principal component analysis (PCA) with a varimax rotation (Vegan package, R v.3.1.0; Oksanen et al., 2007). Eigenvectors were inverted to aid interpretation. The first four principal components (PCs) were retained (Fig. 2) as they accounted for 60% of the variation in the original dataset (40%, 8%, 6% and 6%, respectively). The PCs can

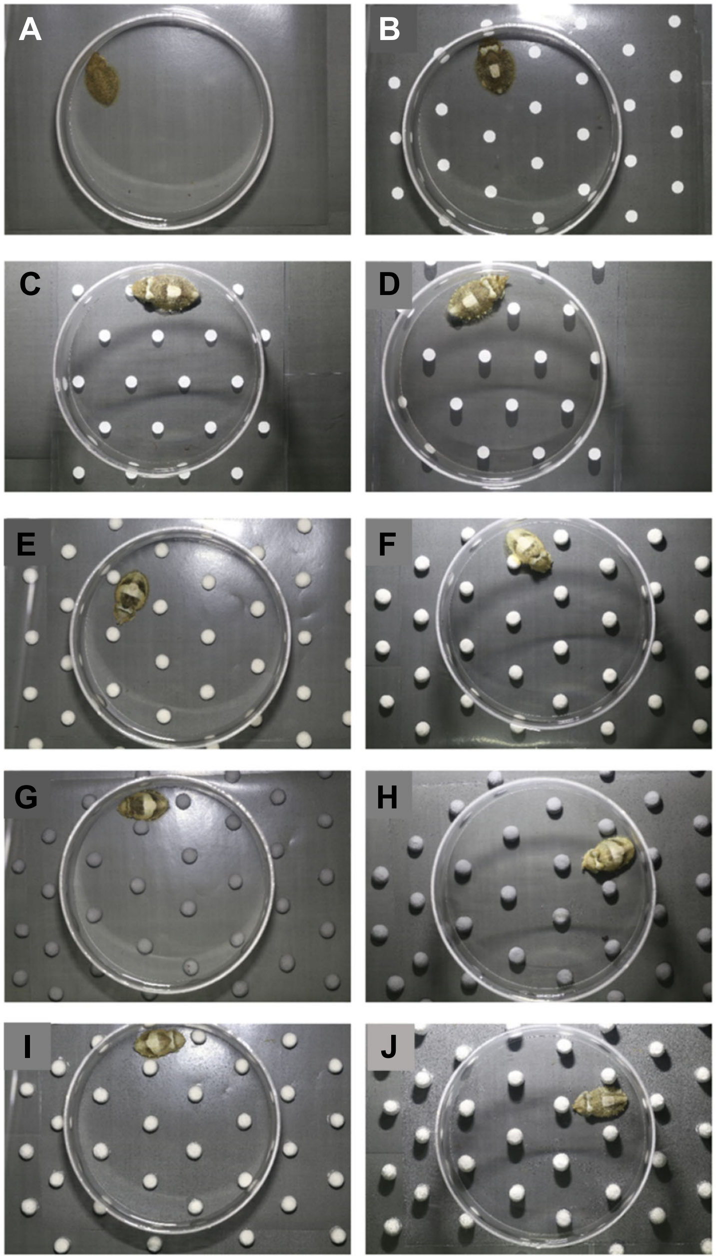
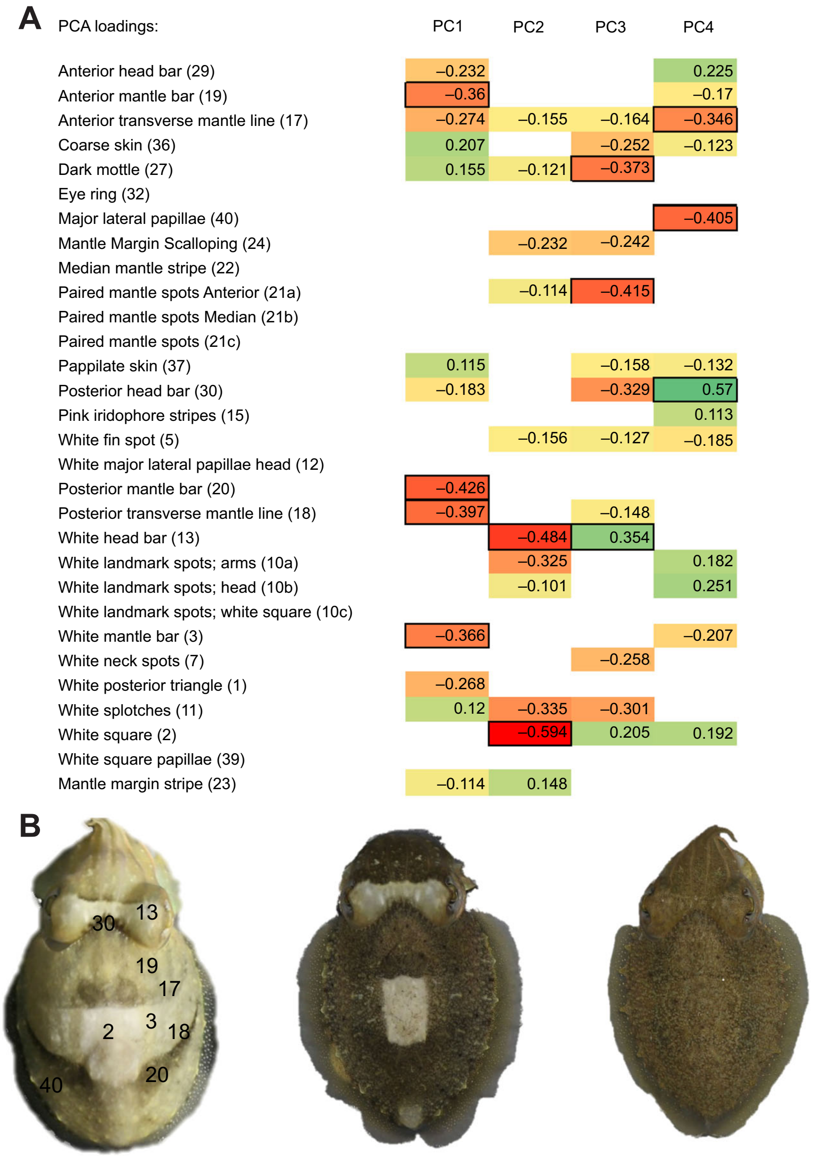


Fig. 1. Experimental backgrounds and the cuttlefish patterning response. (A) Uniform grey; (B) 2D white spots; (C) 2D white spots with average shadow replicas of the 3D 15 mm cylinders; (D) 2D white spots with average shadow replicas of the 3D 30 mm cylinders; (E) 15 mm white cylinders lit from above; (F) 15 mm white cylinders lit obliquely; (G) 15 mm grey moulds lit from above; (H) 15 mm grey moulds lit obliquely; (I) 30 mm white cylinders lit from above; (J) 30 mm white cylinders lit obliquely. The 2D conditions A–D were tested with overhead and oblique illumination, giving 14 conditions in all.



A PCA loadings:

	PC1	PC2	PC3	PC4
Anterior head bar (29)	−0.232			0.225
Anterior mantle bar (19)	−0.36			−0.17
Anterior transverse mantle line (17)	−0.274	−0.155	−0.164	−0.346
Coarse skin (36)	0.207		−0.252	−0.123
Dark mottle (27)	0.155	−0.121	−0.373	
Eye ring (32)				
Major lateral papillae (40)				−0.405
Mantle Margin Scalloping (24)		−0.232	−0.242	
Median mantle stripe (22)				
Paired mantle spots Anterior (21a)		−0.114	−0.415	
Paired mantle spots Median (21b)				
Paired mantle spots (21c)				
Pappilate skin (37)	0.115		−0.158	−0.132
Posterior head bar (30)	−0.183		−0.329	0.57
Pink iridophore stripes (15)				0.113
White fin spot (5)		−0.156	−0.127	−0.185
White major lateral papillae head (12)				
Posterior mantle bar (20)	−0.426			
Posterior transverse mantle line (18)	−0.397		−0.148	
White head bar (13)		−0.484	0.354	
White landmark spots; arms (10a)		−0.325		0.182
White landmark spots; head (10b)		−0.101		0.251
White landmark spots; white square (10c)				
White mantle bar (3)	−0.366			−0.207
White neck spots (7)			−0.258	
White posterior triangle (1)	−0.268			
White splotches (11)	0.12	−0.335	−0.301	
White square (2)		−0.594	0.205	0.192
White square papillae (39)				
Mantle margin stripe (23)	−0.114	0.148		

Fig. 2. Principal components analysis (PCA) of cuttlefish body pattern. (A) Loadings of the pattern components scored on the four principal components (PCs) that accounted for 60% of the variation in the patterns displayed across all 14 treatments in this study. Ten animals were tested in each treatment. Scores refer to loadings of each component on the relevant PC. Notably, PC1 was associated with low expression of the anterior and posterior mantle bars and the transverse mantle line. PC1 expression was reduced in the presence of 3D objects compared with the 2D controls (Fig. 3). (B) Left: a cuttlefish displaying the 3D pattern, illustrating several of the pattern components (numbered after Hanlon and Messenger, 1988) most visible in the pattern it displays in response to 3D form. Middle: an example of the white square pattern expressed in 2D backgrounds with flat white circles of the same diameter. Right: a typical 'uniform' pattern expressed on uniform grey backgrounds.

be simply regarded as orthogonal measures of the animals' coloration patterns, which account for the maximum possible proportion of the variance in the patterns with a given number of factors. Most of the experimentally relevant variation was represented by PC1 and PC2 (Fig. 3).

To ascertain the multivariate difference in expressed patterns between treatments, a MANOVA (R v.3.1.0) was carried out with the PCA scores of these four components. Following that, pairwise MANOVA comparisons were conducted as *post hoc* tests to check for differences between specific treatments.

To test for the effect of 3D form, comparisons were made between 3D and 2D backgrounds, and 15 mm 3D and 30 mm 3D heights. To test for the effect of contrast, a multivariate pairwise test was made between the grey and white objects. To test for the effect of lighting, the lighting regime (overhead or oblique) was compared between 2D contrast backgrounds and 2D shadow representation backgrounds. Finally, to test for the effect of shadows, 3D backgrounds with and without shadows were tested. A Bonferroni correction was applied.

In order to compare contrasts, the reflectance luminance of the grey background, the white and grey modelling clay moulds and two of the 2D backgrounds (one with white spots, and one with white spots and representative shadows) were taken with an RS-105 light meter. Weber contrast was calculated with the standard equation ($(I-I_b)/I_b$ where I is the luminance, and I_b is the luminance of the background.

RESULTS

Of the 36 pattern components that were scored on cuttlefish, 24 were identified in the four principal components that accounted for 60% of the variation (Figs 1 and 2), and hence were affected by the experimental treatment (Fig. 2). PC1, which represented 40% of the variation from the original dataset, was characterised by high positive loadings on the posterior mantle bar and posterior transverse mantle line, while PC2, which represents 8% of the variation, was characterised by high positive loadings on the white square and white head bar (Fig. 2). Expression of the mantle bar gives a pictorial illusion of depth on the cuttlefish body (at least to the human eye). PC3 (6% of the original data set) was positively associated with some skin texture components (e.g. coarse skin and papillate skin) and some smaller pattern components (e.g. white neck spots and white landmark spots). PC4 (also 6% of the

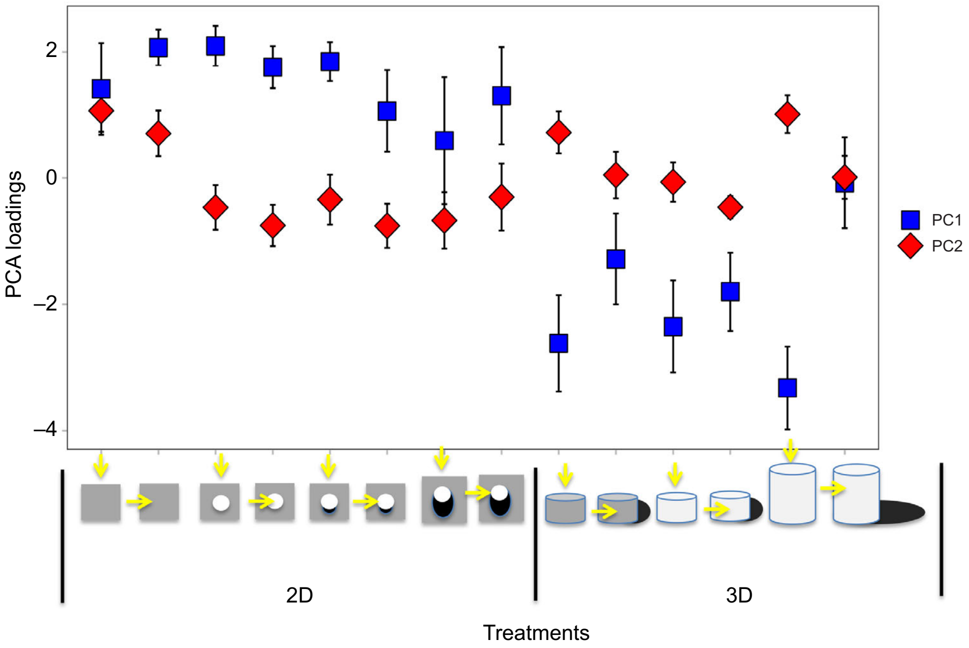


Fig. 3. Graph of the PCA loadings of PC1 and PC2 for all the treatments. The yellow arrows show the direction of the light: either from above or shining obliquely, as illustrated here as from the side. PC1 and PC2 loadings switch depending on whether the backgrounds are 2D or 3D: PC1 (with its associated body pattern components) is expressed more highly than PC2 through the 2D patterns, but the situation is reversed for the backgrounds with 3D relief, except when the attached cast shadow is most pronounced (last treatment on the right), where there was no significant difference between the two components.

original dataset) was positively associated with several pattern components also positively associated with PC1, but negatively associated with others (e.g. anterior head bar and posterior head bar).

Pairwise MANOVA comparisons revealed that all four PC score patterns were highly significantly different between 2D and 3D treatments ($P<0.00001$), and not significant between 15 and 30 mm cylinders ($P=0.09$, 0.45, 0.68) or different contrasts (15 mm white on grey compared with 15 mm grey on grey: $P=0.16$, 0.09, including both light directions). This indicates that 3D relief has a strong effect on the camouflage response and pattern of the cuttlefish. Lighting direction on 2D contrast backgrounds made no significant difference ($P=0.12$–0.77). The presence of cast shadows made no significant difference to the patterns in response to the 3D 15 mm cylinders ($P=0.09$, 0.68). However, there was a pairwise significant difference between shadow and no shadow for the 30 mm cylinder ($P=0.005$). The patterns displayed in the 30 mm 3D shadow treatment were similar to those in response to the 2D treatment with white circles and black long shadows; PC1 and PC2 overlapped for this treatment (see Fig. 3).

DISCUSSION

We examined two factors in order to understand how cuttlefish visually perceive depth and their camouflage response; namely, 3D relief and attached cast shadows.

In response to a grid of 15 mm diameter cylinders (which is around the same area of the white square component of these animals), cuttlefish expressed a specific type of pattern, characterised by a strong dark posterior mantle bar (Fig. 2B, left, component 20). We called this pattern the 3D body pattern. This pattern was significantly different to those expressed in 2D backgrounds, but that would otherwise be classed as the ‘Disruptive’ pattern (with larger components and shapes with contrasts between them). Expression of the 3D body pattern was unaffected by the contrast of the objects against the background, whereas the contrast in camouflage patterns expressed on 2D backgrounds tends to scale with the contrast of the background (Kelman et al., 2007; Mäthger et al., 2006; Zylinski et al., 2009a). The strength of the cast shadow did not affect camouflage pattern expression for cylinders, except when the tall cylinder cast a strong shadow, in which case the expression of the posterior mantle bar was reduced so that the body pattern was more similar to the Disruptive pattern, which is typically expressed on flat backgrounds. By comparison, on 2D patterns that resembled the 3D backgrounds viewed from above, the strong dark mantle bar was negatively weighted and, as expected, animals displayed a Disruptive type of body pattern (Barbosa et al., 2007; Chiao and Hanlon, 2001a; Zylinski et al., 2012, 2009a). The 3D pattern has visual similarities with the Disruptive pattern; both include large high-contrast components, and juxtapose light and dark markings, but the 3D pattern additionally gives an illusion of depth (to the human eye) (see Fig. 1B–D for the Disruptive pattern, and Fig. 1E–I for the 3D pattern). These markings include the dark posterior mantle bar with the light transverse mantle line, the posterior head bar, and the anterior paired mantle spots.

To our knowledge variants of the Disruptive pattern are expressed for a wide range of flat backgrounds in laboratory conditions (e.g. Barbosa et al., 2007; Chiao and Hanlon, 2001a; Zylinski et al., 2012, 2009a), while the 3D pattern has not been reported as a characteristic response to any 2D backgrounds. Natural environment backgrounds are rarely simple, and the cuttlefish mix these basic body patterns in ways that remain poorly understood. The insensitivity of the 3D pattern to object–background contrast and shadow implies that the animals are indeed expressing this pattern in response to the 3D environment, rather than simply matching the 2D image in the retina.

Cast shadows can be visually perceived as shadows by other animals (Mizutani et al., 2015; Yonas and Granrud, 2006). When presented with a long cast shadow produced by a side light on the tall 3D cylinders, the cuttlefish chose a camouflage pattern that was the same as the one they produced over a completely flat 2D image of white circles and printed black virtual replicates of the shadows (Fig. 1J). This suggests that the cuttlefish perceive the stationary shadows not as complementary depth cues, but purely as low frequencies of light similar or equal to the printed black analogous shapes. Moreover, they ignore the presence of these shadows until they become large enough. Then they factor this into their patterns, but lose the distinctive 3D pattern by instead assuming a more general Disruptive pattern displayed in high-contrast 2D environments (compare Fig. 1D and J). This fits into the model that camouflage is a two-stage process governed by thresholds (Buresch et al., 2011; Chiao and Hanlon, 2001a; Josef et al., 2017) as both 3D cues and low-light frequencies are present in this particular background, but the abundance of low-light areas triggers a more suitable camouflage response over the presence of 3D relief. Buresch et al. (2011) found that a single 3D object on a flat surface causes a relevant change of camouflage reaction only if it is in high contrast to the background. In our present study, low-contrast 3D cylinders (grey cylinders on a grey background) were interpreted equally by the cuttlefish to the high contrast white 3D cylinders on a grey background. The objects used by Buresch et al. (2011) were, however, bigger than the white square of the animals – about the size of the whole mantle of the animal – and were presented as only one object at a time in an otherwise uniform scene. Thresholds of size, abundance, 3D form and contrasts are all likely to compete to trigger an adaptive response in order to be less noticeable in a given scene (Josef et al., 2017), with some degree of variation and plasticity to fit within each category as much as possible.

We know that *S. officinalis* may perceive depth through direct depth cues (stereo or motion parallax; Feord et al., 2020; Kelman et al., 2008; Messenger, 1968), and shading as a pictorial cue (Zylinski et al., 2016). In this present study, we found that cast attached stationary shadows are not depth cues for this cephalopod. Further studies will reveal what other cues may be used; perhaps visual cues such as texture differences, polarized light or specular highlights may play a part in visual depth perception in cuttlefish.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.E.N., D.O., S.Z.; Methodology: A.E.N.; Validation: A.E.N.; Formal analysis: A.E.N.; Investigation: A.E.N.; Resources: A.E.N., D.O.; Writing - original draft: A.E.N.; Writing - review & editing: A.E.N., D.O., S.Z., S.S.; Visualization: A.E.N.; Supervision: S.S.; Funding acquisition: S.Z.

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