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Re-Engineering the Stomatopod Eye, Nature's Most Comprehensive Visual Sensor

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14. ABSTRACT

The outcomes of this work includes over 70 publications, many in the highest-impact journals (Science, Current Biology, Nature, PNAS), publication of the now defining text book for Visual Ecology, filed two patents, three post docs have become new faculty members or have start on tenure track paths, and 15 postgraduates have successfully obtained their PhDs. Some of the discoveries from this project include: Clear demonstration of the use of circular polarisation in animal signalling and behavior The discrimination of linear polarisation information from objects at a resolution similar to brightness Evidence for a new form of rapid polarisation and colour processing by the brain of stomatopods Two new methodologies introduced, polarisation distance and intuitive polarisation display Insect-like organisation in stomatopod brain morphology suggesting a common complex ancestor

De-bunking of the concept of polarocrypsis as currently stated. Two new ways of producing polarised reflections, one at molecular and one at nanoparticle level

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“Re-engineering the stomatopod eye, nature's most comprehensive visual sensor”

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Preamble to Final Report: This was a very successful body of work performed in close collaborations with three other laboratories in the UK and USA. It resulted in several exciting discoveries, over 70 peer reviewed publications (39 with direct contribution from Australian section), several in Science, Nature and other leading scientific journals and between us close to 70 conference presentations. This combination of two biologists a physicist and an engineer has worked very effectively and it is hard to ascribe particular publications or discoveries to any one laboratory. Nonetheless in what follows I have tried to clearly disambiguate publications and discoveries principally led by my lab. and which therefore might be attributed to the AOARD section of this overall project.

Abstract: Stomatopod (mantis shrimp) vision is both unique among animals and extraordinarily complex at the receptor level, comprising a total of 20 different photoreceptor types or functional input channels. 12 channels for color (including several in the UV, the whole system sampling from 300-720nm), 6 for linear polarization (4 sampling at 0°, 90°,45° and 135°) with peak spectral sensitivity close to 500nm and 2 in the UV sampling at 0° and 90°, with peak spectral sensitivity close to 350nm) and (in some species), 2 for circular polarization (Left and Right-handed), also with peak spectral sensitivity close to 500nm. Why do stomatopods sample the light that is available to them in such great detail?

This research project built on our previous work in this system and with a combination of our current state of knowledge and fresh intellectual and methodological input to the project, we aimed to explain the complexity of the system for the first time. Stomatopods brains are small and are unlikely to deal in multi-dimensional data sets but, in common with most invertebrates, more likely send a set of simple ‘command messages’ to the brain from the eye and outer visual system neuropils. The mechanisms that

function to reduce and analyse the complexity of 20 data streams make up an important component of the research we propose here. Added leverage to approach both receptor function and data streaming / filtering came from new collaborations with the Gruev Laboratory that can mimic or re-engineer the stomatopod eye optoelectronically. By sharing coding principles between disciplines (engineering and biology), and through continued behavioural, anatomical, molecular and physiological investigations, we aimed to decode the inner principles of stomatopod vision as well as provide spin-offs to inform more efficient and smart sensor design.

Introduction:

Over the course of many years, our collaborative work on the complexity of the stomatopod (mantis shrimp) visual system has provided many new discoveries and exciting research outcomes (for example, ten papers to date in *Nature/Science/Current Biology*). In terms of the number of input channels at the retinal level, their vision is far more complex than any other vertebrate or invertebrate system known. Anatomically, there are 16 different photoreceptor types, arranged into 12 channels for color (including several in the UV, the whole system sampling from 300-720nm), 6 for linear polarization (4 sampling at 0°, 90°,45° and 135°) with peak spectral sensitivity close to 500nm and 2 in the UV sampling at 0° and 90°, with peak spectral sensitivity close to 350nm) and (in some species), 2 for circular polarization (Left and Right-handed), also with peak spectral sensitivity close to 500nm. Altogether, this produces a 20-channel sensor that has the potential to encode most or all spectral and polarization information available from 300-720nm.

Our overarching aim was to answer two integrated questions:

(1) Why these parallel streams of information are optimal for what stomatopods are seeing in their visual environment and the complex visual tasks stomatopods perform.
(2) How their processors (both in the retina and in the central nervous system) are optimized to avoid the seemingly inevitable log-jam of information resulting from such massively parallel input.

A key element in their visual system is the line-scanning (push-broom) sensor array used by stomatopods. This multi-channel line-scan array, thought to be unique in animal vision, avoids the problem of integrating 20 two-dimensional (i.e. spatially extended) arrays of information and extracting salient information from this stack in real time. It presents other problems however, as the line-scan system is embedded within a mostly conventional, extended array of visual sensors. Thus, the overall system requires an internal, temporal and coordinate system on which visual information can be painted during each scan. How this data-management centre functions, or even where it is located, has yet to be discovered.

The stomatopod lifestyle is fast and full of potentially deadly combat (Fig. 1). In fact, their raptorial strike is known to cause cavitation (in essence, boiling) the water in front of its impact point as they defend, attack and find food. Behaviorally, they have been described as ‘primate-like’ in their complexity, and it is almost certainly the interactions between their visual system and their violent capabilities that have pushed these creatures along their unique evolutionary trajectory for the past 400 million years. We want to learn from this evolutionarily based design. As their closest existing, artificial design-neighbours for data throughput and processing complexity are airborne and satellite sensors, there are already engineering-biology parallels available for exploitation.

Fig. 1 Stomatopods process 20 streams of visual information perhaps faster than any animal known. Here *Lysiosquilla maculata* catches a fish in a few thousandths of a second. (Photo Roy Caldwell).

Invertebrate sensory systems are elegant in the means used to filter out and reject unwanted information input at peripheral (e.g. photoreceptor and post-receptor interneuron) stages. In contrast, vertebrate systems typically perform much of the filtering in the brain. The result for humans and many other vertebrates is a huge central nervous system to perform this relatively time-consuming and energetically expensive task. In engineering machine vision systems, we have often attempted to emulate the vertebrate way. As our sensors have become more refined and high-density in recent years, this has resulted in processing problems that prevent fast handling of incoming information. An important advance promised by the research described in this proposal is that by examining the information-coding strategies of stomatopods, it could become possible to emulate their parsimonious, energetically and materially efficient, design. Shrimp-brains are small - so the incoming messages for survival are necessarily kept simple.

Our previous work on stomatopod vision has taught us much about its unique visual inputs and retinal design. The research has revealed unexpected dimensions of vision such as circular polarization sensitivity, which gives these species a covert communication channel and possibly unique ways to solve problems of scatter and object detection under water. There have always been unanswered, important questions, however. Why is this system so different from any other? What visual information has the system evolved to see? Why use 12 color channels when theoretically only 6 are needed? Humans use higher order polarization analyses such as Muller Matrices. With all the available information required to calculate Stokes parameters (S0, S1, S2, S3), is the stomatopod eye also capable of complex polarization analysis?

The specific aims the project attempted are listed below and under each details of the most important outcomes and discoveries are given. Following this there is an overview of the importance of the work.

(1) To learn the design foundations stomatopods use for optimized, rapid processing of multi-channel information. We examined how polarization is viewed by stomatopods, discovering a fundamental explanation for why they rotate their eyes (Daly et al 2016, Marshall et al 2014). We also made the first discovery of a behavioural use for circular polarization vision in intra-specific recognition (Gagnon et al 2015). This led to a suggested modification of the way polarisation information is displayed for humans to understand in any imaging polarisation application. Instead of colour coding, intuitive polarisation shapes are used to express degree, angle and elipticity (Gagnon, Marshall 2016). Furthermore, we have discovered a unique type of UV modulating filters to provide mutli-channel information from a limited palette of UV visual pigments (Bok et al 2014, Cronin et al 2014). In comparative work the relative signalling value of information at either ends of the spectrum underwater were considered (Franklin et al 2016, Wilkins et al 2016, Stieb et al 2017). Speed and acuity of polarisation information processing was examined behaviourally with the surprising finding that linear polarisation cues are examined in as much detail as colour or luminous (brightness) information, but only in some animals (Temple et al 2012, How et al 2012, How et al 2015).

(2) To discover how information is processed in stomatopod visual systems.
We have provided evidence for a new type of multi-channel color processing in animals (Thoen et al 2014, Zaidi et al 2014). We have shown how stomatopod processing of polarization information is optimized not to suffer confusion points as are seen in crabs and cephalopods (How 2014) and erected the idea of a formalised polarisation distance in euclidial space – just as colour has such a distance in colour vision (How and Marshall 2014). We have examined the molecular diversity in the retinas of these animals, which will produce a much better understanding of the development of polarization vision and of the roles of polarization opsins in larval and adult eyes. Finally, we have shown that multiple opsins are expressed in polarization receptors in stomatopods along with evidence for the presence of a "dorsal rim" – a specialized region of the retina that in insects is devoted to polarization vision. In comparative work, the perception of illusions was examined in the reef environment lending support to the idea of processing apparently complex tasks early on in the visual neural train (Simpson et al 2016). Finally, in a series of papers emerging now, we are beginning to describe the neuroanatomy of stomatopod optic neuropils and brain in detail (Thoen et al 2017, Wolf et al 2017).

(3) To discover the natural complexity of visual scenes the stomatopod imaging system has evolved to see. The development of the polarization cameras has been a huge success (Powell et al 2014). Not only have we been able to access a remarkable amount of new information about the visual ecology of polarized light underwater, we have been able to translate this biomimetic vision into fundamental medical research and the field of GPS denied navigation. This culminated in the presentation of the 2016 IEEE G. Fink award (York et al 2014). We have also made an important discovery of how fish achieve an optimal reflective silvery camouflage by controlling the non-polarizing properties of the skin (Jordan et al 2012, 2013, 2014, Roberts et al 2014). We have extended this work to discover the greater importance of intensity contrast over polarization as the important dimension for underwater predators to view prey (Johnsen et al 2016). This has led to a high-level debate in the magazine Science (Cronin et al 2016).

(4) To investigate the co-evolution of visual systems, visual signals and camouflage in the natural environment. We have discovered new optical physics for the way stomatopods (and comparatively their great rivals the cephalopods) spectrally control the polarization and visualisation of light (Chiou et al 2012, Roberts et al 2012, Talbot et al 2012, How et al 2014, Gagnon et al 2016). We also discovered the first evidence of how polarization signals evolved in stomatopods and how these signals are used. We have also extended this work to other aquatic species including cephalopods and other crustaceans (Hanlon et al 2013, Chung et al 2014, How 2015) and with other comparisons to signalling systems and their perception across all animals (Marshall and Cheney 2013, Marshall and Arikawa 2014, Cronin et al 2014, Kemp et al 2015, Marshall et al 2015).

Three reviews of the area of polarisation vision were published by the team including contributions to a new book on the subject and a book on visual ecology as a whole (Marshall et al 2014, Marshall et al 2014, Cronin et al 2014).

Experiment:

Methodological descriptions around each sub-section are included in the Results and Discussion section below. They include:

a) A new behavioural paradigm using front-polaroid-stripped computer monitors. This can be used to assay presence / absence of polarization vision and acuity of polarization vision both in angle of e-vector discrimination and degree or % polarization (Fig. 2).
b) Standard intracellular electrophysiology and electroretinogram (ERG) using extracellular electrodes (Fig ?).
c) A new (the world's first) underwater and terrestrial polarization camera. This has been used to observe and characterize polarized light and polarization signals from animals in the field (the Great Barrier Reef) and In quantifying polarized light field for GPS-free geolocation (Fig. x).
d) Standard and 3-view electron microscopy to characterize nano-structure of photoreceptors and optical elements involved in circular polarsation vision (Fig. x).
e) Standard behavioural paradigms involving two-way choice tests with reward of either food or safe-burrow. Tests were made against colour, linear, eliptical and circular polarisation discrimination ability (Fig. 4,5).
f) Old (e.g. Golgi) and new (triple fluorescent stain – phalloidin, a-tubulin, DAPI) neuroanatomical staining and characterization techniques to characterize sub-retinal connections and information flow through to the brain. (Figs. 3,7,8,9,10).

Results and Discussion:

General Significance and Outcomes as follows:

The outcomes of our previous four years of work include over 70 publications, many in the highest-impact journals (Science, Current Biology, Nature journals), the now defining text book for Visual Ecology (Cronin and Marshall), two patents filed (Gruev), three post docs have become new faculty members or have start on tenure track paths, and 15 postgraduates have successfully obtained their PhDs. These outcomes represent evidence for the impact and innovation generated from this grant.

Our work has influenced areas of science outside our own immediate fields. These include areas of primate visual processing (Zaidi 2014) the field of cancer diagnosis (Charanya 2014), and early diagnosis of age-related macular pigment degeneration, the leading cause of blindness in the western world (Temple 2015).

The bio-inspired development of the world's first real-time underwater (and terrestrial) polarization analysis video camera has forged highly successful links across the subject areas of our team (two biologists, one physicist and one engineer). Evidence and recognition of this successful synergy is demonstrated by the presentation in 2015 of The G. Fink award by the IEEE for the most influential paper published in the Proceedings of the IEEE journal (York 2014).

Results based on the specific questions asked in the Marshall lab. during this project are detailed below:

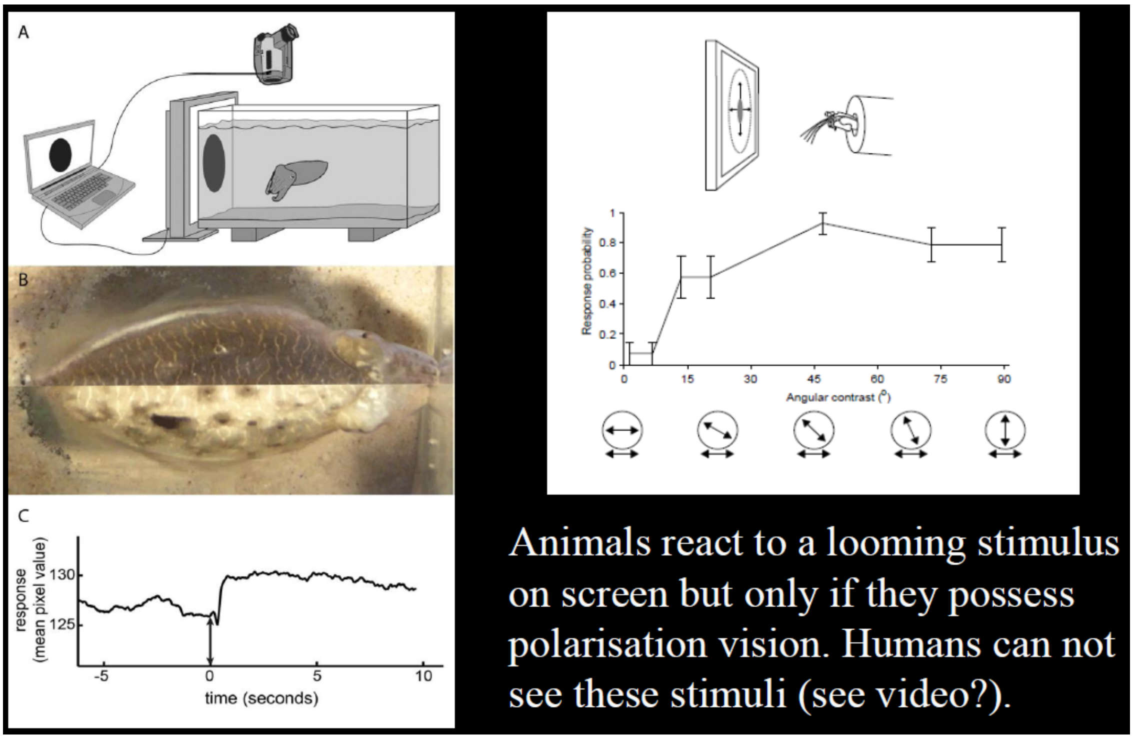
(1) We aimed to learn the design foundations stomatopods use for optimized, rapid processing of multi-channel information.

Question. What is the sensitivity of polarization vision systems? Using new behavioural techniques, stomatopod and other invertebrate polarisation sensitivities were described.

In 2012 we determined that stomatopods have surprisingly coarse spectral and polarisation resolution, using a new behavioural technique. This involved stripping the front polaroid off computer monitors and producing a screen and stimuli on the screen that could only be viewed by animals with polarisation vision. Conversely, using the same technique we demonstrated that polarisation resolution in cuttlefish and fiddler crabs was relatively fine (Fig. 2).

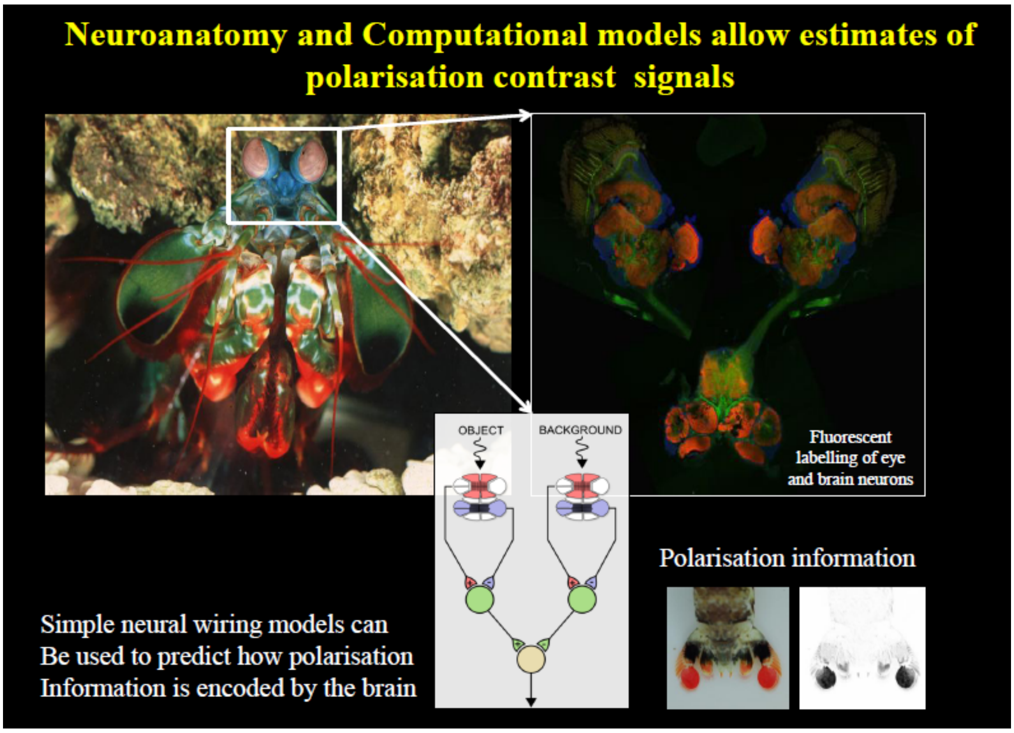
In 2013 we aimed to develop models and circuit-diagrams that account for this difference between stomatopods and other animals, test other stomatopod species and other non-stomatopod species for polarisation resolution.

This objective was largely achieved, a specific model for polarisation distance (discrimination) was developed (How and Marshall 2014) and several animals tested for performance (Fig. 3). As mentioned above, interestingly, as also reported for colour vision, stomatopods under-perform relative to other animals in the tests given. The How-Marshall model allows neuroanatomical results to be combined in a model that estimates polarisation distance or contrast between two objects in a polarisation space. This is similar in principle to chromatic or colour space and colour distances or contrasts. Colour vision in stomatopods has been studied in parallel with publications in Science, Nature and Current Biology resulting – see next specific aim for description.



Animals react to a looming stimulus on screen but only if they possess polarisation vision. Humans can not see these stimuli (see video?).

Fig. 2 Polarisation test paradigm A-C Left, show setup with cuttlefish. The looming black circle can only be seen by animals with polarisation vision and their reaction is recorded. Cuttlefish blanch or change body colour as shown in B – top half before, bottom half after stimulus. This can be quantified using pixel brightness and is sensitive down to one degree of polarisation difference. Stomatopods (Right) also react to similar looming stimuli by retreating or showing eye movements. However, the reaction threshold is far coarser than expected and is closer to 15 degrees.



Neuroanatomy and Computational models allow estimates of polarisation contrast signals

Simple neural wiring models can Be used to predict how polarisation Information is encoded by the brain

Fig. 3 Neural connectivity and modelled polarisation discrimination system. Fluorescent labelling of stomatopod brain structures are revealing the information flow to the central processor. This enables models of the discrimination system to be developed where the polarisation difference between object and background is estimated. The How-Marshall model of polarisation distance was proposed in 2013 (How and Marshall 2014).

In 2014/15 work within this question focussed on details of circular polarisation performance. Having discovered during this project that some species use circular or elliptical polarisation instead of or as well as linear polarisation, the behavioural parameters of this were tested in a different apparatus with results indicating that this form of light was used in resolving aggressive conflict (Fig. 4.)

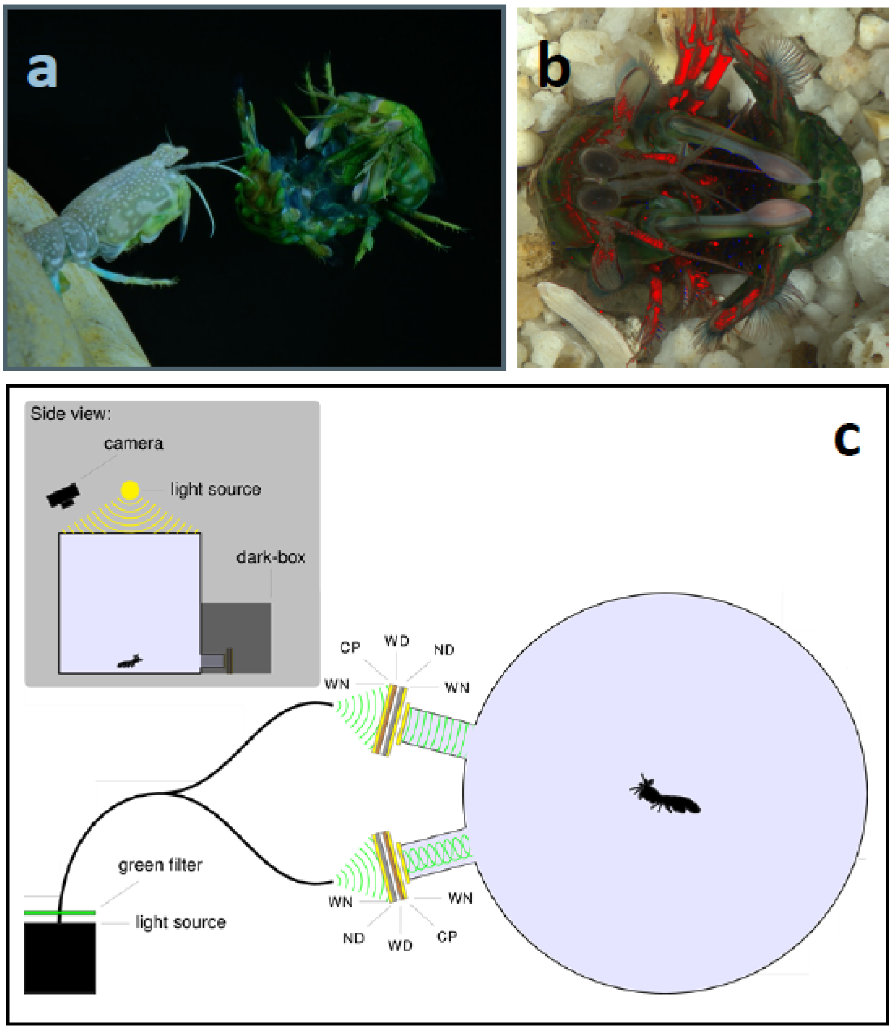


Fig. 4 Stomatopods fight over burrows and cavities that they use as homes on the reef (a). As seen in (a) and (b), they often curl into a defensive posture and (b) shows areas on the legs and body of *Gonodactylus falcatus* that reflect circular polarised light. Experimental details shown in (c) are from recent behavioural tests (Gagnon et al 2016) showing that animals investigating an arena avoid cavities containing circular polarisation, presumably as these burrows are assumed occupied by a potential competitor. This sort of information transfer using cryptic light is important both to prevent potentially deadly conflict between animals (for example, the fight seen in a ended in the death of one of the stomatopods) but also because circular polarised light is not visible to other marine creature as far as we know.

One of the areas of behavioural work this leads onto in the next proposal is to examine is the possible arms-race between stomatopods and cephalopods, both of which prey on each other and both of which possess linear polarisation vision and linear polarisation signals. Only stomatopods (as discovered through this project) exhibit circular polarised reflections and photoreceptors capable of seeing this light modality. Are they one step ahead after 400 million years?

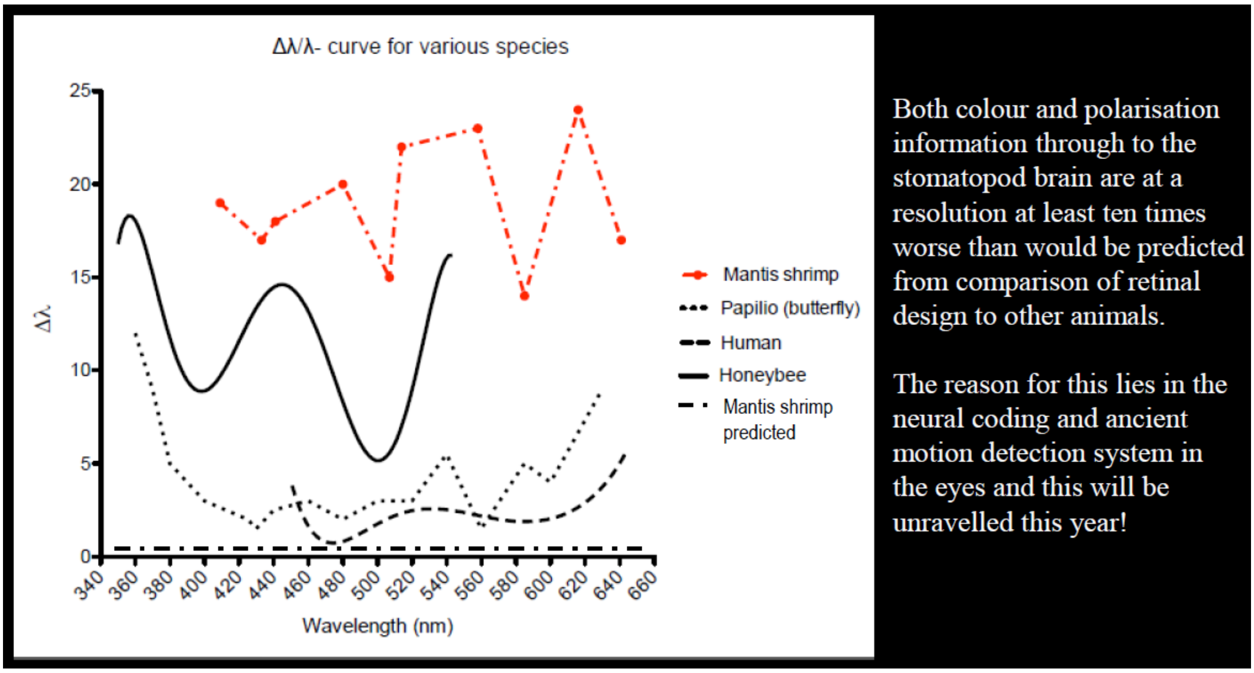
(2) We tried to discover how information is processed in stomatopod visual systems. At higher levels, we examined neural interconnectivity and processing principles at various stages of analysis in the visual system both anatomically and with electrophysiological approaches.

Question. How do the photoreceptor cells of mantis shrimps produce responses that track extremely transient changes in stimulus intensity?

Extracellular recordings of stomatopod visual responses are now complete and tell us that stomatopods have a relatively rapid response time compared to other animals (Chiou et al Unpublished). Given the rapid behaviours they engage in, including ballistic strikes and fighting behaviour, this is expected.

Behavioural results from both colour and polarisation processing streams (Question 1 above) lends support to our emerging hypothesis that rapid information processing should be possible, despite the multi-channel nature of stomatopod vision. Essentially redundant information is discarded, perhaps in a sparse-coding scenario? A surprise observation was that in fact primates (including humans) may encode colour information at higher cortical levels as stomatopods do at retinal level (Zaidi et al 2013).

Behavioural colour discrimination tests in stomatopods also indicate coarse coding of colour information (Fig. 5, Thoen et al 2014).



Both colour and polarisation information through to the stomatopod brain are at a resolution at least ten times worse than would be predicted from comparison of retinal design to other animals.

The reason for this lies in the neural coding and ancient motion detection system in the eyes and this will be unravelled this year!

Fig. 5 Spectral discrimination curves **(Δλ/λ).** Spectral discrimination curve from behavioural testing of *H. trispinosa* (red dot-dash line), theoretically modelled spectral discrimination curve (black dot-dash line) compared to other animals. This demonstrates that stomatopods encode colour at a low bit-rate and possibly do not use the same neural mechanisms for colour sense as other animals.

Resulting from both polarisation and colour behavioural data suggesting stomatopods encode visual information differently, a hypothetical process for this has been raised. This is shown in Fig. 6. Our idea is that both spectral and polarisation information is viewed as an instantaneous pattern of excitation – both along the spectrum and around the polarisation space sphere (Poincare). This pattern is read out during eye scans – just like a bar-code scanner at a store – and enables rapid information processing. Such rapid processing of information from con-specifics and other competitors may be a necessary part of their fast and violent lifestyle.

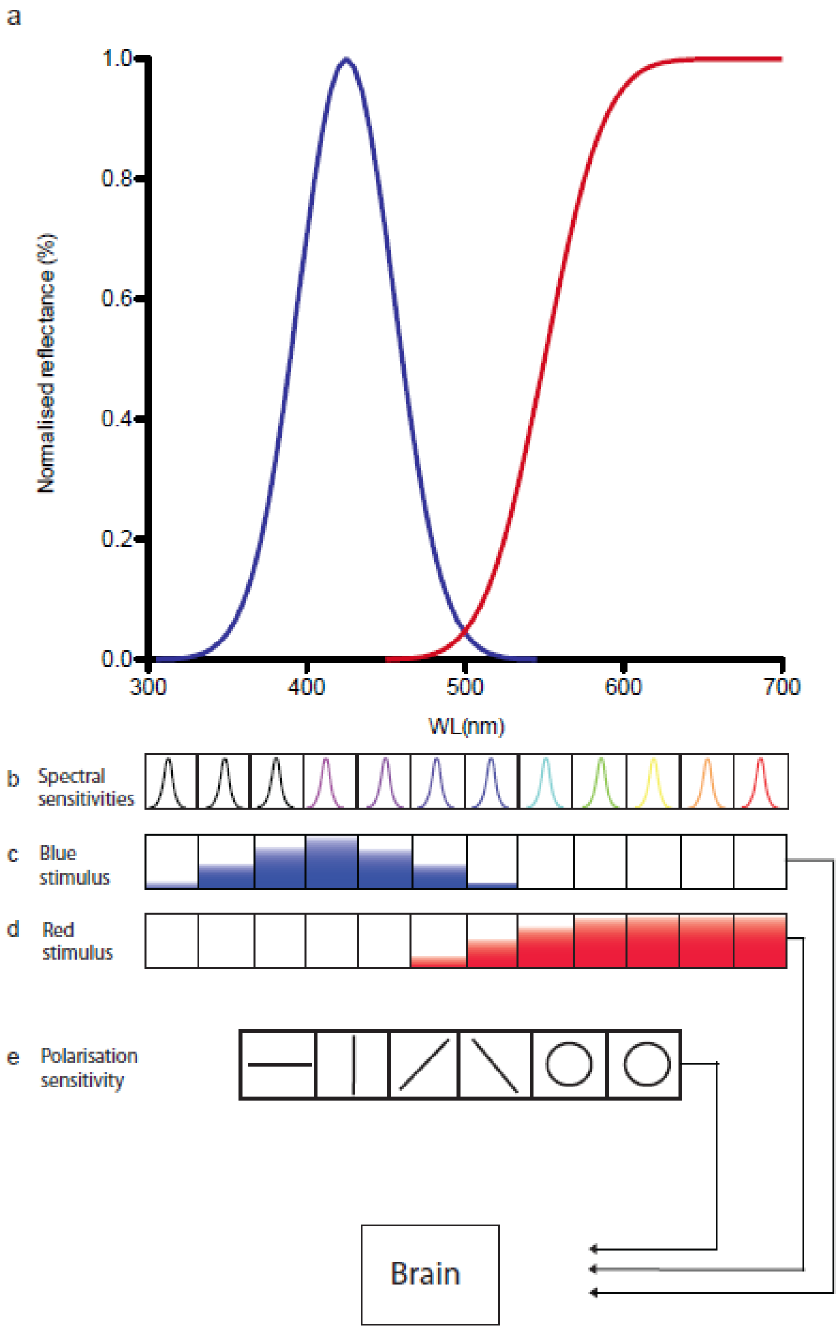


Fig. 6. Proposed processing mechanism behind stomatopod colour and polarisation vision. a) Idealised spectral reflectance from stomatopod body parts b) Spectral sensitivities throughout the spectrum divided into separate bins. c) and d) Excitation patterns of each spectral sensitivity when looking at the blue c) and the red d) reflectance spectra. e) Polarisation system in stomatopods with, respectively, linear (90° angles), elliptical (45° angles) and circular (circles) polarisation sensitivities binned in the same way as the spectral sensitivities.

Question. How are the neural circuits constructed to provide the information processing? This is a large question requiring many years work but good progress was made in 2013 – 2015. PhD students Hanne Thoen and Rachel Templin have begun high resolution transmission electron microscopy and fluorescent staining of the stomatopod nervous system to determine information pathways arising from the various visual modalities. This forms a major part of what the Marshall lab will continue with in 2016-2020 if successful in the next grant application.

There are excellent results from both Hanne and Rachel from the last four years work. This is a huge task, however Hanne went to work with Nick Strausfeld in Arizona to learn his world-leading anatomical techniques.

Discoveries fall into three categories and they are discussed here with some reference to planned future work. This work is being put to press now in a series of 4 manuscripts from Hanne Thoen's thesis.

i) **Stomatopods with different lifestyles show very different designs in neural processing units.**

The hemielipsiod bodies, that in stomatopods may be the equivalent of the memory-forming mushroom bodies in insects, appear to be large in wandering species and small in sedentary species (Figs. 7,9,10). Projections from the olfactory lobes, which are the primary olfactory centres in the crustacean brain, are divided into two branches, each terminating in the hemiellipsoid body. An interesting aspect is the fact that in some insects the mushroom bodies have been found to process visual input, either as part of a complete modality switch or by topographical division of the different modalities into separate areas. The distinct projections of olfactory neurons into the outer layers of the hemiellipsoid body in stomatopods suggests that the inner core could have a different function, perhaps processing visual information? **Hypotheses arising from this include:** i) Stomatopod hemiellipsoid bodies receive and encode visual input. ii) Stomatopod species that roam freely have larger hemiellipsoid bodies than the species living in burrows.

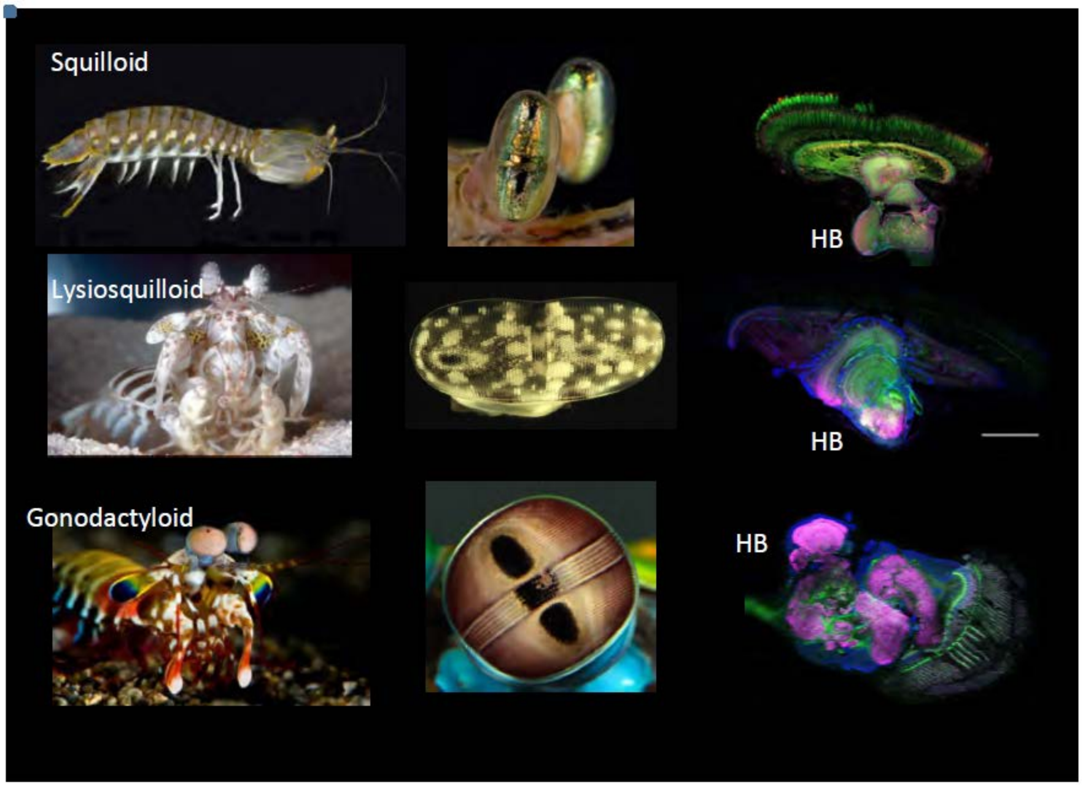


Fig.7. Representative stomatopods from the comparative study that this proposal aims to expand upon. Left – the animal, Centre – the eye, Right – fluorescent immunolabel of eye-stalk neuropils. Note the relative difference in size of the various neural integration centres such as the hemielipsoid bodies (HB). Scale 500um.

We plan to test this in the future with the following experiment. In simple terms stomatopods across several families have two main lifestyles; a) a home or burrow-bound existence as seen in *Haptosquilla* *trispinosa* for example or b) a wandering existence as seen on the reef flats or mud plain species and around the reefs. In insects, this lifestyle difference presents as two very different brain morphologies, with the wanderers having larger memory-modules (the mushroom bodies) as might be expected. Stomatopods also show differences between lifestyle types, however in their case it appears to be the hemielipsoid body, a potential mushroom body equivalent, that shows marked differences between groups. Working closely with insect and invertebrate brain experts, Nick Starusfeld, we propose to not just compare brain area sizes but attempt to manipulate them through developmental constraints.

The stomatopod experiment will involve catching the different stomatopod types (wanderers and home-bound) at larval stages – something we do every year in the field – and then allowing development of each type in relative confinement or freedom. The prediction is that wanderers that are confined to remain home for several weeks will not develop the hemielipsoid complexity seen in individuals that are allowed to wander in larger aquaria. Comparison of the neural architecture in four groups; 1 – normal adult wanderer, 2 – normal adult home-bound, 3 – developmentally constrained adult wanderer and 4 - developmentally constrained adult home-bound will give insight into how stomatopods from different ecological and phylogenetic backgrounds process information and the plasticity of this process at the neuronal level.

ii) **A new neural processing unit (neuropil) was discovered in the protocerebral complex of some stomatopod species** (Fig. 8,9,10). For the moment called Thoen's Organ, the internal anatomy of this structure is highly glomerular with each unit passing axons through the optic nerve. Our current thinking is that each glomerluar unit resolves a sub-category of visual information from the mid-band and other eye regions. Further anatomical description and close electrophysiological examination of this new brain region are planned and fortunately this lobe is situated in an area easy to record from with intracellular electrodes. Glomerular complexes in flies have been shown to receive projections directly from specific types of lobula columnar neurons and also from wide-field neurons in the lobula receiving input from the medulla. These glomeruli were shown to code noisy visual primitives from single lobula output neurons, thereby providing reliably coded information from converging sensory inputs. In *Drosophila,* relays from the glomeruli in the lateral protocerebrum projects to higher centres of processing such as the central complex through the dorsal protocerebral lobes. But they also convey information to the rest of the body through interactions with the giant descending neurons, which project to the thoracic ganglia. Although we still do not know the function of the glomeruli and why they are gathered in a large glomerular complex in the stomatopod protocerebrum, it is likely that the large variety of shapes and sizes of glomeruli indicate different types of information inputs, possibly from different types of visual modalities.

Hypothesis: Large-field lobular neurons encode spectral and polarisation modalities during scanning eye movement. These sub-categories of information are passed to Thoen's Organ in usable packets to be sent to the brain. We hope to test this in the new work proposed for 2016-2020.

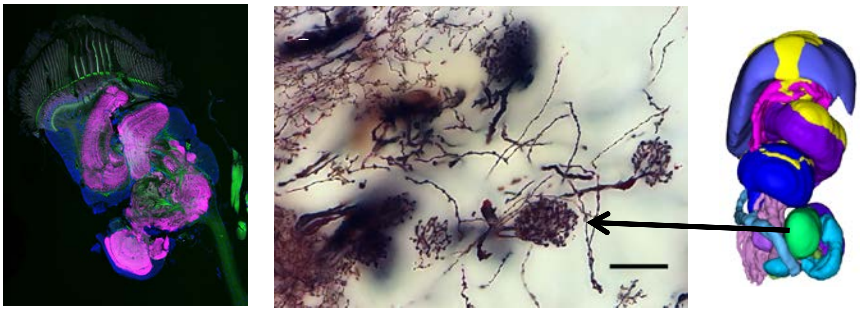


Fig. 8 Details of Thoen's Organ, the glomerular body that forms part of the protocerebral complex in gonodactyloid stomatopods (see Fig.7). Right - Three dimensional reconstruction of eye-stalk structures and rotated to show Thoen's Organ in green. Centre – Golgi stain of nodular structures within Thoen's Organ.

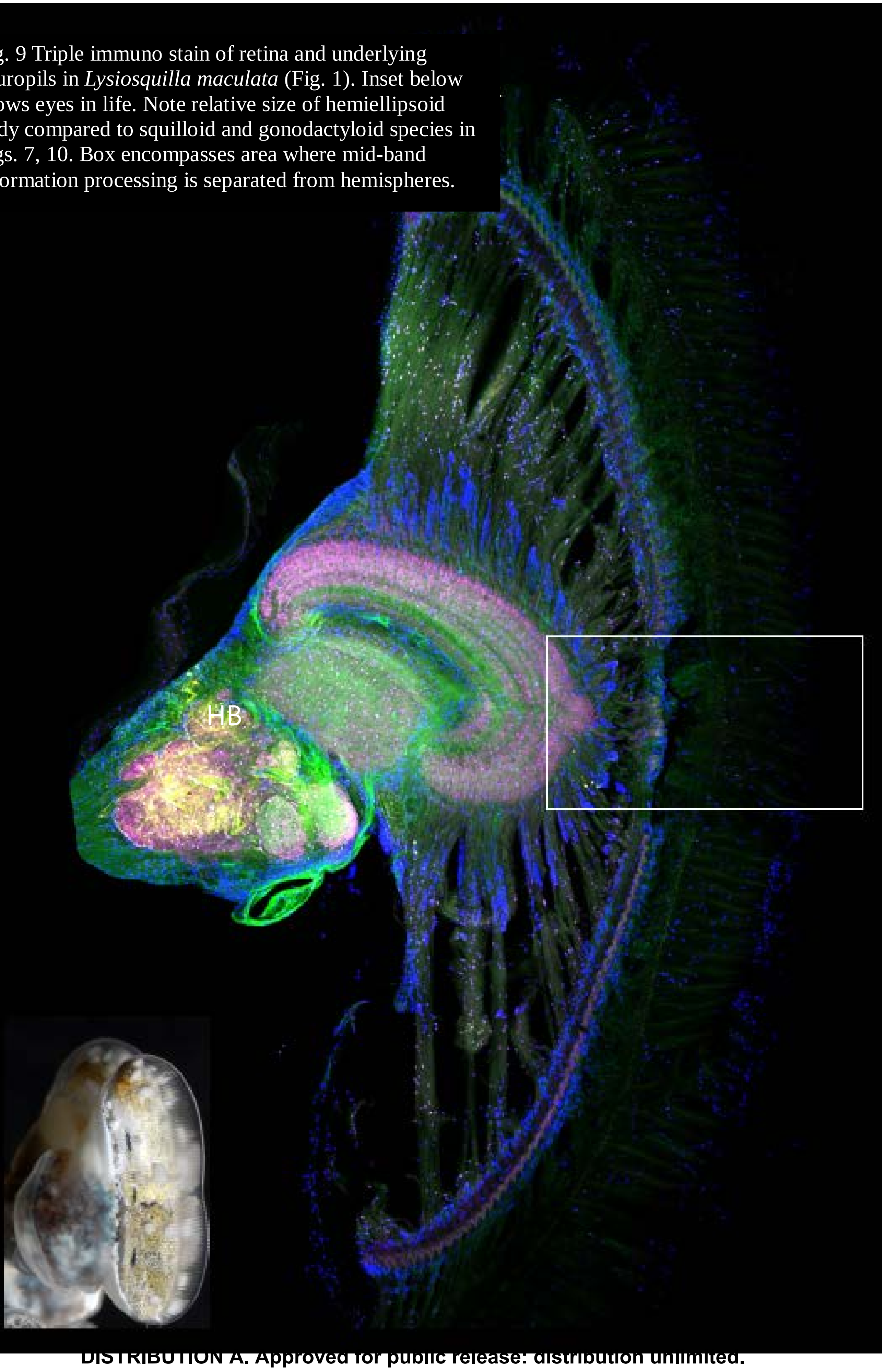


Fig. 9 Triple immuno stain of retina and underlying neuropils in *Lysiosquilla maculata* (Fig. 1). Inset below shows eyes in life. Note relative size of hemiellipsoid body compared to squilloid and gonodactyloid species in Figs. 7, 10. Box encompasses area where mid-band information processing is separated from hemispheres.

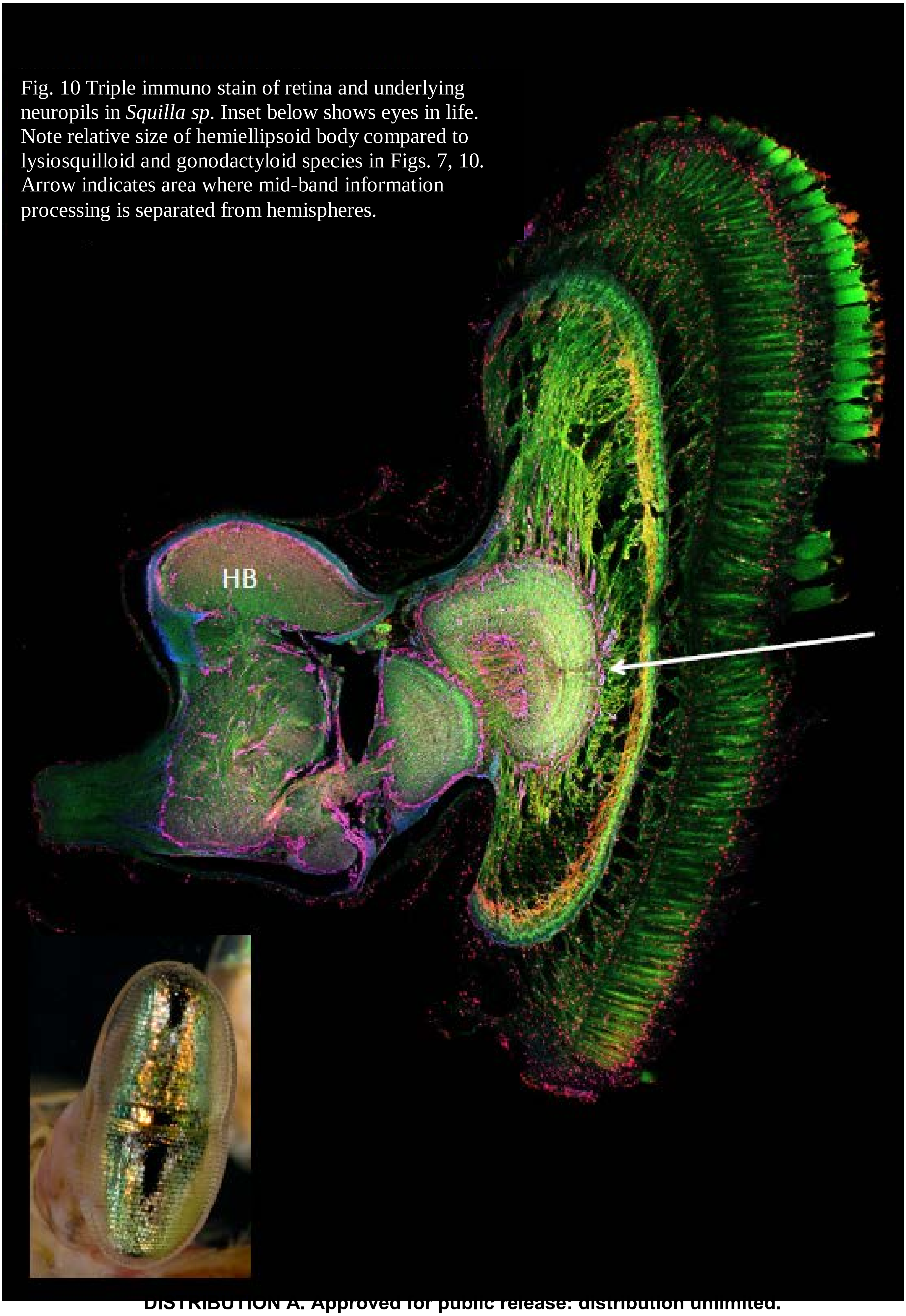


Fig. 10 Triple immuno stain of retina and underlying neuropils in *Squilla sp*. Inset below shows eyes in life. Note relative size of hemiellipsoid body compared to lysiosquilloid and gonodactyloid species in Figs. 7, 10. Arrow indicates area where mid-band information processing is separated from hemispheres.

iii) **Insects are stomatopods of the air.** Very new comparative results suggest that stomatopods may be the progenitors of dicondylic (most) insects. This surprising possibility is the brain-child (pardon the pun) of Nick Strausfeld and Hanne Thoen and comes from a comparison of the central complex of a number of insects and crustaceans. In conjunction with Nick Strausfeld, one aim here is to test this hypothesis against the other possibility that stomatopod brain structure is highly converged with insects, potentially unlikely given their different lifestyles, or is it? This has been proposed in new grant application. Very recent results have been published (Thoen et al 2017) and have led to a new hypothesis on the evolution and phylogeny of all arthropods which we are trying to get published in Nature now (Wolff et al 2017)

Hypothesis: Central complex (CX) in arthropods fall into two gross structural categories. The CX in stomatopods is more like that of insects than other crustaceans and further comparative investigation of this over several insect and crustacean lineages will provide evidence for one or the other hypothesis.

(3) To attempted to discover more of the natural complexity of visual scenes the stomatopod imaging system has evolved to see.

Question, development 1. Building a real-time polarisation camera for polarisation visual information analysis underwater. Development of real-time polarisation cameras with collaborator Gruev has been successful (Fig.11) and field tests on The Great Barrier Reef. Several new applications of this camera have resulted including the medical avenue of early cancer detection. (York et al 2014).

Question, development 2. Camouflage and communication underwater using polarized light. Imaging of animals in their natural habitat is continuing and has resulted in a series of papers and chapters published and due this year this year. Silvery camouflage was examined in 2012 with a Nature publication resulting from this work. In 2013, further camouflage and communication in polarisation space will be examined in both underwater and terrestrial habitats.

Fig. 12 is a sample of the many animals and objects examined. These include underwater polarisation targets for calibration of the system and animals that use polarisation as a source of information. In the case of the stomatopod (third from bottom) this information is used in mate selection. The cuttlefish, immediately below the stomatopod, also appears to use polarisation information for communication. As these animals lack colour vision but have very acute polarisation vision (Temple et al 2012) we hypothesise that they use polarisation in the same way as other animals use colour. Advantages of this new mode of visual communication are being investigated now and form a major component of the current grant proposal.

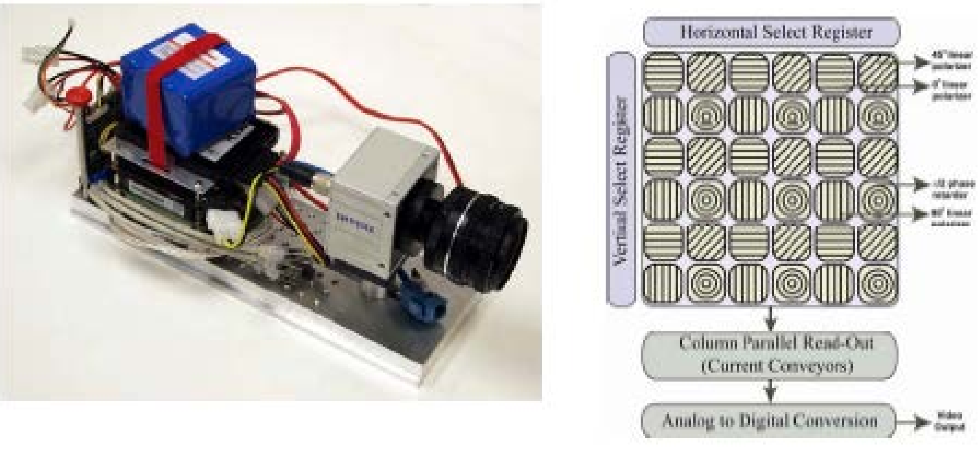


Fig. 11 First underwater real-time polarisation camera. Left – the camera, computer and battery are fitted and controlled in an underwater housing. Right – the innovative core of the system is a nanofabricated pixel mask including vertical, horizontal and 45 degree polarisation elements (in place of RGB). As implied here, a circular polarisation camera is in design now.

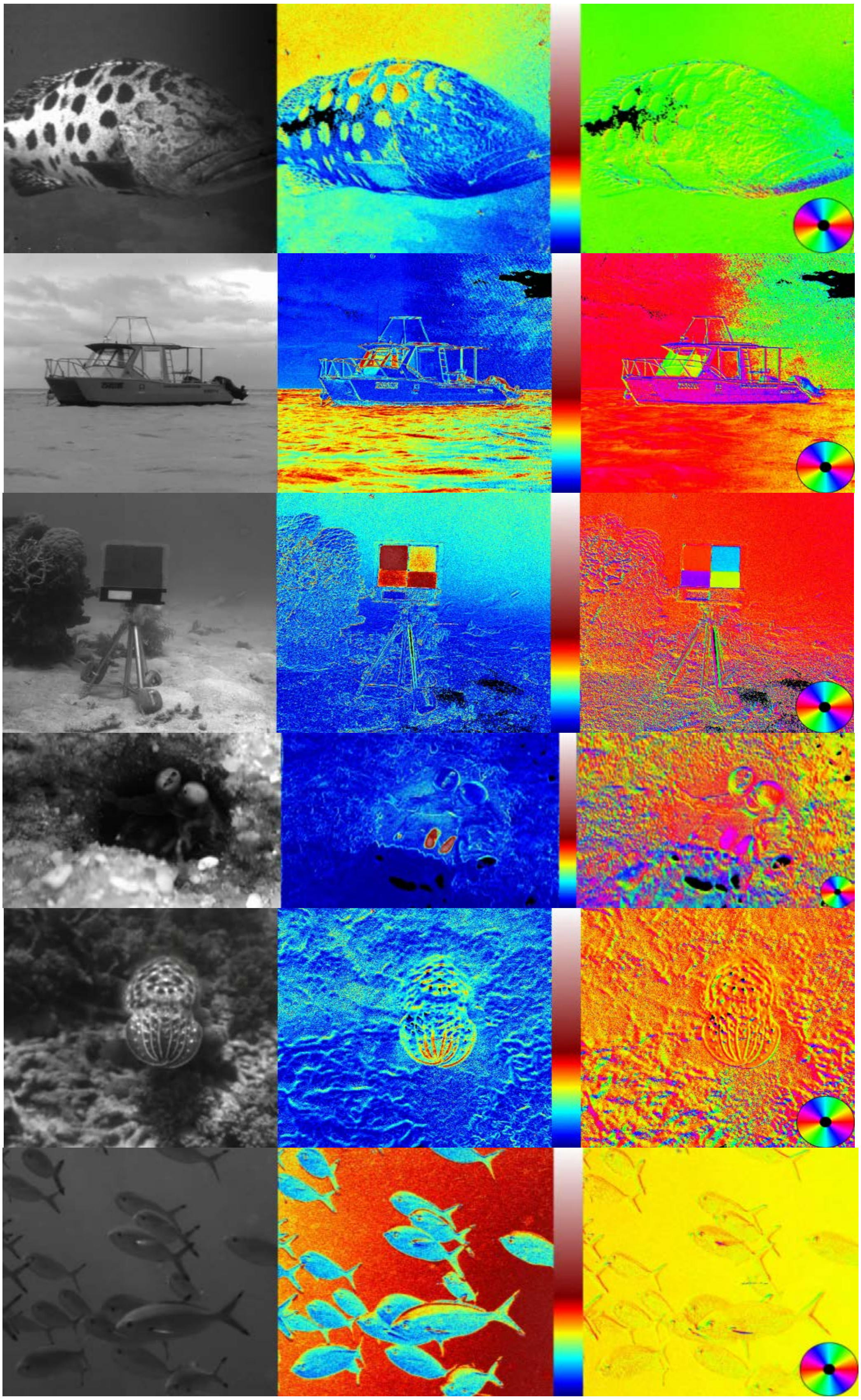


Fig. 12 Results from underwater polarising camera. False colour images of various animals and other objects showing strong degree of polarization contrast against background (middle column) and intrinsic polarization information in stomatopods, cuttlefish, reflections and underwater polarization targets.

(4) We investigated the co-evolution of visual systems, visual signals and camouflage in the natural environment.

This work was largely coordinated in the Cronin and Roberts labs, however Marshall lab. PhD student Rachel Templin has spearheaded a successful project examining the co-evolution of circular / elliptical polarisation signals and the R8 photoreceptor cells responsible for facilitating this form of vision, and its relative elipticity, in different stomatopod species. We set out with two specific questions:

Question 1. Are the polarization signals from different stomatopod species matched to species-specific elliptical polarization vision capability? New anatomical studies will be initiated this year to examine this question.

Question 2. As well as between species R8 differences (and therefore elliptical information tuning), very recent results suggest within-species differences in some species. Is this the outcome of an ‘arms race’ in which there are generalist species, able to interpret the messages of prey, break prey camouflage, and ‘read the mail’ of the unsuspecting messengers?

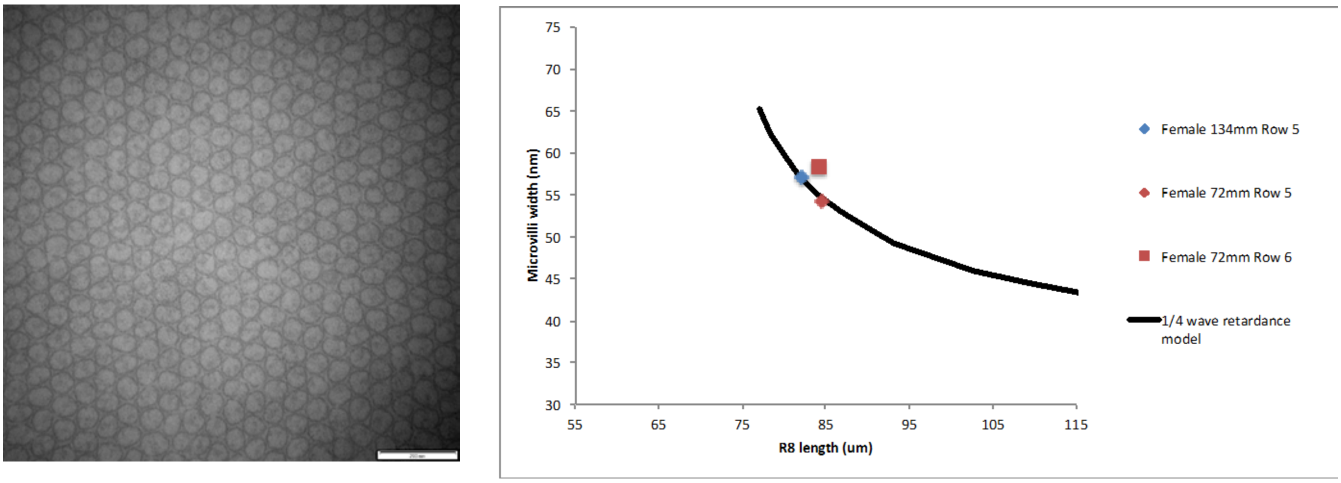


Fig. 13. Left – electron micrograph detail of the R8 cell showing crystalline arrangement of microvilli. The anatomical parameters of this structure, tube or microvillar width and the total length of the R8 cell, give different stomatopod species specific optical retardation characteristics as plotted – Right – against a theoretically perfect ¼ wavelength retardation. ¼ wavelength retardation results in circular polarisation vision (Marshall et al et al 2014) as is the case here for *Lysiosquilla ma*culata (Fig. 1).

Rachel’s PhD which is beginning to be published this year examines different stomatopod species and their R8 photoreceptors (Fig. 13) as well as their signalling characteristics and behaviours (Fig. 7) relative to circular polarisation. Our current hypothesis is different stomatopods use different elipticities and R8 cell characteristics to tune polarisation vision to specific signals, in much the same way as colour vision may be tuned to specific colours.

List of Publications and Significant Collaborations that resulted from AOARD supported project:

Overall between the four groups of CI/PIs over 80 publications resulted from this project. The 39 initially listed here are those to which I contributed, or that were lead from the Marshall laboratory. The full listing is given below.

Papers, books and monographs. All peer reviewed

1 T-H Chiou, AR Place, RL Caldwell, NJ Marshall, and TW Cronin 2012. A novel function for a carotenoid: astaxanthin used as a polarizer for visual signalling in a mantis shrimp. J. Exp. Biol. 215:584-589.

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5 Talbot, C., Jordan, T. M., Roberts, N. W., Collin, S. P., Marshall, N. J. & Temple, S. E. 2012 Corneal microprojections in coleoid cephalopods. Journal of Comparative Physiology A 198(12): 849-856.

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7 RT Hanlon, C-C Chiao, L Mathger and NJ Marshall 2013 A fish-eye view of cuttlefish camouflage using in situ spectrometry. Biological Journal of the Linnean Society.109(3):535-51.

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13 NJ Marshall, NW Roberts and TW Cronin 2014 Polarisation Signals. In: Polarized Light and Polarization Vision in Animal Sciences, G Horvath (ed). Springer, New-York. 407-442.

14 WS Chung and NJ Marshall 2014 Range-finding in squid using retinal deformation and image blur. **Current Biology**. 24 (2): R64-R65. (Front Cover).

15 HH Thoen, MJ How, TH Chiou and NJ Marshall 2014 A different form of colour vision in Mantis shrimps. **Science** 343: 411-413
(With Science Commentary and multiple other News and Views attached).

16 S Powell, V Gruev, TW Cronin and NJ Marshall 2014 Underwater polarization camera for real-time and high definition imaging. IEEE 9099-1.

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26 YL Gagnon, RM Templin, MJ How & NJ Marshall. 2015 Circularly polarized light as a communication signal in mantis shrimps. **Current Biology**. 25, 3074-3078

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35 EE Simpson, NJ Marshall, KL Cheney 2016 Coral reef fish perceive lightness illusions. Nature - Scientific Reports. 6:35335.

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Conference presentations from Marshall lab – 32 talks or poster presentations since 2012. Full listing of 74 publications resulting from four-laboratory collaboration:

Full listing of output from the project including publications from all four PIs and their group. These result from co-funding of the project through AFOSR and EOARD.

2017

SM Stieb, F Cortesi, L Suess, Carleton KL, W Salzburger, NJ Marshall 2017 Why UV- and red-vision are important for damselfish (Pomacentridae): structural and expression variation in opsin genes. Molecular Ecology doi: 10.1111/mec.13968

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T.M. Jordan, D. Wilby, T.-H. Chiou, K.D. Feller, R.L. Caldwell, T.W. Cronin and N.W. Roberts. 2015. A shape-anisotropic reflective polarizer in a stomatopod crustacean. Scientific Reports 6, 21744. doi:10.1038/srep21744

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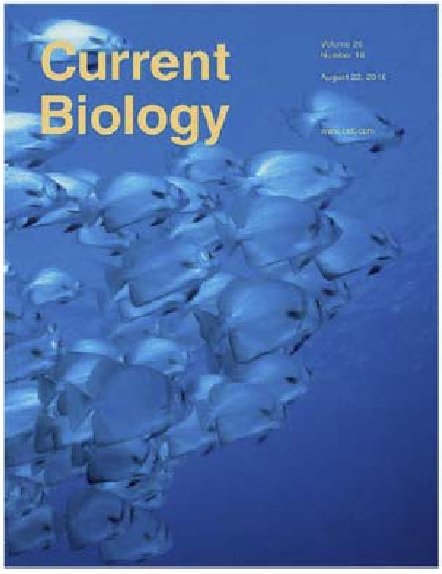
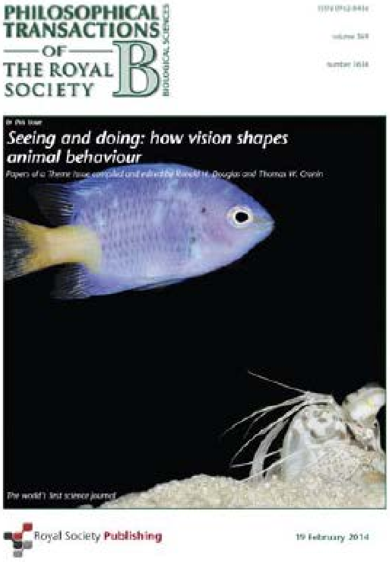
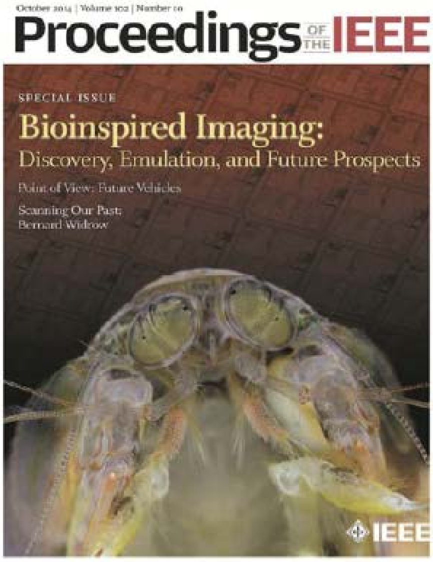
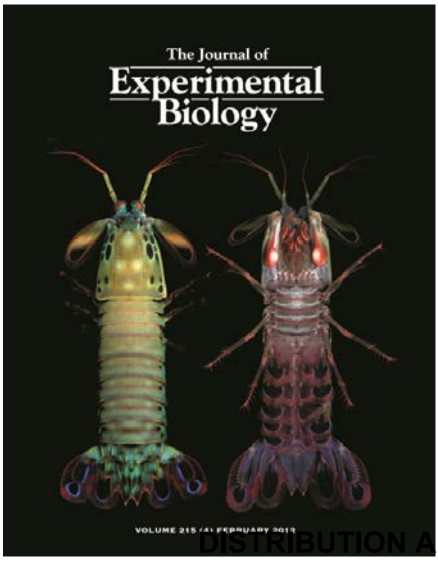
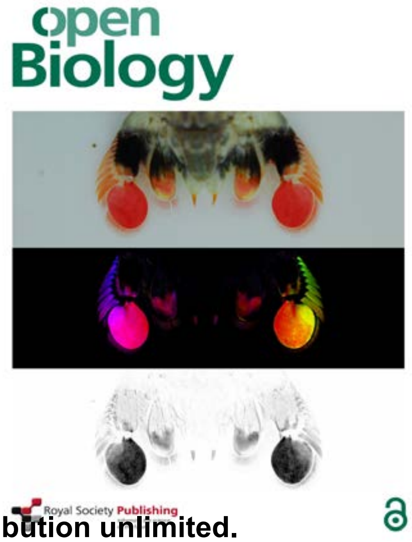
Front covers resulting from the work of combined team.





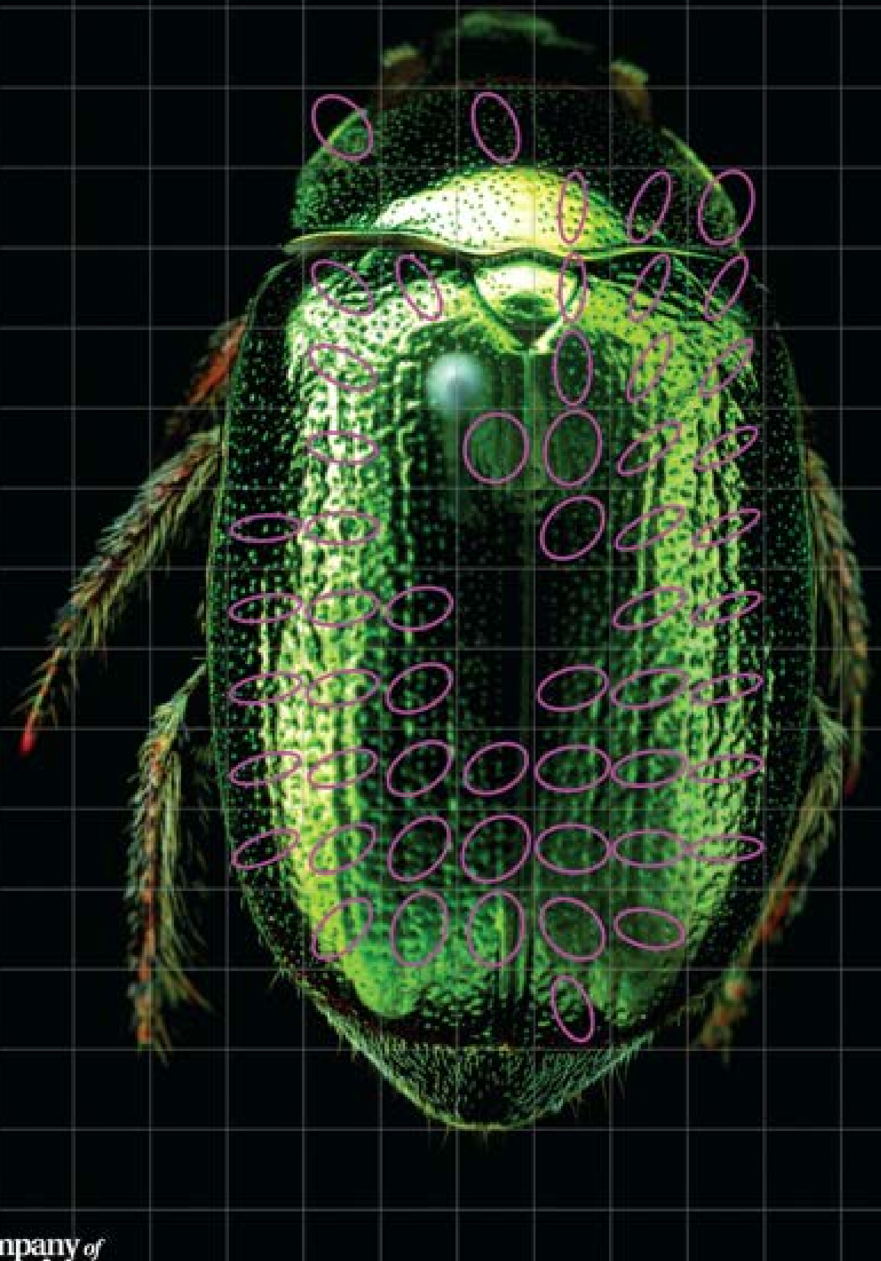






Volume 219 (16) August 2016

Journal of Experimental Biology



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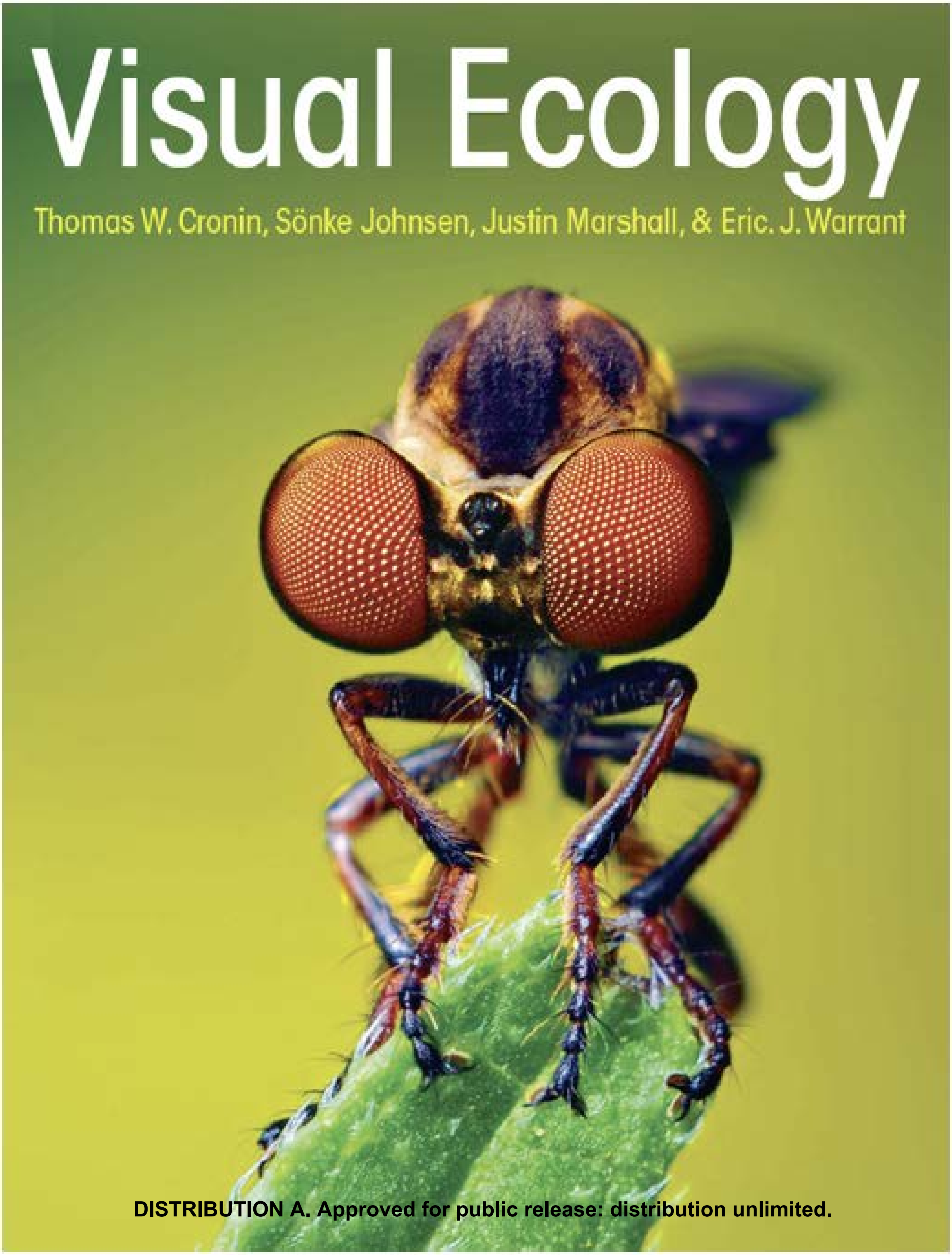
Book cover from *Visual Ecology.* Published by Princeton University Press in 2014, this book was a short-listed finalist for “Best Book in Biological and Life Sciences, 2015” and was awarded the 2015 PROSE award for “Best Textbook in Biological and Life Sciences”. Much of the information in this book was discovered through work from AFOSR-sponsored research.



Visual Ecology

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