Cuttlefish responses to visual orientation of substrates, water flow and a model of motion camouflage

A. J. Shohet[1], R. J. Baddeley[2], J. C. Anderson, E. J. Kelman and D. Osorio*

School of Life Sciences, University of Sussex, Falmer, Brighton, BN1 9QG, UK

[1]Present address: Smart Materials Group, QinetiQ, Cody Technology Park, Ively Road, Farnborough, Hampshire GU14 0LX, UK
[2]Present address: Department of Experimental Psychology, Social Sciences Complex, 8 Woodland Road, Clifton, Bristol, BS8 1TN, UK
*Author for correspondence (e-mail: d.osorio@sussex.ac.uk)

Summary

Low-level mechanisms in vertebrate vision are sensitive to line orientation. Here we investigate orientation sensitivity in the cuttlefish *Sepia pharaonis*, by allowing animals to settle on stripe patterns. When camouflaging themselves cuttlefish are known to be sensitive to image parameters such as contrast and spatial scale, but we find no effect of background orientation on the patterns displayed. It is nonetheless clear that the animals see orientation, because they prefer to rest with the body-axis perpendicular to the stripes. We consider three possible mechanisms to account for this behaviour. Firstly, that the body patterns are themselves oriented, and that the cuttlefish align themselves to aid static camouflage. This is unlikely, as the patterns displayed have no dominant orientation at any spatial scale. A second possibility is that motion camouflage favours alignment of the body orthogonal to background stripes, and we suggest how this alignment can minimise motion signals produced by occlusion. Thirdly we show that cuttlefish prefer to rest with their body-axis parallel to the water flow, and it is possible that they use visual patterns such as sand ripples to determine water flow.

Key words: *Sepia*, cephalopod, orientation, motion camouflage, vision.

Introduction

It is readily apparent that an animal's camouflage pattern can give insight into visual mechanisms of its adversaries (Osorio and Srinivasan, 1991; Stevens and Cuthill, 2006). For species such as cuttlefish *Sepia* spp. that can control the expression of coloration patterns one can also study their own perception. For example by looking at the effects of adjusting a specific cue or image parameter on the patterns expressed (Chiao and Hanlon, 2001a,b; Mäthger et al., 2006). This study considers cuttlefish visual behaviour of from both points of view. We ask what the animals can see, and how they use this information. Camouflage is often studied with respect to static images features, such as colour and texture, edges and shape, but motion is a highly salient visual cue. Regardless of the accuracy of the match to a background, motion will often break camouflage (Julesz, 1971). This raises the question of whether there is any strategy of motion camouflage, other than remaining stationary relative to the background (Srinivasan and Davey, 1995; Mitzutani et al., 2005). A simple possibility is that stripes aligned with the direction of motion would give a weak motion signal. In the light of these questions about visual perception and camouflage this study investigates orientation sensitivity of cuttlefish.

The eyes and the visual behaviour of cephalopod molluscs have much in common with those of fish. Thus *Octopus* uses a broad array of features to recognize objects (Hanlon and Messenger, 1996), whereas the cuttlefish *Sepia officinalis* shows size constancy when selecting prey (Messenger, 1977). In addition to tests of object recognition, a natural way to investigate cephalopod vision is *via* their visual polymorphism or 'polyphenism', which allows a complete change of body pattern in less than a second (Hanlon and Messenger, 1988; Hanlon et al., 1999; Chiao and Hanlon, 2001a,b; Messenger, 2001). In particular one can ask how cuttlefish (*Sepia* spp.), which often lie on the sea-bed rather like flatfish, alter their appearance according to the background substrate. Under these conditions the patterns adopted by juveniles at rest are probably cryptic, although this is hard to prove (Kelman et al., 2006).

In visual psychology a central idea is that neural codes represent images by a small number of parameters. Best known are the primary visual cortices of cats and monkeys where neurons encode spatial location, spatial scale, colour, contrast, stereo, motion and orientation (Hubel, 1988). It is, therefore, natural to ask if cephalopods use similar measures. Many cephalopods, including *Sepia officinalis*, lack colour vision (Marshall and Messenger, 1996; Mäthger et al., 2006), but, unsurprisingly, they are sensitive to achromatic contrast (Chiao
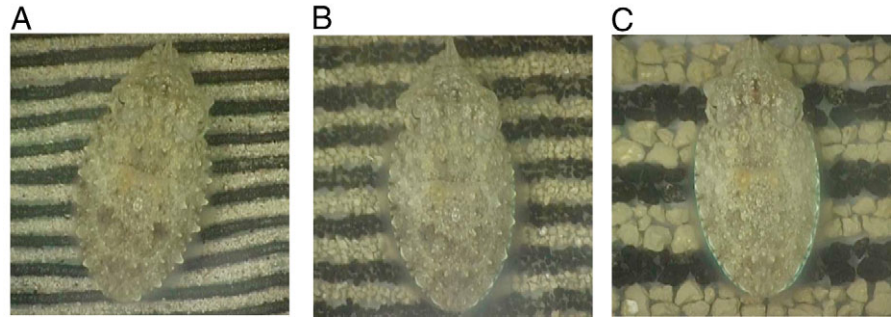
Fig. 1. Images of cuttlefish resting on backgrounds: (A) fine, (B) medium and (C) coarse.

and Hanlon, 2001a; Chiao and Hanlon, 2001b; Mäthger et al., 2006). We do not know of tests of stereovision, motion or orientation sensitivity in cuttlefish, but octopus can learn the orientation of a line (Wells, 1960).

This paper reports on orientation sensitivity of cuttlefish lying on striped backgrounds (Fig. 1). Two types of response are of interest: orientation dependence of the body pattern, or orientation dependence in body position. It turns out that the animals detect orientation but do not use this control the expression of body patterns. Instead they prefer to lie with their body axis perpendicular to the stripes. This behaviour is consistent with visual information being used to orient parallel to the water flow, and we show that cuttlefish do indeed orient in this way. To conclude, we discuss further the significance of the cuttlefishes' behaviour with regard to camouflage on oriented backgrounds, and also for motion camouflage.

Materials and methods
Visual responses to orientation

Five juvenile, Pharaoh cuttlefish *Sepia pharaonis* Ehrenberg (mean mantle length 8 cm) were reared from eggs supplied by the National Resource Centre for Cephalpods (Galveston, TX, USA), and maintained at the Brighton Sea Life Centre (Brighton, UK). The animals were held in a circular tank 1.2 m in diameter, with 0.6 m depth of seawater pumped from offshore. *S. pharaonis* is a tropical species and the temperature was held at 23°C with a 12 h:12 h L:D lighting regime. They were fed *ad libitum* on mysid (*Mysis* sp.) and ghost shrimps, (*Natantia* sp.). Eighty percent of the water was changed daily, and concentrations of nitrite, nitrate and ammonia were at nominal background levels. Animals were 8 weeks old at the beginning of the experiments.

Five cuttlefish were tested twelve times each on three different backgrounds (Fig. 1), which were presented in a random order. When we were filming the water was reduced to a depth of 0.25 m. We placed individual cuttlefish into a circular filming arena (0.6 m diameter, 0.3 m height) of opaque white plastic that lay within the holding tank. To minimise cast shadows three 150 W halogen floodlights were spaced equally around the arena. Backgrounds, randomised for design and orientation, were placed underneath the arena, and the animal left to acclimatise for at least 10 mins. The cuttlefish was allowed to settle on the substrate until it was expressing a

consistent camouflage pattern. A still image was then taken with a digital video camera (Canon XL-1) from directly above (Fig. 1). The process was repeated to give a set of images for each animal on each of the three backgrounds. To ensure that we studied each animal once, after filming the cuttlefish was then moved to a separate holding tank.

Experimental backgrounds were made of three substrate types fixed onto 0.5 m^2 Perspex sheets by aquarium sealant (Geocel Ltd, UK). Substrates were either 1 mm diameter: 'fine'; 3 mm: 'medium'; or 9 mm: 'coarse'. The particles were coloured either black or beige with pond paint. Each background consisted of alternating black and beige stripes of equal width (Fig. 1). The period of the patterns were 5 mm for sand, 15 mm for gravel and 45 mm for pebble.

Image analysis

The study produced 180 images (one image of each cuttlefish ✕ 12 trials ✕ 3 backgrounds ✕ 5 cuttlefish). The orientation of the animal with respect to the background was given by the acute angle between the longitudinal midline of the cuttlefish and the longitudinal direction of the background stripes.

Warping

The images were, by necessity, taken from multiple points of view, and the animals vary in size, and can stretch and twist their skin. To deal with these distortions and hence to allow point-by-point comparisons of the body patterns, images were warped (by bi-cubic interpolation) to a standardised reference frame by placing a mesh of 14 reference points on the image of the cuttlefish (Anderson et al., 2003). After warping, each image was converted to a matrix (385✕287) of pixel intensity values and filtered by convolution with a Gaussian filter (see Appendix). We did not analyse the pattern on the head.

A number of points are relevant. Firstly, warping is critical: small inaccuracies give substantial artefacts along luminance boundaries, even between identical images. Luckily these registration artefacts are easy to spot. Secondly, any errors are caused mainly by inaccuracies in the location of reference point, rather than the warping algorithm. Thirdly, warping is very good at interpolation, but less good at extrapolation, which means that information about the pattern at the edge of the animal should be treated with caution.
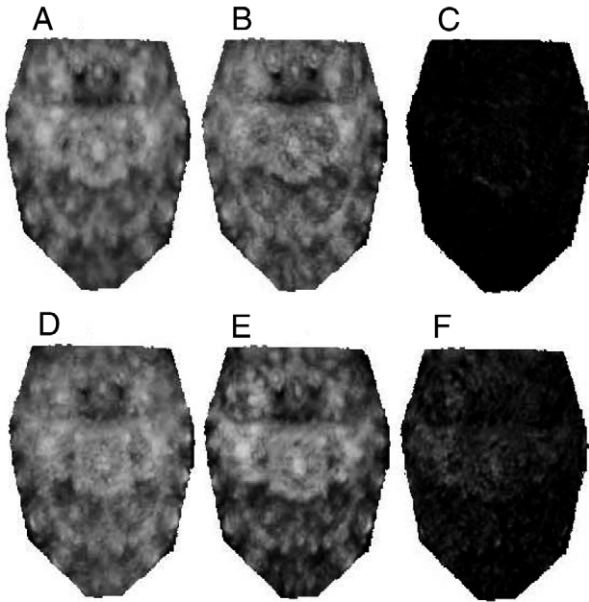

Fig. 2. Evidence that there is no systematic effect of orientation relative to background on the coloration patterns expressed by cuttlefish. Upper row: Average images of all cuttlefish camouflaging (A) parallel and (B) perpendicular to the small-scale background and, (C) the mean difference between these two sets of patterns. Lower row: average images of cuttlefish camouflaging (D) parallel and (E) perpendicular to the medium background and (F) the mean difference between these two sets of patterns. Differences were even smaller for the coarse stripes.

Statistics

To visualise the effect of background orientation on the body pattern, we need: (a) to average all the images where the animal lay parallel (1–30°) to the background stripes ($<I_{parallel}>$; Fig. 2A); (b) to average all the images where the animal lay at right-angles (61–90°) to the background stripes ($<I_{perpendicular}>$; Fig. 2B), and (c) to estimate the difference between them ($<I_{parallel}> - <I_{perpendicular}>$; Fig. 2C). This creates a difference-image where positive values indicate regions that were brighter when the animal was lying parallel, and darker regions represent locations where the skin was darker when the animal was lying parallel to the background stripes. This analysis identifies possible effects of orientation, but does not distinguish real structure from random variation. Moreover, the magnitude of this difference signal is not a good criterion for identifying statistically significant effects, since it ignores variability. Therefore, as well as the difference image, a t-statistic image (I^t) is created where the value of each pixel is simply the difference image, divided by the estimated standard deviation at that location.

$$I^t = \frac{|<I_{parallel}> - <I_{perpendicular}>|}{\sqrt{\frac{1}{2}}\sqrt{\sigma(I_{parallel})^2 + \sigma(I_{perpendicular})^2}} ,$$

where $\sigma(I_{parallel})$ is the standard deviation of the images where the animal was parallel to the stripes, and $\sigma(I_{perpendicular})$ is the

standard deviation where the animal was perpendicular to the stripes, and |.| represents the absolute function.

To distinguish responses to the stimulus orientation from random variation we explicitly calculated the magnitude of effects one would expect to encounter simply due to random effects using a permutation test {also called a randomization test, re-randomization test, or an exact test [for an example of its application to spatial data, see Holmes et al. (Holmes et al., 1996)]}. This works by calculating the sampling distribution of the largest difference between the two conditions, under the null hypothesis that there is no difference. This is done by randomly splitting the data into two sets and calculating the maximum difference between the average images in the two sets (e.g. it estimates the magnitude of the difference expected if the was no difference in the two conditions). By repeating this process a large number of times, an estimate of sampling distribution under the Null hypothesis can be generated, and hence an appropriate threshold for 95% significance. To calculate an appropriate significance threshold, the data are randomly split into two equally sized groups. Using this random split, the maximum t statistic in the resulting t image is calculated. To get an estimate of the distribution of the maximum values due to chance, this process of splitting the data into two random groups, and calculating the maximum value of the t image was repeated 1000 times. Given 1000 maximum values, an appropriate 0.05 significance threshold can be calculated by ordering these values in terms of increasing magnitude, and setting the threshold to the 95 percentile (the 950th value). This is a robust non-parametric significance test that takes account of the actual (potentially non-Gaussian) distribution of image values. This method also deals with the problems of within-image correlation and of correction for multiple comparisons.

Measuring orientation in cuttlefish body patterns

To determine whether the *S. pharaonis* coloration patterns contain orientation-specific structure that matches the background stripes, images of the cuttlefish were convolved with vertical and horizontal spatial filters (see Appendix). These filters were derived by differentiating a Gaussian distribution, either vertically or horizontally. A range of filter widths spanning the separation of the background stripes enabled us to detect structure at several spatial scales.

Orientation to water flow

Tests of orientation preference in water flow were done after the work on visual behaviour and, because *S. pharaonis* were no longer available, used ten juvenile common cuttlefish, *Sepia officinalis* (mean mantle length 60 mm). These two species of *Sepia* are much alike in their general behaviour and coloration patterns (e.g. Chiao and Hanlon, 2001a,b). Subjects were placed singly in a 560 mm×120 mm laminar flow chamber. An Eheim aquaball powerhead 1212 (Eheim Ltd, Germany) provided a recirculatory water flow, propelling water at one end and drawing water from the other at 80 mm s⁻¹. This flow rate (~0.3 km h⁻¹) is not high for tidal and wave currents in shallow

water. To control for the effects of the visual environment in the laboratory, water flow was at 0°, 90°, 180° and 270° to an arbitrary main axis in the tank.

Individual cuttlefish were placed in the laminar flow chamber, with no water flow and allowed to settle. A cuttlefish was deemed to be settled when all movement stopped, including fin undulation. The cuttlefish was then disturbed by rotating the chamber to the position of the desired direction of water flow. The flow was switched on and the animal allowed to settle. Orientation relative to the flow was measured after the cuttlefish had remained settled for 5 min.

Results and discussion

Estimating the quality of camouflage of the juvenile *Sepia pharaonis*, or indeed any animal, is difficult (Kelman et al., 2006). The patterns expressed were a reasonable match to the brightness and texture, but there was no obvious effect of the background stripe width (Fig. 1). Image analysis found no effect of orientation relative to the background on the patterns expressed (Fig. 2), nor was there any sign that the body patterns were themselves oriented (Fig. 3). The insensitivity to orientation in the background was puzzling. The same species, indeed the same animals, are clearly sensitive to spatial frequency and contrast of their background (Chiao and Hanlon, 2001a) (A.J.S., unpublished data).

Had we investigated only body patterns, the conclusion would be that *Sepia pharaonis* is insensitive to the orientation in the substrate. Given a predator sensitive to orientation, then it should be advantageous to generate body patterns that mimic the orientation structure of the substrate. Where backgrounds are themselves oriented (as with ripple patterns) it would seem sensible to use a similar camouflage pattern, but cuttlefish in our experiments do not do this. Nonetheless it is clear that the animals are sensitive to visual orientation, because on the medium and the fine stripes they align themselves across the stripes (Figs 1, 4; fine stripes: χ^2=15.8, d.f.=2, P<0.001; medium stripes: χ^2=19.3, d.f.=2, P<0.001). There was no such preference on the coarse background (Fig. 4; χ^2=1.7, d.f.=2, P=0.4). Since the null hypothesis is that all orientations are equally likely, a χ^2 test for independence of orientation and frequency is an appropriate statistic.

This presents a puzzle. The animals can see orientation but do not produce a cryptic pattern to match the oriented backgrounds. We can consider five possible reasons for this: (1) they are incapable of matching the orientation structure; (2) they naturally have anisotropic structure in their patterns, and can effectively camouflage themselves simply by rotating until this natural anisotropy matches the environment; (3) generating orientated patterns is not effective for camouflage; (4) this behaviour should not be understood in terms of static matching, but as a response to the more demanding problem of concealing movement; (5) orientation across stripes is beneficial for reasons other than camouflage.

The first possibility, that the cuttlefish cannot generate orientated patterns is implausible. Body pattern components such as the head bar are orientated, and are commonly used in (what we assume to be) cryptic coloration. So it is not that the animals *cannot* display orientated displays to match the background, but that they *do not*.

The second potential reason for the lack of orientation dependence is that normal camouflage displays have strongly orientated structure. Rather than generating a specific orientated pattern, animals could orientate so that their default pattern matches the background orientation. This is not the case. Fig. 3 shows that there are similar amounts of vertical and horizontal structure in the body patterns at the scale of the background substrate.

Fig. 3. The effect of applying horizontal and vertical spatial filters to representative images of a cuttlefish camouflaged perpendicular and parallel to the sand and gravel backgrounds (Fig. 1). Fine background (sand) – the horizontal filter (A) found no horizontal structure in the cuttlefish camouflage pattern (B) and the vertical filter (C) found no vertical structure in the cuttlefish camouflage pattern (D). For the medium background (gravel) – the horizontal filter (E) found no horizontal structure in cuttlefish camouflage pattern (F) and the vertical filter (G) found no vertical structure in cuttlefish camouflage pattern (H). This analysis was run for a range of filter widths; the images shown are those where the filtered scale most closely matched the width of background stripe, and so one might expect an effect of orientation on the pattern.
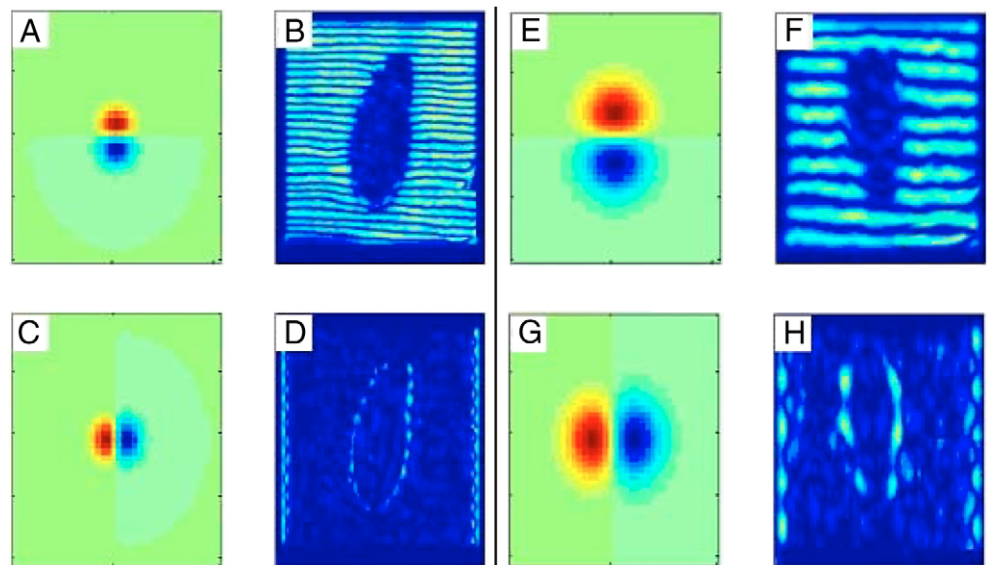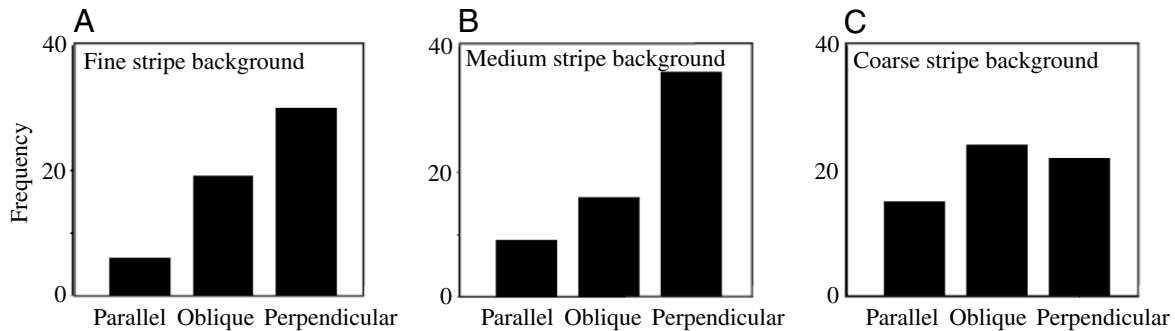
Fig. 4. The effect of applying horizontal and vertical spatial filters to representative images of a cuttlefish camouflaged perpendicular and parallel to the fine and medium backgrounds (see Fig. 1). The number of times in 60 tests that the five subjects settled at each of the three orientations relative to backgrounds: (A) fine, (B) medium and (C) coarse stripes.

The third possibility is that generating orientated structure is not desirable for camouflage (Fig. 5). Camouflage is excellent if the body pattern perfectly matches the background (Fig. 5A), but because small alignment errors generate highly visible corners and edges around the mantle, a less perfect match can be worse than having no pattern at all (Fig. 5B). If in addition to alignment errors, the spatial frequency and orientation are also poorly matched, the conspicuousness of the pattern is higher still (Fig. 5C). Matching the environment therefore may be risky: a small error can cause high visibility. Natural backgrounds are not as clearly striped as those in our experiments, but similar principles will apply to other types of cryptic camouflage.

A model of motion camouflage

The previous three hypotheses refer to static crypsis. This neglects the highly deleterious effects of motion on crypsis. Almost regardless of the coloration pattern, small movements will render animals highly visible. Visual motion reveals the form of an object, at least to human observers, and minimising its salience is essential to concealment, especially where water currents cause involuntary displacements.

In humans, detection of relative motion against a background greatly exceeds sensitivity to absolute motion [simply detecting that a feature has moved (Leibowitz, 1955)], and given the nature of the underlying task, the same almost certainly applies for the cuttlefish's predators. Consider two situations: for the detection of absolute motion one has to compensate for both self-motion, and the movement of one's eyes. All these processes are inherently noisy; a single bright light in a dark room appears to move because of this noise. Relative motion signals are not confounded by this noise. Also relevant to how motion affects camouflage is that the revealing and occlusion of the substrate gives a very large motion signal. Minimising movement occlusion will minimise the degradation of camouflage caused by movement.

Both these characteristics are relevant to camouflage on an oriented background. Even if the direction of motion is random, then as shown in Fig. 6, for an animal placed on a striped background, the main source of relative motion is along the edge of the animal aligned with the stripes. If the animal is longer than it is wide, then the relative motion signal is minimized when the body axis is orthogonal to the stripes, as we observed (Fig. 4). Minimising a relative motion signal may explain why the animals do not use stripes for camouflage. Stripes may give good camouflage when the animal is static, but relative motion of body pattern stripes against background stripes is likely to be conspicuous.

The effect of relative motion on camouflage could explain why orientated body patterns are not used, and also why the body-axis is held orthogonal to the background. However, a further possibility is that this posture will minimise involuntary movements. Near the shoreline, orientated structure has two main causes: shadows generated by waves and sand ripples

Fig. 5. Where camouflage relies on matching stripes on a body pattern to stripes in the background, mismatches due to small errors may severely compromise camouflage. (A) A cartoon of the camouflage situation faced by our cuttlefish, together with the optimal camouflage pattern (stripes that exactly match the substrate). If this were possible, it would be the best strategy. To achieve this perfect match, the animal needs to both accurately estimate the frequency, orientation and phase of the substrate, and also generate to a matching pattern. (B) Shows the results of a small error (10%) in estimating the frequency of the substrate. As can be seen, this small error results in highly visible structure around the cuttlefish. (C) Shows the result of a 10% error in frequency, phase and orientation. These small errors can result in a pattern that is more visible than one that either simply matched the average luminance, or employs a disruptive pattern.
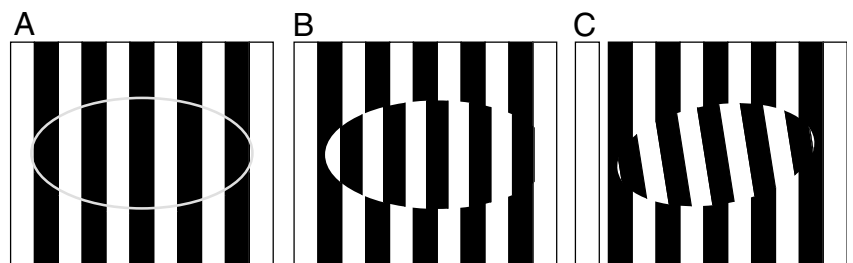
Fig. 6. The effect of motion on visibility. (A) An optimal static camouflage pattern where the pattern matches the background, and the orientation minimises the number of lines obscured. Unfortunately, if the animal moves, this pattern is far from optimal: the relative motion between the stripes on the animals back and the background is highly visible, and there is a strong relative motion signal together with occlusions along the side (marked by the arrows). (B) A pattern without stripes minimises motion signals. Further, orientating the body orthogonally to the substrate, the area of high relative motion and occlusion is minimised. (C) Sand ripples in the natural environment are oriented at 90° to the water flow (Ayrton, 1910). Thus an orientated substrate provides important information about the current. Similar principles apply to shadows cast by waves. Orientating the body in the direction shown by the arrow, as was observed, minimises drag, and maximises the efficiency with which the animals can compensate for involuntary movements.
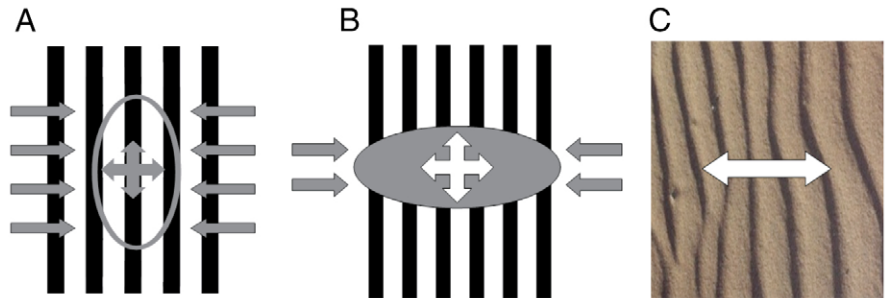
aligned orthogonally to the predominant direction of flow. Displacement by currents and waves is therefore more likely to be at right angles to the stripes. To minimize such involuntary motion the body should be orientated to minimise drag and maximise propulsion force (Fig. 6C). Having eyes directed laterally also gives effective visual feedback on any movements, and helps minimise motion in turbulent costal waters where *Sepia* live. We have no explanation for the absence of an orientation response to the broadest stripes (Fig. 4), although the number of edge and corner features (Fig. 5 declines as width increases.

Orientation to water flow

The preceding observations raise the possibility that cuttlefish prefer to align their bodies with the flow. In a follow-up study, juvenile common cuttlefish (*Sepia officinalis*; *S. pharaonis* was no longer available) placed in a flow of $0.08~\mathrm{m~s^{-1}}$ did indeed orientate their body axis parallel to the flow (Fig. 7). An obvious interpretation is that the animals use the visual pattern to judge the direction of flow. This could be advantageous if the actual flow is unstable, as in shallow water with wave action.

To conclude, whereas a terrestrial predator can minimise motion by moving slowly, and perhaps minimise motion by actively choosing a trajectory (Srinivasan and Davey, 1995; Mitzutani et al., 2005), cuttlefish, in coastal waters are likely to be subject to involuntary displacements by waves and currents. The animals appear to use both visual patterns and information about water flow to align themselves at 90° to background stripes, and with the flow. There is no compelling evidence that the demands of camouflage are an overriding consideration, but given the quality of crypsis by juvenile cuttlefish (Hanlon and Messenger, 1988) it would not be surprising if they were important.

Finally we note that this work makes predictions about the occurrence of oriented textures in natural substrates. First that they do occur where cuttlefish live, and second that they are normally caused by water flow (e.g. ripples) and give information about this flow. Static, oriented patterns, such as those associated with tree bark or rock strata, may be rare, and hence of little relevance to camouflage.

Appendix
Gaussian filtering of images

After warping, images were Gaussian filtered: (1) to remove the effect of high frequency noise, (2) to minimise effects of registration artefacts, and (3) because image statistics after convolution are more Gaussian than those before (owing to the central limit theorem). Our analysis does not require normally distributed image statistics, but normality improves the power of the tests used.

This leaves the choice of the spatial scale (standard deviation of the filter) used for blurring. We used a cross validation-based technique that allows the data to determine an optimal estimate for removing noise but preserving any informative variation. This technique exploits the fact that where data are corrupted by independent additive noise, the best estimate of the underlying signals is simply the mean signal. Therefore, one can
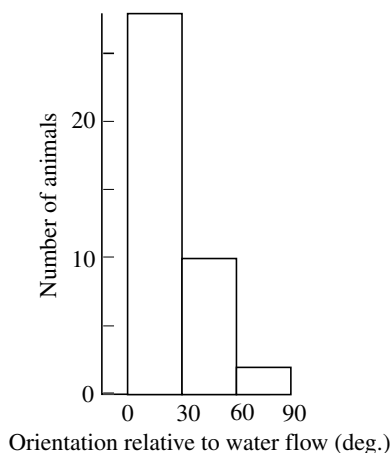
Fig. 7. Body orientation of cuttlefish in flowing water. Data are for ten animals each measured four times. There is a clear preference for a posture parallel to the direction of flow ($\chi^2 = 26.6$, d.f.=2, $P<0.001$).

measure the performance of a particular filter scale by measuring how closely (mean squared error) an individual blurred image is to the average of all other measurements made in that condition. After averaging this error over all three conditions, this cross validation statistic measures how well a particular width of filter removes noise. The filter that minimises this cross validation statistic is used for subsequent analysis.

Lastly, to minimise any small effects of inhomogeneous illumination within the tank, image intensity values were divided by their median. This then resulted in 180 images, warped to the same reference frame, filtered to remove noise, and scaled to remove the effects of variable illumination. These intensity matrixes represented the animal's response to that particular stimulus.

References

Anderson, J. C., Baddeley, R. J., Osorio, D., Shashar, N., Tyler, C. W., Ramachandran, V. S., Crook, A. C. and Hanlon, R. T. (2003). Modular organization of adaptive coloration in flounder and cuttlefish revealed by independent component analysis. *Network – Computation in Neural Systems* **14**, 321-333.

Ayrton, H. (1910). The origin and growth of ripple marks. *Proc. R. Soc. Lond. A* **84**, 285-310.

Chiao, C. C. and Hanlon, R. T. (2001a). Cuttlefish camouflage: visual perception of size, contrast and number of white squares on artificial checkerboard substrata initiates disruptive coloration. *J. Exp. Biol.* **204**, 2119-2125.

Chiao, C. C. and Hanlon, R. T. (2001b). Cuttlefish cue visually on area – not shape or aspect ratio – of light objects in the substrate to produce disruptive body patterns for camouflage. *Biol. Bull.* **201**, 269-270.

Hanlon, R. T. and Messenger, J. B. (1988). Adaptive coloration in young cuttlefish (*Sepia officinalis*) – the morphology and development of body patterns and their relation to behavior. *Phil. Trans. R. Soc. Lond. B* **320**, 437-487.

Hanlon, R. T. and Messenger, J. B. (1996). *Cephalopod Behaviour.* Cambridge, UK: Cambridge University Press.

Hanlon, R. T., Forsythe, J. W. and Joneschild, D. E. (1999). Crypsis, conspicuousness, mimicry and polyphenism as antipredator defences of foraging octopuses on Indo-Pacific coral reefs, with a method of quantifying crypsis from video tapes. *Biol. J. Linn. Soc.* **66**, 1-22.

Holmes, A. P., Blair, R. C., Watson, J. D. G. and Ford, I. (1996). Non-parametric analysis of statistic images from functional mapping experiments. *J. Cereb. Blood Flow Metab.* **16**, 7-22.

Hubel, D. (1988). *Eye, Brain and Vision.* New York: W. H. Freeman.

Julesz, B. (1971). *Foundations of Cyclopean Perception.* Chicago: University of Chicago Press.

Leibowitz, H. W. (1955). The relationship between the rate threshold for the perception of movement and luminance for various durations of exposure. *J. Exp. Psychol.* **49**, 209-214.

Kelman, E. J., Tiptus, P. and Osario, D. (2006). Juvenile plaice (*Pleuronectes platessa*) produce camouflage by flexibly combining two separate patterns. *J. Exp. Biol.* **209**, 3288-3292.

Marshall, N. J. and Messenger, J. B. (1996). Colour-blind camouflage. *Nature* **382**, 408-409.

Mäthger, L., Barbosa, A., Miner, S. and Hanlon, R. T. (2006). Color blindness and contrast perception in cuttlefish (*Sepia officinalis*) determined by a visual sensorimotor assay. *Vision Res.* **46**, 1746-1753.

Messenger, J. B. (1977). Prey-capture and learning in the cuttlefish, *Sepia. Symp. Zool. Soc. Lond.* **38**, 347-376.

Messenger, J. B. (2001). Cephalopod chromatophores: neurobiology and natural history. *Biol. Rev.* **76**, 473-528.

Mizutani, A., Chahl, J. S. and Srinivasan, M. V. (2005). Insect behaviour: Motion camouflage in dragonflies. *Nature* **423**, 604.

Osorio, D. and Srinivasan, M. V. (1991). Camouflage by edge enhancement in animal coloration patterns and its implications for visual mechanisms. *Proc. R. Soc. Lond. B* **244**, 81-85.

Srinivasan, M. V. and Davey, M. (1995). Strategies for active camouflage of motion. *Proc. R. Soc. Lond. B* **259**, 19-25.

Stevens, M. and Cuthill, I. C. (2006). Disruptive coloration, crypsis and edge detection in early visual processing. *Proc. R. Soc. Lond. B* **273**, 2141-2147.

Wells, M. J. (1960). Proprioception and visual discrimination of orientation in octopus. *J. Exp. Biol.* **36**, 501-511.