

Correspondences

High-resolution polarisation vision in a cuttlefish

S.E. Temple^{1,2}, V. Pignatelli³,
T. Cook³, M.J. How³, T.-H. Chiou³,
N.W. Roberts¹, and N.J. Marshall³

For animals that can see it, the polarisation of light adds another dimension to vision, analogous to adding colour to a black and white image [1,2]. Whilst some animals use the orientation of the electric field vector (e-vector) for navigation and orientation [3], the ability to discriminate angular differences in e-vector has been implicated in object recognition for predator/prey detection [4,5] as well as signalling and communication [6]. In all animals previously tested, however, the resolution of e-vector angle discrimination has been found to be in the range 10–20° [5,7,8], which is inadequate for the typical e-vector differences measured in relevant natural visual scenes [9]. In this study, we found that mourning cuttlefish (*Sepia plangon*) are able to detect differences between e-vector orientations as small as 1°. Not only is this the most acute e-vector angle discrimination measured behaviourally in any animal, but it provides a high enough resolution to be relevant to real world visual tasks. We analysed natural underwater scenes using computer based polarisation imaging. When we increased the resolution of our system, we discovered information not detected using normal-resolution imaging polarimetry and invisible to animals lacking fine e-vector angle discrimination. For example, we found that high-resolution e-vector discrimination provides a new way of breaking typical intensity-based background matching. *S. plangon* lacks colour vision, like most other cephalopods, and high-resolution polarisation vision may provide an alternative source of contrast information that is just as fine-scale.

To test the abilities of cuttlefish to discriminate between two e-vectors of different orientations,

we presented looming stimuli (expanding circle, simulating a rapidly approaching object) in e-vector difference-only videos (see Supplemental Movie 1 published online with this article), and used the innate deimatic antipredator

display (a sudden change in body colour pattern thought to startle potential predators; Figure 1A) [10] as an indication of stimulus detection. To produce images with e-vector difference instead of intensity contrast, the outer (front)

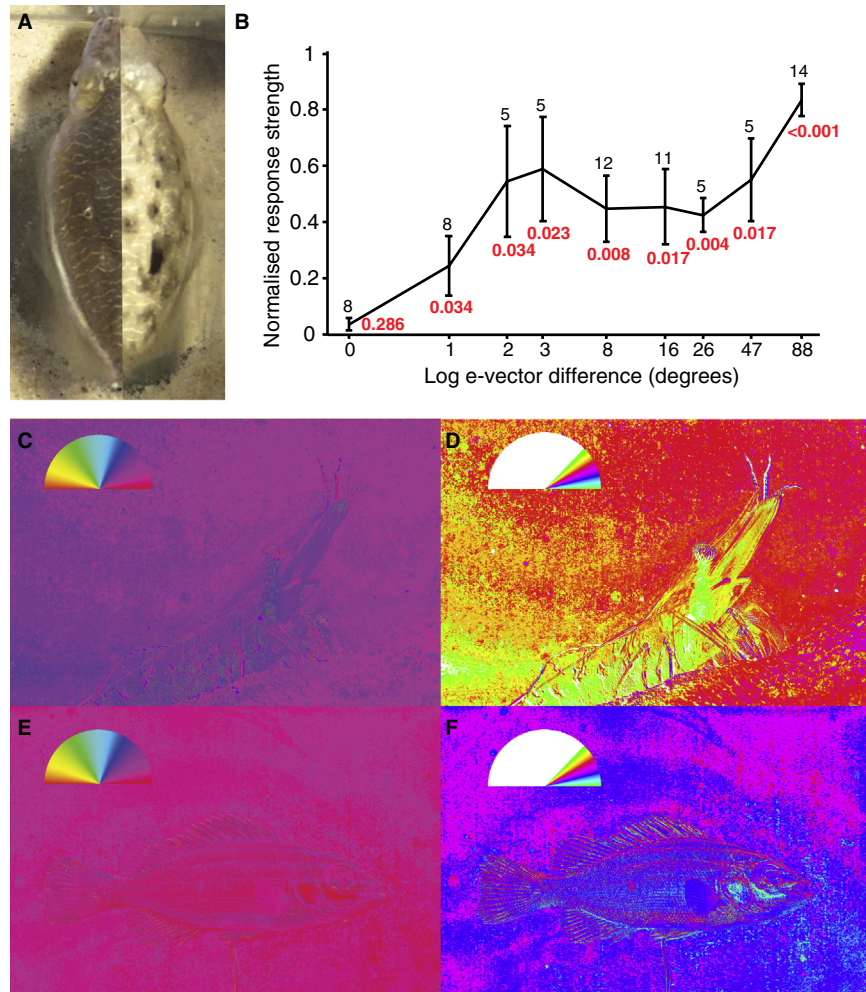


Figure 1. High-resolution polarisation vision in *Sepia plangon* improves image contrast. (A) *S. plangon* responded to looming stimuli that differed in angle of polarisation from the background with an innate deimatic display (brightening of body colour). Left portion = pre-stimulus; right portion = post stimulus. (B) Normalized response strength (see Supplemental Information for further details) decreased as the difference between the e-vector angle of the stimulus and background decreased (solid line). The minimum e-vector discrimination was 1.05° (one-sided paired t-test between normalized level of response and a baseline level of body colour change one and a half seconds prior to stimulus onset). A Benjamini-Hochberg correction for repeated measures was used (see Supplemental Information for further details). Error bars represent mean \pm 1 S.E. Black numbers over error bars indicate the number of individuals tested. Red numbers below error bars are p-values. (C-F) Imaging polarimetry of an unidentified penaeid shrimp (C and D) and a small perciform fish, black bream (*Acanthopagrus australis*) (E and F). The reflections from both animals appear to match the angle of the background e-vector closely when the images are processed with standard, low-resolution imaging polarimetry (C and E). However, more information is available in the polarisation dimension when using high-resolution analysis/sensitivity (D and F), where the false colour palette (colour wheel insert in C and E indicating e-vector angle) is compressed into a 45° range (See Supplemental Information for further details). As evident from C and E almost all the polarisation information falls within this angular range. These images model polarisation information (which humans are unable to detect) and convert it to colour, but it is important to note that they are only a model that highlights the information available at higher resolutions and are not an accurate representation of what cuttlefish see.

polarising filter was removed from a liquid crystal display (LCD) computer monitor, a modification of previous methods [4,7]. By varying greyscale values from 0–255 (black to white), the modified LCD displayed images with e-vector orientations varying from 0–90°, but with no change in degree of polarisation (>96%), and no relevant changes in intensity (see Supplemental Figure S1A in the Supplemental Information and Supplemental Movie 1). Therefore, the stimulus was only visible to animals possessing polarisation sensitivity, where the visual system's e-vector sensitivity effectively replaces the front polariser of the LCD. Differences in e-vector angle between stimuli and backgrounds were achieved by varying greyscale values independently.

Cuttlefish responded strongly when presented with a looming stimulus in e-vector difference-only (Figure 1A; see also Supplemental Figure S1D, and Supplemental Movie S2), and as the angular difference between the e-vectors of the stimulus and background was decreased, there was a corresponding decrease in the relative strength of the response (Figure 1B). The minimum angular difference detectable between two e-vectors was 1.05° (one-sided paired t-test with Benjamini-Hochberg correction for multiple comparisons, $t = 2.23$, $df = 7$, $p = 0.034$), which is more acute than previous measures in other cephalopods [5], crayfish [7], and fish [8]. When presented with a negative control, which consisted of a looming stimulus with an e-vector orientation that matched that of the background, the response did not differ from baseline levels ($t = 0.59$, $df = 7$, $p = 0.286$).

Investigations are underway to determine how widespread high-resolution polarisation vision is among animals with polarisation sensitivity. Preliminary results (unpublished) indicate that the common cuttlefish (*S. officinalis*) may be as acute (~1.0°) as *S. plangon*, but fiddler crabs (*Uca vomeris*; ~3°), and octopus (*Octopus aculeatus*; ~10°) do not appear to possess equally high-resolution polarisation vision when tested using the same approach. At present, physiological/morphological explanations for the superior e-vector

discrimination in cuttlefishes are unknown.

To investigate the functional significance of high-resolution e-vector discrimination, we simulated how natural scenes differ with either low or high-resolution polarisation vision. When analysed with higher-resolution there was a considerable enhancement in visual information (Figure 1C–F). Objects that were otherwise relatively indistinguishable from the background with standard imaging polarimetry (Figure 1C,E), equivalent to lower-resolution polarisation vision (each colour equals 10–20°), became conspicuous with high-resolution imaging polarimetry (each colour equals 2–5°; Figure 1D,F). The low-resolution images indicated that some aquatic animals, which exhibit intensity based background matching, also match the e-vector orientation of the background. However, high-resolution e-vector discrimination breaks this form of polarisation background matching. Camouflage in the polarisation dimension has not previously been investigated and we suggest that the need to detect animals, such as fish camouflaged in the polarisation dimension, may be one selective pressure driving the evolution of high-resolution e-vector angle discrimination in *S. plangon*. Sensitivity to small differences between e-vectors may be the result of an evolutionary arms race between polarisation camouflage and polarisation sensitivity.

Some cuttlefish, including *S. plangon* (our unpublished observations), produce polarised patterns on their bodies that are thought to be used as part of a covert communication channel, invisible to animals lacking polarisation vision [6]. High-resolution e-vector angle discrimination combined with high-definition polarised patterns could increase the amount of information transmitted through this channel. It appears that we may now need to look at camouflage and communication in a new light.

Supplemental Information

Supplemental Information includes one figure, two movies, Supplemental Experimental Procedures, and can be found with this article online at doi:10.1016/j.cub.2012.01.010.

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¹School of Biological Sciences, University of Bristol, Bristol, BS8 1UG, UK. ²School of Biomedical Sciences, The University of Queensland, St. Lucia, Queensland, 4072, Australia. ³Queensland Brain Institute, The University of Queensland, St. Lucia, Queensland, 4072, Australia.
E-mail: shelbytb@hotmail.com