Final Report for AOARD Grant 09-4073

"Natural Models for Autonomous Control of Spatial Navigation, Sensing, and Guidance, Part 1"

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Chris Talbot	PhD, research supported 50%
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This is the final report on the latter stages of a major international review of polarization vision and polarized light ? ?New Directions in Biological Research on Polarized Light.?

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As this list of personnel suggests, the project has grown and through attracting other personnel, achieved far more than originally intended. Viktor Gruev, originally from Nader Engheta’s lab. is included as new collaborations are starting there and these will hopefully develop in the next 2 years.

Abstract: This grant has supported the latter stages of a major international review of polarization vision and polarized light "New directions in biological research on polarized light" published by The Philosophical Transactions of the Royal Society of London and edited by the two PIs. The papers from this issue are included with this report as a series of PDFs.

Other publications of note include an invited summary of the area in Current Biology.

Conceptual advances in the research include:

a) The development of a behavioural screening technique for polarization sensitivity in any animal (trialed on crustacean, cephalopods, fish and next turtles).
b) Demonstration of polarization sensitivity ten times more acute than previously documented in cephalopods (cuttlefish and octopus) and crustaceans (mantis shrimps and crabs). This opens a potentially new chapter in polarization communication and camouflage.
c) Electrophysiological characterization of linear polarization, circular polarization and colour photoreceptors in 3 species of mantis shrimp (stomatopod). This includes confirmation of elliptical encoding in 2 species, again suggesting a covert communication language?
d) Behavioural acuity threshold of linear polarization in a stomatopod partially achieved.
e) Anatomical basis of circular polarization characterized in 3 stomatopod species.
f) Modeling of ideal ¼ wave retardation advanced using biological parameters as input – it is this area that has the highest chance of practical application through data-storage and nanotechnological biomimetics.
g) Demonstration of new forms of linear and circular polarization reflection in several stomatopod species.
h) Characterisation of the polarization reflection properties of marine creatures other than cephalopods and stomatopods has begun with over 20 species of fish so far.

Each of these is expanded upon in the following report.

Introduction:

This final report covers the first 2 years of what is a 4 year project. It is a joint research project with Prof Tom Cronin of UMBC USA. The second 2 years will come under AOARD 11-4039. Prof Tom Cronin will provide a progress report to cover his lab. Output but it should be noted that much of the following output is highly collaborative with the Cronin lab. And also with named collaborator Dr Nick Roberts (University of Bristol, UK) whose expertise at the physics end of this research has become essential for its continuing success.

The ultimate goal of this research is to understand polarization vision, polarization communication and polarization camouflage (information transfer) in marine animals, with a view to using what we learn in technological applications. Spatial navigation, sensing and guidance are tasks animals behaving in the real world accomplish every day and some of this is achieved using polarized light, a form of electromagnetic radiation that humans are not capable of accessing without resorting to technology such as filters, cameras and specialized sensors. Our aim is to use the power of biological design in a realm of vision to which we are only now becoming dimly aware.

The project is conducting research focused on the visual systems of several groups of vertebrate and invertebrate animals with the goal of understanding how they perceive, process, and analyse visual stimuli. Much of the proposed research will focus on polarized light sensitivity in visible and ultraviolet spectral regions. To carry out this research, two laboratory groups, both of which have worked for several years in collaboration with the Air Force, will join forces internationally. These laboratories, one in the United States and one in Australia, have served as research centers in the areas of visual physiology and ecology of marine and terrestrial animals, with special expertise in visual aspects of ultraviolet and polarized light. The two groups have worked together for over two decades and have an outstanding history of producing new, exciting, and unexpected research findings and publishing in the very best international scientific journals.

Results, including Experiments and Discussion

Results are described and discussed relative to the original specific objectives identified.

(Objective 1) To measure and explain structural properties and their diversity in natural materials that preferentially reflect or absorb linearly and circularly polarized light. *Our research has revealed that certain animals use very unusual structures to control the reflection, transmission, or absorption of linearly or circularly polarized light from their surfaces or in their photoreceptors. These structures often have no man-made counterparts, and the optics underlying polarization absorption or reflection are poorly understood. In this project we will examine new types of natural polarizers and polarization-sensitive photoreceptors, characterizing their spectral, ultrastructural, and theoretical optical properties.*

The significance of this side of the project is to identify the way in which polarising signals (both linear and circular) are produced by animals. This may inform nanofabrication of such materials and reveal how polarisation information is encoded.

Material properties of polarised body patterns in stomatopods

In our previous research we have found that the polarisation body patterns in stomatopods were produced by two different mechanisms, the first produce iridescent blue reflections based on photonic vesicles underneath a thin layer of transparent cuticle, the second is red in colour and is based on the absorption of dichroic pigments within the cuticle (Cronin et al., 2009). While it is easy to see how polarisation reflections are produced by photonic structures, a dichroic polariser can only produce polarised light after the light has passed through a filter. Since stomatopods do not produce bioluminescent light, the polarised body patterns we observed must come from the reflection of light from the environment. With such a passive design, a highly reflective material under the polariser is to be expected.

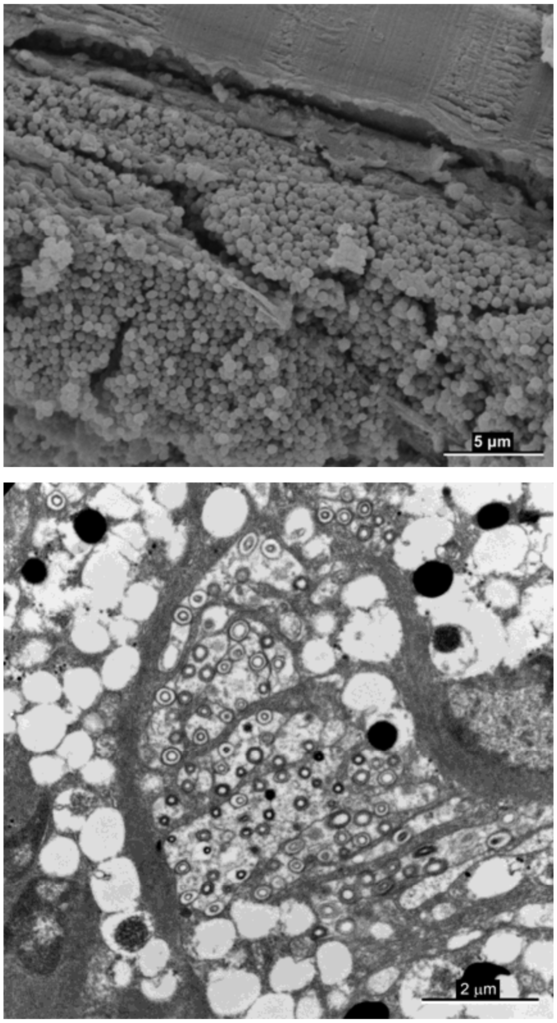

Figure 1. Scanning (top) and transmission (bottom) electron microscope images of light reflectors underneath the dichroic polarization cuticle in the antennal scale of the stomatopod *O. scyllarus*.

Based on our scanning electron microscopy results, we recently found that the light-reflecting material under the polarized antennal scale of *Odontodactylus scyllarus* is composed of photonic sized spheres. The diameters of these spheres was roughly equal to visible wavelengths (Fig 1, top).

Under a transmission election microscope, we found that these spheres are made from double layered membrane structures (Fig 1, bottom). Except for their near-zero eccentricity, this structure is almost identical to that of the blue polarization reflectors we discovered previously (Chiou et al., 2005). Due to the symmetry of the geometry, this photonic structural reflector should have roughly equal reflectance to incoming light of various zenith angles. Having such a broad-band diffuse reflector behind a dichroic linear polarizer, the animal can produce a steady polarised visual signal irrespective to the source of illumination. Physical models for the optical properties of these light reflectors are still under development.

(Objective 2) To investigate the physiological processing of polarization information. *One group of our focal animal models, stomatopod crustaceans, possesses an astonishingly broad range of visual information-sensing channels. There are 16 information input channels in all: 12 are for the analysis of color (one also associated with polarized light) plus at least two for detecting linearly polarized light and two for circularly polarized light. Understanding how information is tracked in this parallel input array will be the basis for guiding research into sensor fusion, stimulus analysis, and post-processing of sensory information. Efficient processing and resultant "command decisions" for the brain to interpret and act on are essential for these fast-living, combative animals. Using electrophysiological and neuroanatomical studies on the properties of neurons in the visual pathway, we expect to discover new forms of sensory filtering, integration, and sorting. We now understand the basics of these properties, but new work will examine temporal features and spatial aspects of sensory processing with the goal of uncovering approaches to hyperacute imaging of stimuli in both time and space.*

The significance of this part of the project is that is builds on previous basic descriptions of the complex visual system of stomatopod and now begins to interrogate it anatomically and physiologically.

Our major discovery is to confirm my previous hypothesis that different species of stomatopod appear to use circular polarised light of different ellipticities. This may allow these animals access to a new language of light where the variable is ellipticity rather than wavelength (colour) or linear polarised light angle and %.

Circular/elliptical polarisation vision

Mantis shrimps possess the remarkable ability to sense circularly polarised light. Because few, if any, marine animals are able to do this, these animals can potentially use this modality as a 'secret' communication channel. Indeed, we have now found several species that possess circularly polarise body patterns used for communication (Fig.2).

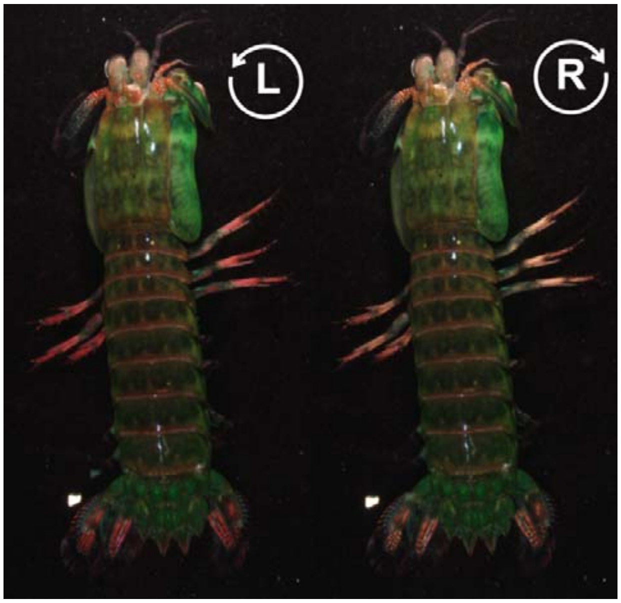

Figure 2. The circularly polarised red colour patterns of *Gonodactylus falcatus*

As yet, no examples of direct circular polarisation detectors have been discovered in nature, so mantis shrimps rely on optical filters to convert circular to linear polarised light. These filters use sub-wavelength scale membrane structures, which - through optical birefringence - alter the phase of the light's electric vector (e-vector). These filters – known as wave retarders - can therefore be used to convert circularly polarised light to linear, and vice versa. Man-made equivalents can be found in various optical appliances including DVD players and Blu-Ray disks. Previous studies by our group have indicated that these filter structures are located in the eighth retinular cells (R8) in the mid-band rows 5-6 (see proposal).

In collaboration with Nick Roberts, at the University of Bristol, we have developed a physical model for the birefringent properties of the R8 cells. We have used this model to predict the optimal dimensions of these cells for the full conversion of circularly to linearly polarised light (¼ wave retardance). As a result, we are now able to compare actual R8 dimensions with those expected for full ¼ wave retardance (see below).

We set out to measure the R8 cells of various species of mantis shrimp to test the hypothesis that their eyes have evolved for full circular polarisation vision. To do this, we collected 5 species from Australian waters and used transmission electron microscopy techniques to visualise and measure the length of the R8 cells in midband rows 5-6, as well as the diameters of the sub-wavelength membrane structures within them, known as microvillae.

Our results to date suggest that many species lack the required filters for the full conversion of circular to linear polarised light. In particular, smaller species tend to have R8 cells approximately half the required length (i.e. 1/8 wave retarders). This would imply that, rather than possessing a perfect circular polarisation vision system, these species compromise on a half-way point between circular and linear – elliptical polarisation vision.

A possible explanation for this compromise is the size constraint on various photoreceptor cells in the eyes of some of the smaller species – there simply is not enough space to fit the 100μm-plus length R8 cells necessary for full circular polarisation vision. Another possibility is that, rather than being a compromise, this may be an adaptation to enable both linear and circular polarisation sensitivity within the same ommatidium. In systems where full ¼ wave retardance occurs, incoming linearly polarised light is converted to full circularly polarised light, which cannot be discriminated by the subsequent linear polarisation system, rendering these cells incapable of detecting linearly polarised light. However, 1/8 retarders convert linear to elliptical, and circular to elliptical, both of which can be detected.

To further test this hypothesis, we are in the process of performing elecrophysiological recordings from the relevant photoreceptor cells in smaller species thought to possess this elliptical polarisation sensitivity.

Electrophysiological evidence for elliptical polarisation vision

Using intracellular electrophysiological and neural anatomical methods, we have continued our survey on the sense of circular polarization in stomatopod crustaceans.

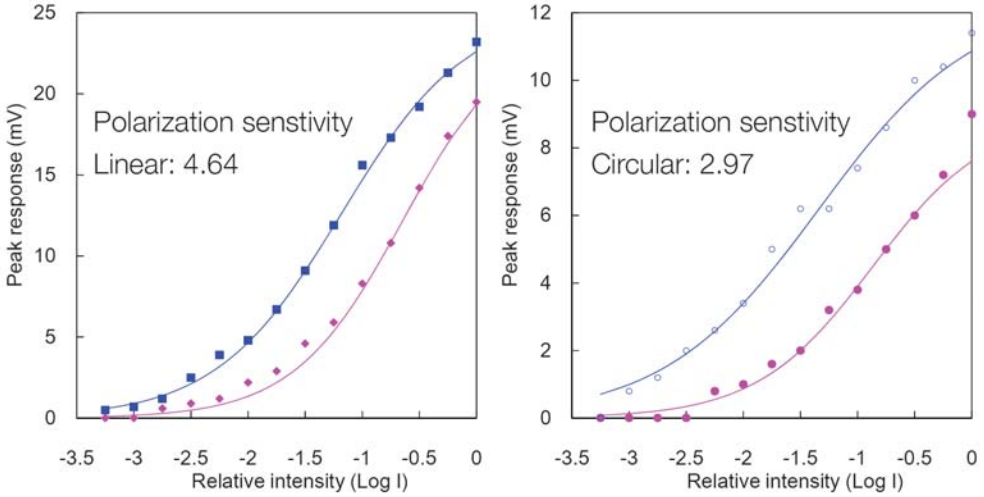

Figure 3. Electrophysiology of elliptical polarization-sensitive photoreceptors. (Left) Peak response voltage and stimulus intensity (V-Log I) curve of a photoreceptor showing differential responses to linearly polarized lights of perpendicular angles. (Right) V-Log I curve recorded from the same photoreceptor as in (A) but showing differential responses to circular polarized light of opposite handedness.

For the past year, we focused on recording photo-responses from receptors that show differential responses to circular polarized light of opposite handedness. The measured polarization sensitivities (be it linear or circular) showed a large amount of variation, even within species. Based on recordings from over one hundred photoreceptors, we are confident that the circular polarization sensitive photoreceptors in three of the four stomatopod species tested are also sensitive to linear polarized light (Fig 3). This result indicates that, rather than being tuned specifically to circularly polarised light, different stomatopod species have their eyes tuned to polarized light of different ellipticity. Preliminary report of this result has been presented as two posters in the 31st annual meeting of the Australian Neuroscience Society.

(Objective 3) To examine the design and specializations of molecular receptors used for visible and ultraviolet polarization sensing. *Recent molecular research on photopigments in our laboratories, as well as newly published information on the 3-dimensional molecular structure of polarization-sensitive visual pigments, will form the background for new studies on molecular specializations of visual pigments and associated molecules that are designed for enhanced polarization sensitivity in both the visual and ultraviolet spectral ranges. With at least five UV photoreceptor classes, stomatopods have a particular interest in this spectral region that we currently do not understand. By working out the molecular underpinnings of polarization sensing, we will gain insight concerning functional differences among materials which could have application for fabrication or design.*

This work has been mostly conducted in the Cronin lab. and we are continuing collaborative work in the field within this topic this summer

(Objective 4) To characterize and explain polarization optics and visual sampling of natural stimulus fields in model organisms. *A general principle of neural sampling is that both pre-receptor and post-receptor mechanisms operate in series to enhance signal detection. Our objective here is to examine some of the prefiltering mechanisms used, both optically and behaviorally. The work is expected to involve a variety of animals to explore diverse systems of managing difficult environmental challenges. These systems include <u>object detection</u>, <u>covert signalling</u>, and <u>navigation</u>.*

Optical / anatomical results; variation of R8 dimensions within eyes

Another area of interest in the circular/elliptical vision question is the variation in R8 filter dimensions observed within individual eyes. Variations within eyes raise the possibility that the circular/elliptical polarisation sense may not be evenly distributed along the mid-band of the stomatopod eye. To investigate this, we used light microscopy, image registration and point digitisation techniques to reconstruct the three-dimensional arrangement of R8 cells across the whole stomatopod eye (Fig.4).

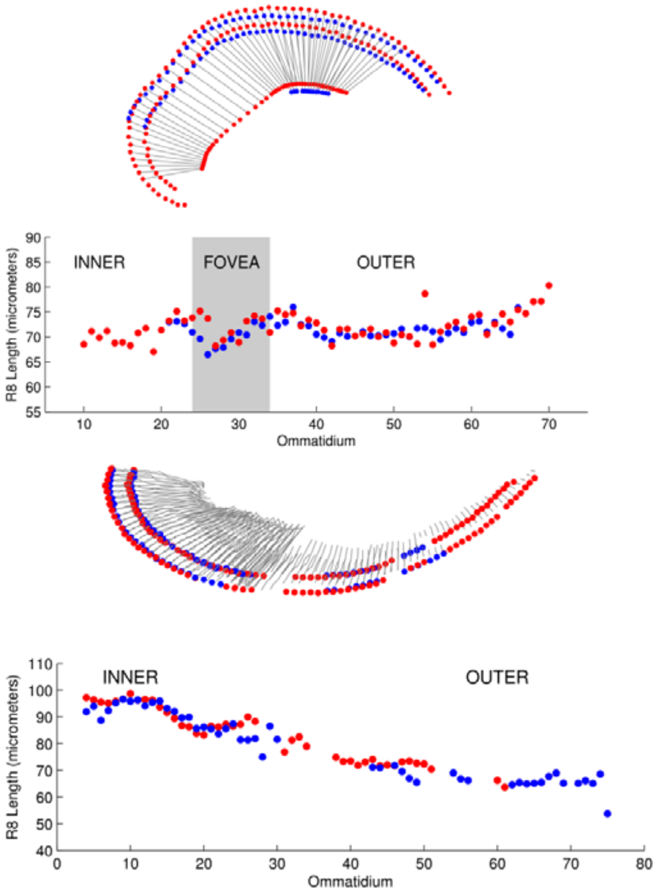

Figure 4. Serial reconstructions of stomatopod eye photoreceptors to show the varying length of R8 cells. Top *H. trispinosa*. Bottom: *G. smithii*.

For some species, such as *Haptosquilla trispinosa*, R8 dimensions are evenly distributed alone the midband. This is one species that uses a specific ellipticity for potential covert communication, as recorded electrophysiologically and demonstrated here anatomically through R8 cell length.

In the example in Fig. 4, the R8 cells mostly fall between 65 and 75µm in length. However, other species show a gradual change in R8 dimensions along the midband. *G. smithii*, for example, has long R8 cells (~90-100µm) in the forward-facing part of the eye, which become gradually shorter in the lateral visual field (~60-70µm) (Fig 4, right). What this implies for the visual capabilities for these animals remains unknown.

Behavioural results: experiments with LCD polarisation monitors

Conventional liquid crystal display (LCD) computer monitors are based on the manipulation of linearly polarised light by the electrical activation of liquid crystal filters. Light passes, first through a vertically oriented linear polaroid filter, then through an LCD array, and finally through a second horizontally oriented polaroid filter. Without electrical activation the LCD layer causes the e-vector of the incoming vertically polarised light to be rotated by 90 degrees, allowing most of it to be transmitted through the second horizontally oriented polaroid filter. However, when

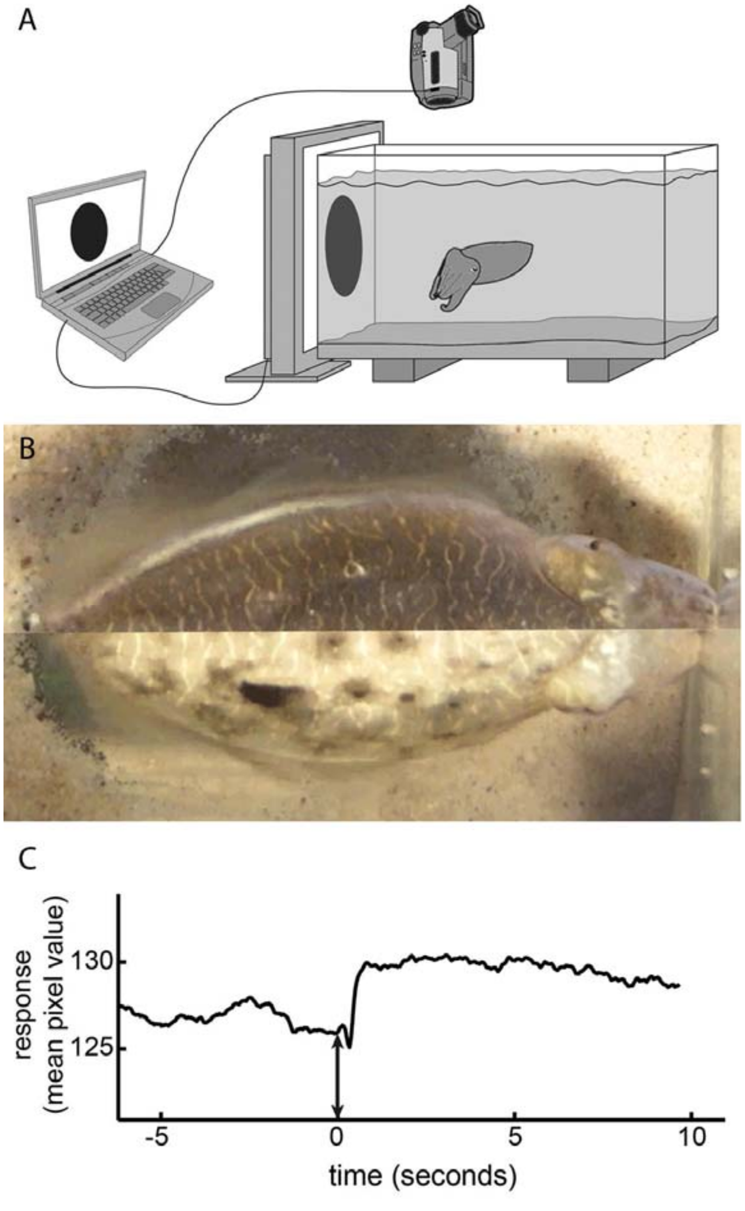

Fig. 5. Cuttlefish (*Sepia plangon*) body patterns as a behavioural assay for testing polarisation vision. (**A**) Schematic of testing tank and relative position and size of stimulus. (**B**) Body colour pattern change showing deimatic (brightening) response to potential predator, top is pre-stimulus body pattern bottom is post stimulus body pattern. (**C**) Time course of change in body colour pattern, stimulus onset marked by double headed arrow. Line follows the mean change in intensity value of pixels on the mantle.

electrically activated, the liquid crystals reorient themselves so that the plane of polarised light is rotated to lesser amounts depending on the level of electrical stimulation. This results in different amounts of light being transmitted through the second polaroid filter.

It follows that the removal of the second polaroid filter will produce a polarisation-only monitor, in which, what was previously brightness contrast, now corresponds to polarisation e-vector contrast. In collaboration with Drs. Nick Roberts and Shelby Temple (University of Bristol) we adapted several standard computer monitors in this way to test the response of various species of marine organism to polarised light stimuli (Fig. 5).

Polarisation vision in the cuttlefish *Sepia plangon*

Cuttlefish from the waters near the UQ fieldwork station on Stradbroke Island were housed in glass seawater aquaria. A polarisation monitor was then placed against one side of the aquarium and fast looming circular stimuli (equivalent to an approaching predator) were presented at 3 minute intervals (Fig. 5). The angle of polarisation contrast was altered for different presentations, so that polarisation contrast varied from 90° to 0°. Cuttlefish responded to perceived looming stimuli in a number of ways, including swimming movements, skin colour and texture changes, which were recorded using digital video cameras. We developed an automated system for measuring cuttlefish responses from the digital video sequences, based on changes in the distribution of image pixel intensity values within the body region of the cuttlefish.

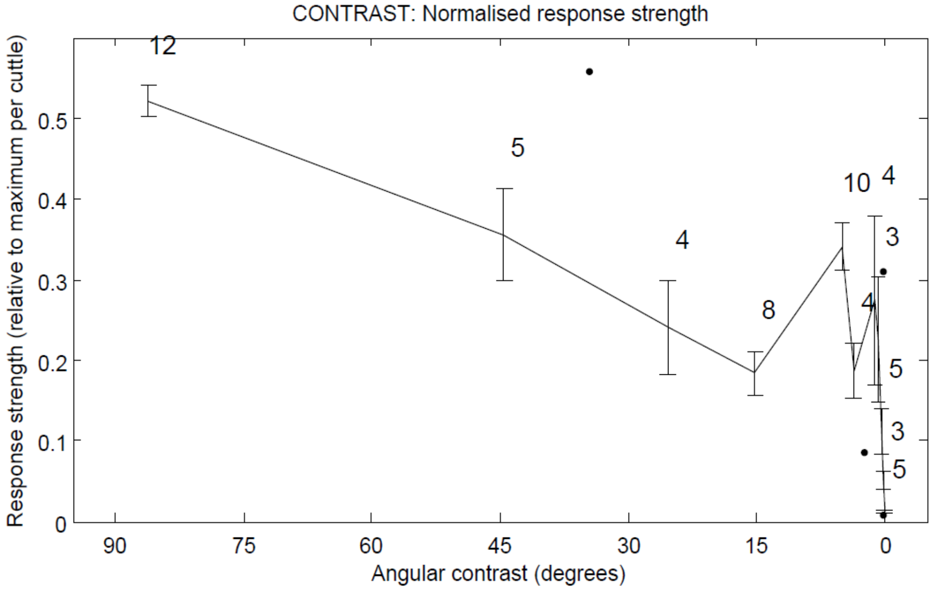

Figure 6. Response of cuttlefish *S. plangon* to varying polarisation angular contrasts.

We found that the cuttlefish, *Sepia plangon*, is extremely sensitive to small angular differences in the e-vector of polarised light down to one degree (Fig 6).

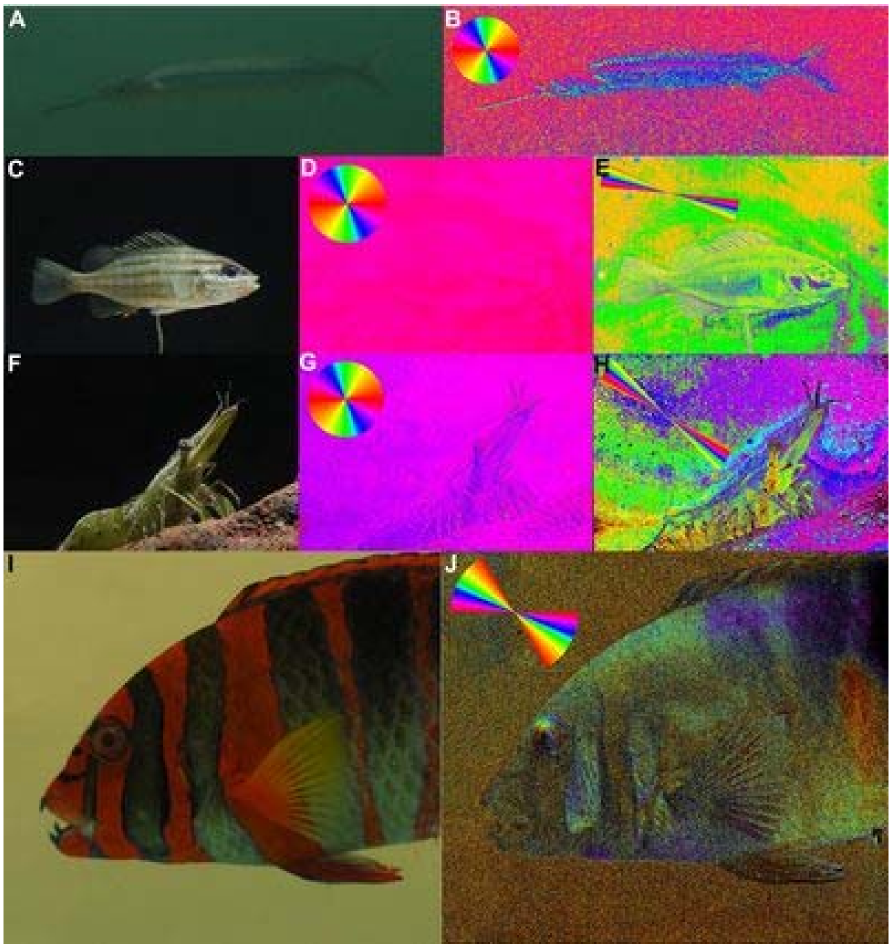

Fig. 7. Imaging polarimetry of potential predators and prey of mourning cuttlefish (*Sepia plangon*). (**A**) Half beak (*Hemiramphus* spp.) in colour and (**B**) polarization contrast with false colours indicating e-vector angle. E-vector angle legend is provided in the corner of each image. (**C**) Black bream (*Acanthopagrus* spp.) in colour and (**D**) polarization contrast, as well as (**E**) high-resolution polarization contrast (155-175 degrees). (F) Shrimp (*Macrobrachium*) in colour and (**G**) polarization contrast, as well as (**H**) high resolution polarization contrast (135-155 degrees). (**I**) Tuskfish in colour and (**J**) in high resolution polarization contrast (140-180 degrees).

This work is currently being submitted to Science as it represents a significant increase in polarisation discrimination, suggesting added interest in the polarised light field. We are also working on characterising the polarising signals from potential predators and prey in the marine world (an extension on previous AOARD Contract – 064040) (Fig. 7) with over 20 species now characterised for their reflective properties. Fig. 7 shows how effectively some animals are camouflaged –

both in terms of ordinary luminance contrast and in polarisation contrast, but also how a high-resolution polarising imaging system can break that camouflage.

Polarisation vision in intertidal crustaceans – fiddler crabs

Using a very similar experimental protocol, we investigated the polarisation sense of an intertidal crustacean, the fiddler crab *Uca vomeris*. Because this species normally inhabits intertidal mudflats and is active during the low-tide period, we could not use a standard aquarium system. Instead, we suspended the crab on top of a polystyrene ball supported over a steady flow of compressed air, so that the crab was able to 'walk' freely causing the ball to rotate underneath it. We were then able to present polarisation stimuli (again the predator-like looming stimulus) of varying angular contrast to the tethered animal. The crabs responded to perceived looming stimuli, either by running away from the monitor, or by 'freezing'.

Using this system, we found that, like the cephalopods, fiddler crabs are extremely sensitive to the angular contrast of polarised light (Fig 8).

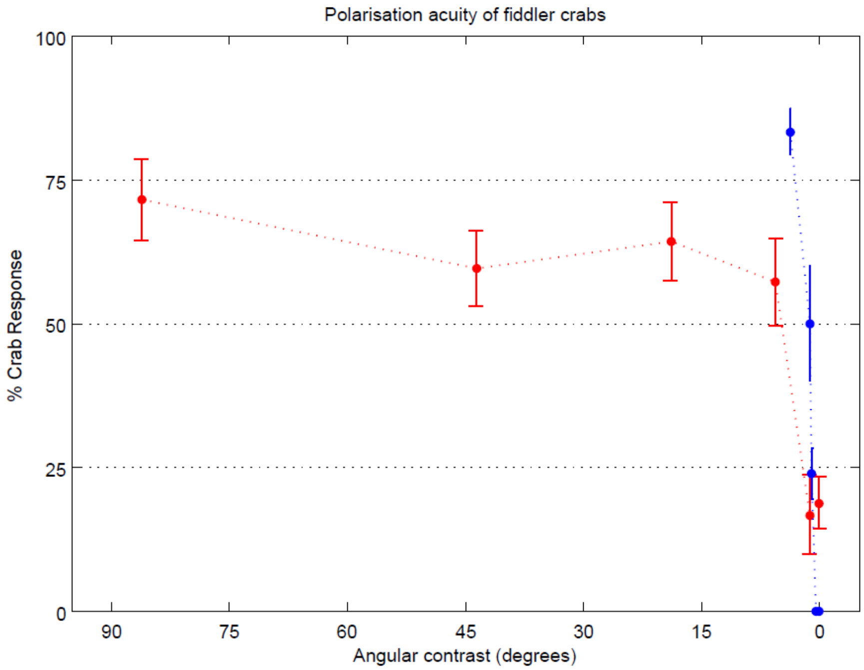

Figure 8. Response of the fiddler crab *Uca vomeris* to varying polarisation angular contrasts.

Testing mantis shrimp linear polarisation acuity

While polarisation monitors are useful for testing the acuity of the linear polarisation detection systems of cuttlefish and fiddler crabs, this technique runs into complications when applied to mantis shrimps. The main issue is that the liquid crystal does not perfectly rotate the e-vector of the incoming light, so that for certain orientations the outgoing light is elliptically polarised rather than linearly polarised. This is not an issue for studying the polarisation sense of animals that do not have a circular or elliptical polarisation sense. But for mantis shrimps this complicates things.

To study the linear polarisation acuity of mantis shrimps we therefore took a different approach using an associative learning experiment. We trained mantis shrimps to select between a pair of visual stimuli differing only in linear polarisation contrast. Upon selecting the correct stimulus, the animal is provided with a food reward. Incorrect choice results in food being withheld until the next choice opportunity. The visual stimuli were constructed from linear polaroid filter, cut so that half of the stimulus was oriented in one direction, and half in another (Fig 8, left). Full polarisation contrast occurred when the two polaroid filters were oriented 90° to each other; zero contrast when the filters were oriented in parallel; and various grades in between.

In preliminary experiments we found that after approximately 10 days of training, the mantis shrimp *H. trispinosa* was easily able to discriminate between a 90° and 0° stimuli. Subsequent variation of the contrast angle suggested that, despite the sophisticated polarisation detection machinery in the eye, this species does not show particularly high behavioural sensitivity to small differences in the angle of polarised light. In fact, polarisation contrasts of 45° or lower were indistinguishable from a 0° contrast stimulus (Fig 8, right). Further behavioural experiments are required to confirm this observation, but if shown to be true, this points to some fairly interesting post-processing mechanisms below the photoreceptor cells.

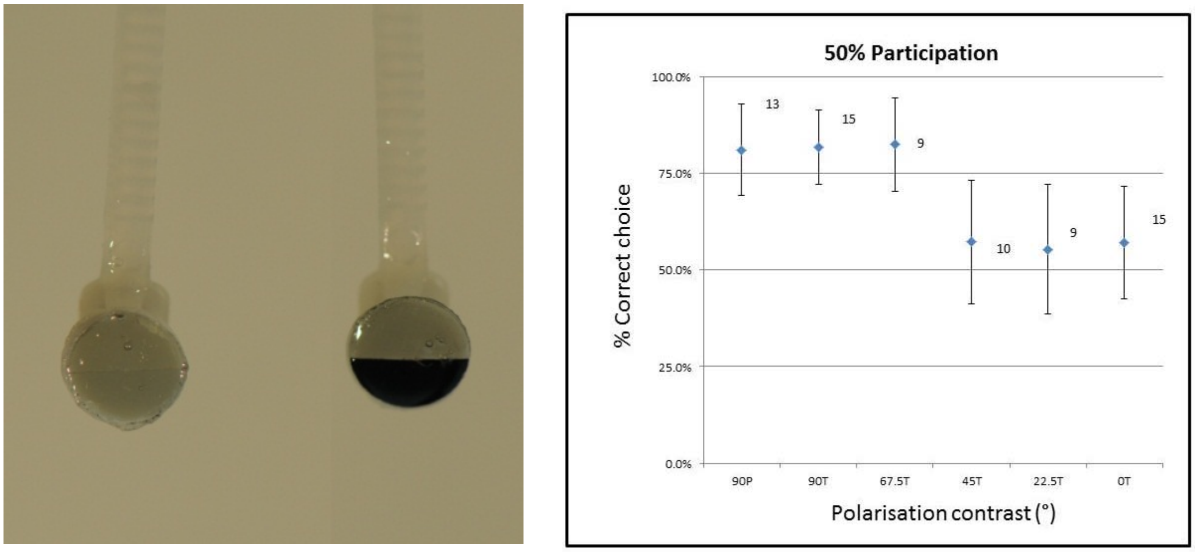

Figure 8. *H. trispinosa* associative learning experiment. Left: photograph of a 0 stimuli and 90 stimuli viewed through a polaroid filter. Right: mantis shrimp success rate for distinguishing between stimuli of varying angular contrast. Numbers on the x axis represent angular contrast in degrees.

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Chiou, T.-H., T. W. Cronin, R. L. Caldwell and J. Marshall. 2005. Biological polarized light reflectors in stomatopod crustaceans. In Polarization Science and Remote Sensing II, J. A. Shaw and J. S. Tyo, eds., Proc. SPIE. 5888, 58881B.

Cronin, T. W., T.-H. Chiou, R. L. Caldwell, N. W. Roberts and J. Marshall. 2009. Polarization signals in mantis shrimps. In Polarization Science and Remote Sensing IV, J. A. Shaw and J. S. Tyo, eds., Proc. SPIE. 7461, 74610C.

List of Publications:

CM Talbot and NJ Marshall 2010 (Front Cover) Polarization sensitivity in two species of cuttlefish – *Sepia plangon* (Gray 1849) and *Sepia mestus* (Gray 1849) – demonstrated with polarized optomotor stimuli. J. Exp. Biol. 2010 213: 3364-3370.

CM. Talbot and NJ Marshall 2010 (Front Cover) Polarization sensitivity and retinal topography of the striped pyjama squid (*Sepioloidea lineolata* – Quoy/Gaimard 1832) J. Exp. Biol. 213: 3371-3377.

TW Cronin and NJ Marshall 2011 Patterns and properties of polarised light in air and water. Phil.Trans.R.Soc.Lond.B. 366:619-626.

CM Talbot and NJ Marshall 2011 The retinal topography of three species of coleoid cephalopod: significance for perception of polarised light. Phil.Trans.R.Soc.Lond.B. 366:724-733.

S Johnsen, NJ Marshall, EA Widder 2011 Polarisation sensitivity as a contrast enhancer in pelagic predators: lessons from in situ polarization imaging of transparent zooplankton. Phil.Trans.R.Soc.Lond.B. 366:655-670.

V Pignatelli et al and NJ Marshall 2011 Behavioural relevance of polarisation sensitivity as a target detection mechanism in cephalopods and fishes. Phil.Trans.R.Soc.Lond.B. 366:734-741.

TH Chiou, NJ Marshall, RL Caldwell, & TW Cronin 2011 Changes in light reflecting properties of signalling appendages alter mate choice behaviour in a stomatopod crustacean *Haptosquilla trispinosa*. Mar. Fresh. Behav. Physiol. 44:1-11.

NJ Marshall & TW Cronin. 2011 Polarisation vision. Curr. Biol. 21:R101-R105.

NJ Marshall & TW Cronin. 2011 Introduction. New directions in research on polarised light. Phil.Trans.R.Soc.Lond.B. 366:615-616.

DD882: As a separate document, please complete and sign the inventions disclosure form.

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