

REVIEW

Polarisation signals: a new currency for communication

N. Justin Marshall^{1,*}, Samuel B. Powell¹, Thomas W. Cronin², Roy L. Caldwell³, Sonke Johnsen⁴, Viktor Gruev⁵, T.-H. Short Chiou⁶, Nicholas W. Roberts⁷ and Martin J. How⁷

ABSTRACT

Most polarisation vision studies reveal elegant examples of how animals, mainly the invertebrates, use polarised light cues for navigation, course-control or habitat selection. Within the past two decades it has been recognised that polarised light, reflected, blocked or transmitted by some animal and plant tissues, may also provide signals that are received or sent between or within species. Much as animals use colour and colour signalling in behaviour and survival, other species additionally make use of polarisation signalling, or indeed may rely on polarisation-based signals instead. It is possible that the degree (or percentage) of polarisation provides a more reliable currency of information than the angle or orientation of the polarised light electric vector (e-vector). Alternatively, signals with specific e-vector angles may be important for some behaviours. Mixed messages, making use of polarisation and colour signals, also exist. While our knowledge of the physics of polarised reflections and sensory systems has increased, the observational and behavioural biology side of the story needs more (and more careful) attention. This Review aims to critically examine recent ideas and findings, and suggests ways forward to reveal the use of light that we cannot see.

KEY WORDS: Polarised light, Signalling, Vision

Introduction

We humans are largely blind to the polarisation of light, and most vertebrates probably share this inability to see a form of light that is all around us (Foster et al., 2018; Temple et al., 2015). Conversely, many invertebrates, including the insects, spiders, crustaceans and cephalopods, and, in fact, a few vertebrates such as fish, are thought to use polarisation for local or global navigation or habitat selection (Dacke et al., 2001, 2002; Hawryshyn, 1992; Horváth and Varju, 1997; Labhart, 1988; Labhart and Meyer, 2002; Schwind, 1983a; Wehner and Rosset, 1985). These behaviours rely on extended-source stimuli (see Glossary), such as the celestial hemisphere or reflective lake surfaces. However, some objects in nature, such as animal skin or cuticle, as well as leaves and flowers, reflect polarisation in smaller, discrete areas. These polarised reflections may be used as signals (see Glossary) between or within species, in many respects similar to the way colours are used for communication. There is a clear distinction between an extended-source cue (see Glossary), such as a polarising light environment or

lake surface, and an animal- or plant-based signal (see Glossary) – the former is not subject to selective change through evolution, whereas the latter may be subject to selective pressures. This Review examines this divide and points to a middle ground – the polarisation contrast of small objects against large-field polarised backgrounds. In this case, while the polarisation visualised may be an extended source, it is the blocking or modification of this polarisation by a small object that may form the signal (Fig. 1). A critical question for this emerging field is whether the polarisation reflections found on animals or plants have evolved for a behavioural reason. Alternatively, as with both ultraviolet signals (Bennett and Cuthill, 1994; Cuthill et al., 2000; Hausmann et al., 2003) and fluorescent signals (Marshall and Johnsen, 2017), they may or may not be visually significant, and could be a by-product of another feature or function of the tissue (Cronin et al., 2009, 2003; Horváth, 2014). These are complex questions, but this is not to say that we shouldn't attempt to address them. With this in mind, at the end of the Review we provide a user guide for the study of polarisation signalling.

Polarised light

Polarised light in nature (Fig. 1) has recently been summarised in the extensive book by Horváth and co-authors (Horváth, 2014) and in condensed form in Johnsen (2012) and Cronin et al. (2014). Foster and co-workers also provide a comprehensive and constructive guide to aid in the design and set-up of experiments where the polarisation of light is used and controlled (Foster et al., 2018). For those wanting an introduction to the physics behind polarisation and polarised light, books such as Goldstein, (2010) and Hecht (2017) are good places to begin.

Briefly, along with colour (wavelength or frequency) and intensity ('brightness'), polarisation is a third physical property that characterizes light. Light emitted from the sun is unpolarised. As it is scattered by particles in the atmosphere and in aquatic environments, or reflected and refracted by solid and liquid surfaces, it may become polarised to different degrees. Three quantities define polarisation: angle, degree and ellipticity (see Glossary). The angle of polarisation describes the average direction in which the electric field of light oscillates, often referred to as the e-vector angle. The degree of polarisation (0–1), or percentage polarisation (0–100%), describes the distribution of those angles, ranging from 0 (or 0%) for an unpolarised light beam to 1 (or 100%) for a beam where all the waves oscillate with a single angle of polarization. In nature, it is rare to find degrees of polarisation above 70%, whereas man-made polarisers may approach 100%. Light can also carry angular momentum, a value we term ellipticity. Ellipticities of –1 and 1 describe circularly polarised light, with intermediate values describing elliptically polarised light. Linearly polarised light has an ellipticity of 0.

Polarisation vision

Polarisation vision (see Glossary) has been reviewed recently (Marshall and Cronin, 2011; Cronin et al., 2014; Labhart, 2016; Foster et al., 2018; and for specific animal groups, Horváth, 2014),

¹Queensland Brain Institute, The University of Queensland, Brisbane, Queensland, 4072, Australia. ²Department of Biological Sciences, University of Maryland Baltimore County, MD 21250, USA. ³University of California Berkeley, Department of Integrative Biology, Berkeley, CA 94720-3140, USA. ⁴Department of Biology, Duke University, Durham, NC 27708-0338, USA. ⁵Electrical and Computer Engineering, University of Illinois, Urbana, IL 61801, USA. ⁶Department of Life Sciences, National Cheng-Kung University, Tainan City 701, Taiwan. ⁷School of Biological Sciences, University of Bristol, Tyndall Avenue, Bristol BS8 1TQ, UK.

*Author for correspondence (Justin.marshall@uq.edu.au)

 N.J.M., 0000-0001-9006-6713

Glossary

Celestial field

In the context of this Review, this refers to the pattern of polarised light in the 180 deg vault of the sky above an observer in terrestrial environments. This pattern is the result of scatter in the atmosphere.

Circular/elliptical polarisation

As well as degree and e-vector angle, an electromagnetic wave may have angular momentum due to out of phase electric field components of the wave. Ellipticities of -1 and 1 (phase differences of $\frac{1}{4}$ of a wavelength) describe circularly polarised light, with intermediate values describing elliptically polarised light. Linearly polarised light has an ellipticity of 0 .

Degree of polarisation/% polarisation

The proportion ($0-1$ or $0-100\%$) of waves in a light source of a particular polarisation state. In this Review, only the degree of linear polarisation – the proportion of waves in a light source of a particular angular orientation – is considered.

Dichroism

A material is described as dichroic if it absorbs one e-vector orientation preferentially to others. Photoreceptor microvilli and some other animal and plant tissues are dichroic.

E-vector angle/angle of polarisation

The angle, relative to an external reference such as horizontal or vertical, of the oscillation of waves in a polarised light beam. E-vector is the property of a single wave but is used synonymously with angle of polarisation in biology.

Extended source/large field

Polarisation cues for e.g. navigation generally come from visual systems examining large or extended areas of sky. Other large fields of polarisation may come from reflective (e.g. lake) surfaces or from scattered light underwater.

Iridophore

A sub-class of chromatophores, colour- or light-reflecting cells that generate skin colour. Iridophore colours are produced using physical light interactions such as thin-film interference or scatter rather than absorptive pigments alone.

Maxilliped

Modified limbs or appendages that function as or close to the mouth-parts in crustaceans. In stomatopods, the second maxillipeds may have polarised and coloured reflections on some segments and these are shown off during encounters with other stomatopods and/or as general threat displays.

Null-point

A two-channel, orthogonal polarisation-sensitive visual system with maximal linear absorptions at, for example, 0 deg and 90 deg is described as having null-points relative to incoming linear polarisation stimuli at 45 deg and 270 deg, as the comparative outputs of the visual system to these different polarisation angles (e-vectors) are indistinguishable.

Phototaxis

A behavioural response or bodily movement towards or away from light or a specific quality of light.

Polarisation cue

A feature that is often (but not exclusively) an extended source of polarisation such as that in the celestial field or a lake surface used to guide behaviours such as navigation. Cues are not subject to evolution as polarisation signals are. A small polarised cue for e.g. egg laying in butterflies might be a specular leaf surface.

Polarisation sensitivity

Visual sensitivity to linearly or circularly polarised light. May be sensitivity to extended sources such as the sky or to small objects or specific signals. May or may not be distinct from polarisation vision.

Polarisation signal

One feature that distinguishes signals from cues in general is that they are subject to evolution. Polarisation signals known so far include small surfaces of integument or skin that may be used in mating display and are hence subject to sexual selection.

Polarisation vision

The ability to distinguish polarisation degree or angle independent of intensity. In its strictest sense, polarisation vision has only been shown in cephalopods and stomatopods. In this Review, a more liberal definition is used, and includes some instances of sensitivity to linearly or circularly polarised light that may confound both intensity and colour.

Snell's window

Looking up at the water surface from underwater, a viewer will see the whole 180 deg celestial hemisphere refracted into a 97 deg cone of light. Outside this window on the world above, total internal reflection makes the surface appear dark.

Specularity

Specular reflection is a property of shiny surfaces. A mirror-like reflection coming from the outer shiny surface of an object and at the reflection angle often masking or obscuring the colour beneath. Such reflections (aside from metallic surfaces) are usually plane-polarised at the angle of the surface.

so we give only a brief summary here. Photoreceptors contain visual pigment molecules that consist of two parts, a transmembrane protein, or opsin, and a chromophore bound within the opsin that absorbs the photons of light. Absorption is most likely when the e-vector or vibration direction of that photon is parallel to the long axis of the chromophore, making the whole molecule dichroic (see Glossary; Kirschfeld, 1973; Cronin et al., 2014). The term 'e-vector' in fact refers to single waves of light, but has been extended, in polarisation biology, to refer to the overall or average angle of oscillation within a beam of linearly polarised light.

The rod and cone photoreceptors of vertebrates are constructed from stacked plate-like lamellae, within which the visual pigments and their chromophores are randomly arrayed relative to incoming photons. They are therefore, on average, insensitive to polarisation, or non-dichroic, without secondary modification (Roberts and Needham, 2007; Roberts et al., 2004; Roberts, 2014). Such modification is found in the anchovy, where the membrane plates of a specific population of cones are arranged side-on and parallel to incoming light, and the cones themselves are oriented at right angles to each other (Flamarique and Harosi, 2002; Kondrashev et al., 2012). This confines the chromophore relative to incoming e-vectors. Although similar orthogonal arrays of double cones exist in many other fish species, the mechanisms for polarisation sensitivity (see Glossary) in these species are less clear (Hawryshyn, 1992, 2000; Roberts, 2014).

Invertebrate photoreceptors (rhabdomeres) are made from tubules of membrane or microvilli that also restrict or partially orient the chromophore. The microvilli are arranged side-on to the light within a photoreceptor, generally in a single direction, like a pack of drinking straws (Fig. 2). The intrinsic molecular dichroism of visual pigment within the microvilli is enhanced at the cellular level by such unidirectional membrane structures. Insects, crustaceans and cephalopods provide good examples of microvillar-type photoreceptors exhibiting such overall linear polarisation sensitivity (Fig. 2). The eyes of these animal groups often have photoreceptors arrayed with polarisation sensitivity at right angles to each other. In some species, two sensitivity directions are common and maintained throughout the whole eye and may be arrayed horizontally (H) and vertically (V) relative to the outside world (Bernard and Wehner, 1977; Wehner, 2001; Talbot and Marshall, 2010, 2011; How et al., 2014a). When considering polarisation-driven behaviours, it is important to work up from the molecular level to cellular (photoreceptor) dichroism and beyond to whole eye, head and indeed animal orientation relative to the outside world (Alkaladi et al., 2013).

Visual systems may possess more than two angles of polarisation sensitivity, potentially to remove null-points (see Glossary; Bernard and Wehner, 1977; How and Marshall, 2014). Several insect species, including bees, crickets and ants, have the potential to compare

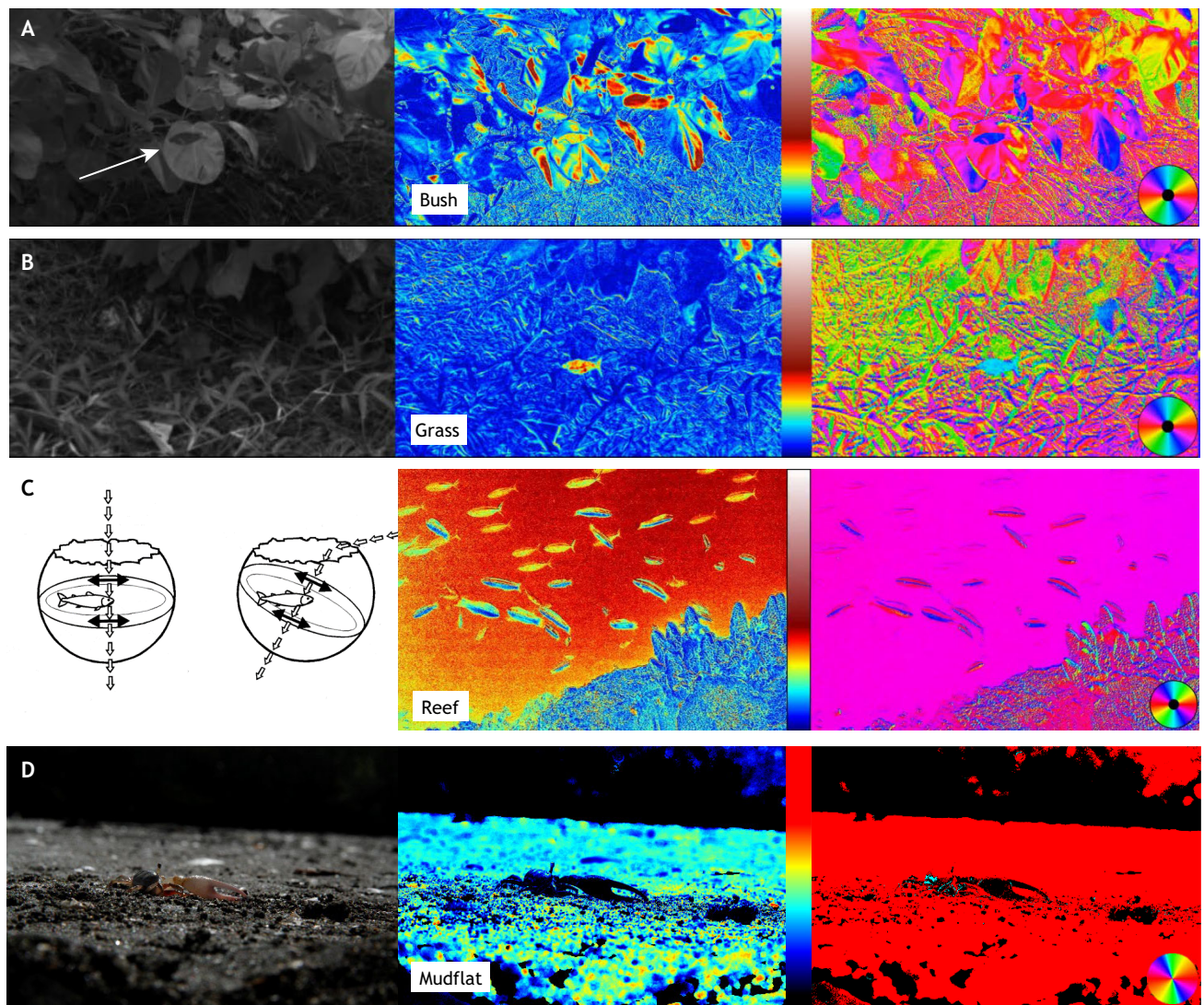


Fig. 1. Polarised light in the environment. (A) Polarisation camera images of a terrestrial scene, a waxy-leaved bush with a small cut-out polaroid fish-shape on one leaf (arrow). Left: intensity (black and white image). Centre: degree (%) polarisation, scale 0–100%, blue to white with deep-red at ~45%, the limit of most natural polarised signals. Right: angle or e-vector direction, the circular key shows, for example, orange/red as horizontal and cyan as vertical (camera details in Gruev et al., 2010 and Johnsen et al., 2016). Note the potential polarocryptic camouflage of ‘fish’ under these circumstances. (B) The same cut-out polaroid fish in a shaded-grass background with a low degree of polarisation, showing the potential for polarisation contrast and signalling. (C) Left: diagrammatic representation of the horizontal band of polarisation underwater at midday with the sun above, and the tilt of polarisation at low sun angles (modified from Hawryshyn, 1992). Centre and right: a typical reef scene at mid–late afternoon, approximately corresponding to the tilted angle in the left-most panel (scales as in A). Note the low degree of polarisation of reef substrate and high degree of background water. (D) A mud flat environment with a fiddler crab with a dry and contrasting claw. Scales and images are similar to those in A, but the left image is in normal colour. Note slightly different colour scale in middle panel so the background mudflat is ~45%.

adjacent photoreceptors that, while maintaining a local orthogonal sensitivity pair, differ in primary e-vector angle sensitivity (Labhart, 1999; Wehner, 2001). Mantis shrimps (stomatopods) possess four linear receptor types; horizontal and vertical, -45 deg and $+45$ deg, as well as left and right circular types (\odot and \ominus), arranged in spatially discrete but optically overlapping eye regions (Marshall et al., 2007, 1991; Marshall, 1988). Stomatopods are exceptional and appear to encode the variables of light differently to any other animal.

Labhart (2016) recently provided a careful summary examining whether invertebrates observing extended field cues see e-vector angle as a separate modality. He concluded that they probably do not extract angle information per se, and he extends the discussion to include potential functions of polarisation vision, including contrast enhancement and communication. While we agree with the first part of his conclusions, we suggest that polarisation does provide

information beyond that used in what may be termed ‘hard-wired’ behaviours. This is notably the case where differences between polarised objects may be learned through behavioural tests (Marshall et al., 2014).

One way to consider whether polarisation does provide information comes through a comparison with colour vision. Kelber and Osorio (2010) suggested four grades of colour vision based on the behavioural uses and underlying mechanisms involved. These were: (1) phototaxis (see Glossary); (2) innate colour preference; (3) colour learning and cognition; (4) colour categorisation, or learning and memory beyond simple choice. While there remains much to be discovered about polarisation behaviour and underlying visual mechanisms, the distinction between Labhart’s view and ours is that we do think polarisation vision crosses the grade 2–3 boundary.

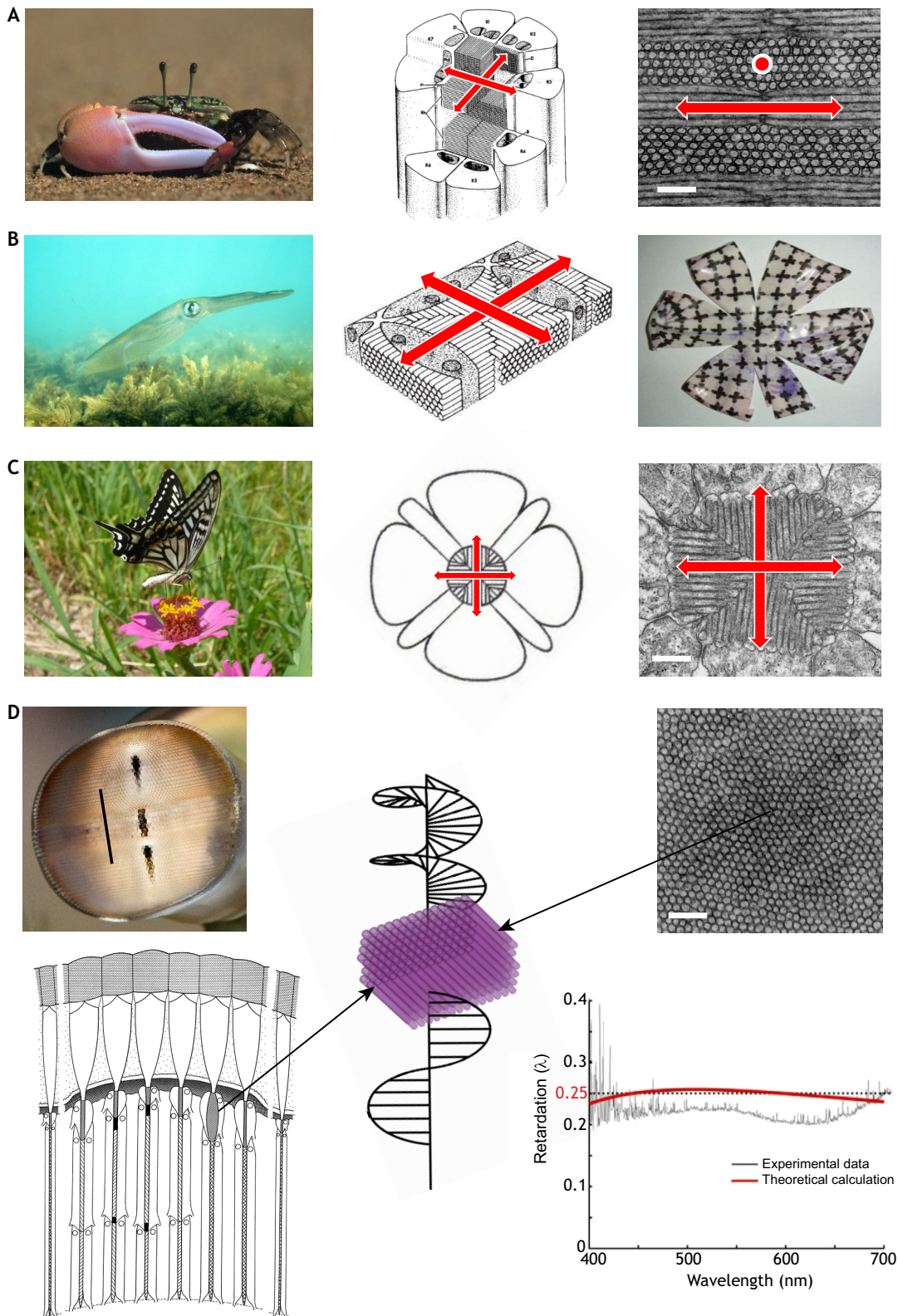


Fig. 2. See next page for legend.

Polarisation in aquatic environments

Many of the putative polarisation signals currently known are in aquatic organisms. The aquatic realm provides four sources of polarisation: (1) refraction and reflection at the surface; (2) entry into the water of the celestial polarisation pattern through Snell's window

(see Glossary); (3) the intrinsic polarisation resulting from the scatter of light from particles in the water column (similar but not identical to the sky, Johnsen, 2012); and (4) the polarisation signals that animals or other objects may generate themselves (Figs 3, 4, 5D and 6). Waterman and colleagues made excellent early studies of the

Fig. 2. Polarisation photoreceptors in a variety of species. (A) Fiddler crab (*Uca polita*; photo courtesy of Jochen Zeil) and diagrammatic 3D structure of a typical crustacean rhabdom showing interdigitating orthogonal microvilli (Centre—after Stowe, 1983) seen in transmission electron micrograph (TEM) in longitudinal section (right). Scale bar here and in TEMs below: 0.2 μm . Red arrows here and below denote bidirectional angle sensitivity. (B) Squid *Loligo paeleii* along with a 3D diagrammatic representation of abutting orthogonal microvilli in its photoreceptors (middle; after Moody and Parriss, 1961) and the retina mounted flat with local photoreceptor angles superimposed to show V- and H-orientation relative to the eye view of the environment (right) (Talbot and Marshall, 2011). (C) Swallowtail butterfly *Papilio xuthus* (photo and TEM courtesy of Kentaro Arikawa), 2D diagrammatic representation of ventral retina proximal photoreceptor in transverse section (centre) and TEM of microvilli (right). (D) Details of circular polarisation sensitivity in stomatopod retina showing the eye and mid-band region, a diagram of longitudinal section of the retina through mid-band from the area indicated by the line on photograph of the eye, the position of the specialised R8 photoreceptors in mid-band rows 5 and 6, TEM of the unidirectional microvilli of this photoreceptor (top right) and arrows to a diagrammatic representation of its quarter-wave retardation optical ability, converting circularly polarised light to linearly polarised light that is absorbed by photoreceptors below (Chiou et al., 2008b). The graph shows the remarkable spectral flatness resulting from this retardance (Roberts et al., 2009).

first three, noting that the angle of the e-vector underwater due to scatter changed with the position of the sun during the day and that with increasing depth, intrinsic polarisation rapidly dominates the polarisation light field (Ivanoff and Waterman, 1958; Waterman, 1954). In later studies, Hawryshyn, (1992) and Cronin and Shashar (2001), Shashar et al. (2004) point out that, during the day, the pattern of polarisation in background water is, on average, horizontal for much of the time and only departs from this at the relatively low solar elevations around dawn and dusk (Fig. 1C, Fig. S1).

As with the celestial field (see Glossary), this backdrop of predictable polarisation is indicative of sun position and, although rarely considered, may be used in aquatic navigation (Powell et al., 2018). More relevant here, the mostly horizontal angle backdrop may also aid the visualisation of small objects against this predictable polarised curtain (Figs 1 and 8; Fig. S1). The angle of the often orthogonal horizontal (H) and vertical (V) polarisation receptors in the eye, relative to the outside world, would provide a strong object contrast against this backdrop and is examined further below (Fig. 2; and see Sharkey et al., 2015).

Animal and plant tissues contain mostly water, and the refractive index difference between them and an aquatic habitat is less than it is in air. The result is fewer specular reflections (see Glossary) underwater than would result from, for example, wet or waxy leaves, water or mudflat surfaces that polarise light for a terrestrial viewer (Fig. 1). While the background in water may be relatively highly polarising (40–60% maximum in open ocean and more like 30% near reefs; Cronin and Shashar, 2001; Ivanoff and Waterman, 1958; Waterman and Westell, 1956), underwater structures and benthic areas, such as kelp and reef structures, are very low in degree of polarisation (Fig. 1C). One corollary of this is that intentional signals of polarisation may contrast well, boosting the efficiency of polarisation over colour for signalling in such a low-polarisation but colour-confusing background (Figs 3B and 4D). Both stomatopods and cuttlefish display against the benthos, and both may be superbly camouflaged in terms of colour, pattern and intensity; thus, polarisation may provide a means of communication that only they can see (Figs 3 and 4).

Polarising signals and polarisation information

The information conveyed by polarisation signals in any species is poorly understood. Detecting a polarised object against a

background or detecting an unpolarised object against a polarised background is different to discriminating some form of polarisation information within the object. In common with colour, it is important to consider whether the potential signal conveys information about, for example, mate quality, territoriality or a food source. If so, is there evidence that evolution has optimised conspicuousness and to which visual systems?

Polarised food

At the moment, with the exception of humans (who use polarisation cameras to judge fruit quality on a factory conveyor-sorting system; Boyer et al., 2016), little evidence exists for polarisation vision being used to locate food or judge its quality. A few authors have noted that flowers, and indeed other areas of plants, reflect polarisation patterns. In behavioural experiments using bumblebees, Foster et al. (2014) constructed flower-like targets containing polarisation patterns to show that the bumblebees could learn to associate polarisation information with a food reward. This idea needs further confirmation – given all the other stimuli a flower presents at close range, such as colour, smell and taste, the addition of polarisation seems superfluous. Also, as these and other authors note, the receptors that mediate this behaviour have not been determined (Heinloth et al., 2018; Mathejczyk and Wernet, 2017). It should also be noted that reward may drive learning that is out of context. For example, behavioural choice experiments in stomatopods used polarised stimuli and a food reward (Marshall et al., 1999a,b; Chiou et al., 2008b). However, polarised food in the natural environment of stomatopods has yet to be found. Stomatopods, bees and other animals may be able to associate polarisation and food in the laboratory despite polarisation being irrelevant in a normal foraging context.

It is important to distinguish whether the polarisation of the object itself is the substrate for choice or whether contrast against a polarised background is enough. The detection of a small polarised or non-polarised object against an unpolarised or polarised background, respectively, may enable identification of something worth eating. Squid (Shashar and Cronin, 1996; Shashar et al., 2000, 1998), and both terrestrial and aquatic insects (Buschbeck et al., 2007; Schwind, 1983b, 1984; Horváth, 2014) or their larvae may use polarisation contrast in predatory events.

Mate choice, habitat choice, polarisation and colour

It has been proposed that the freshwater swordtail fish uses polarisation reflections for mate choice, with females preferring to associate with males that reflect a higher degree of polarisation (Calabrese et al., 2014). These fish are a well-known model system for the study of sexual selection, and manipulations of the strikingly asymmetrical tail ‘sword’ length and colour influence mate choice (Rosenthal and Lobel, 2006). Some of their colours are structural, produced using thin film interference, a reflective mechanism that also polarises light. These sorts of colours and their concomitant polarisation are common in both freshwater and marine fish (e.g. pufferfish *Canthigaster papua*; Fig. 5D). Whether polarisation and colour signals are combined in such mate-choice systems is not clear. The experiments manipulating the polarisation reflections of swordtails relied on an increase in polarised light illumination in a choice chamber environment. It is difficult to determine which element of the environment – fish or background – elicited the response difference. Furthermore, while some attempt was made to monitor colour and brightness changes during experimental manipulations, these variables were kept below an assumed threshold of detection rather than varied over a large range. In order

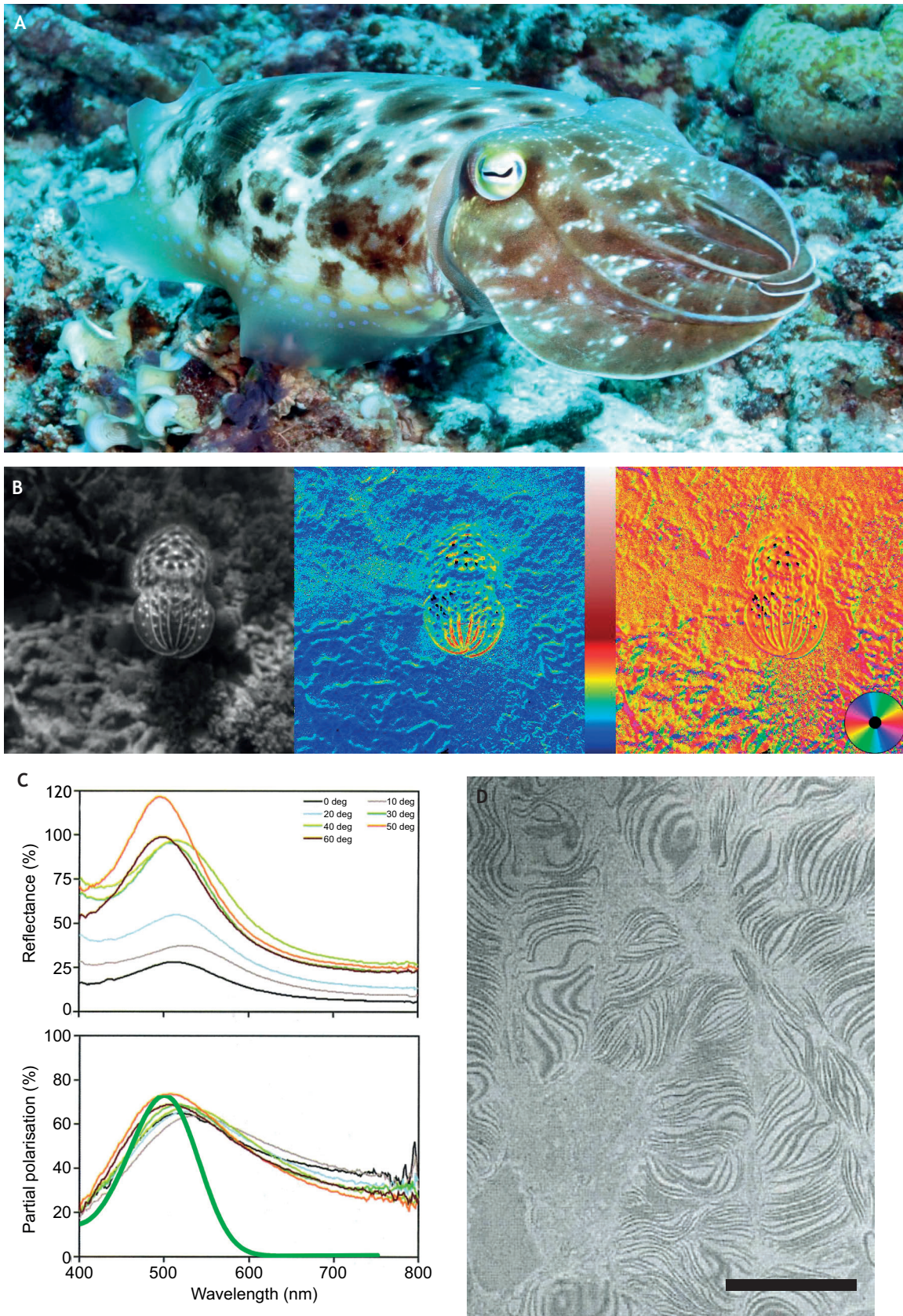


Fig. 3. Linear polarisation signals in cephalopods. (A) *Sepia latimanus*, the broad-club cuttlefish. (B) Polarisation video images (as detailed in Fig. 1) showing highly polarised arm-stripe signals in the centre (% polarisation) panel. (C) Details of arm-stripe reflector in cephalopods, reflectance (top graph) and % polarisation (bottom graph) measured at several angles of tilt. The similar % or degree of polarisation at all angles of measurement clearly shows the independence of this signal to angles of view also. The thick green curve shows the spectral sensitivity of cuttlefish, showing a good match to maximum polarisation efficiency at ~500 nm. TEM of arm-stripe iridophores showing localised random reflection direction allowing the angle independence of % polarisation (Chiou et al., 2007). Scale bar: 7.5 μ m.

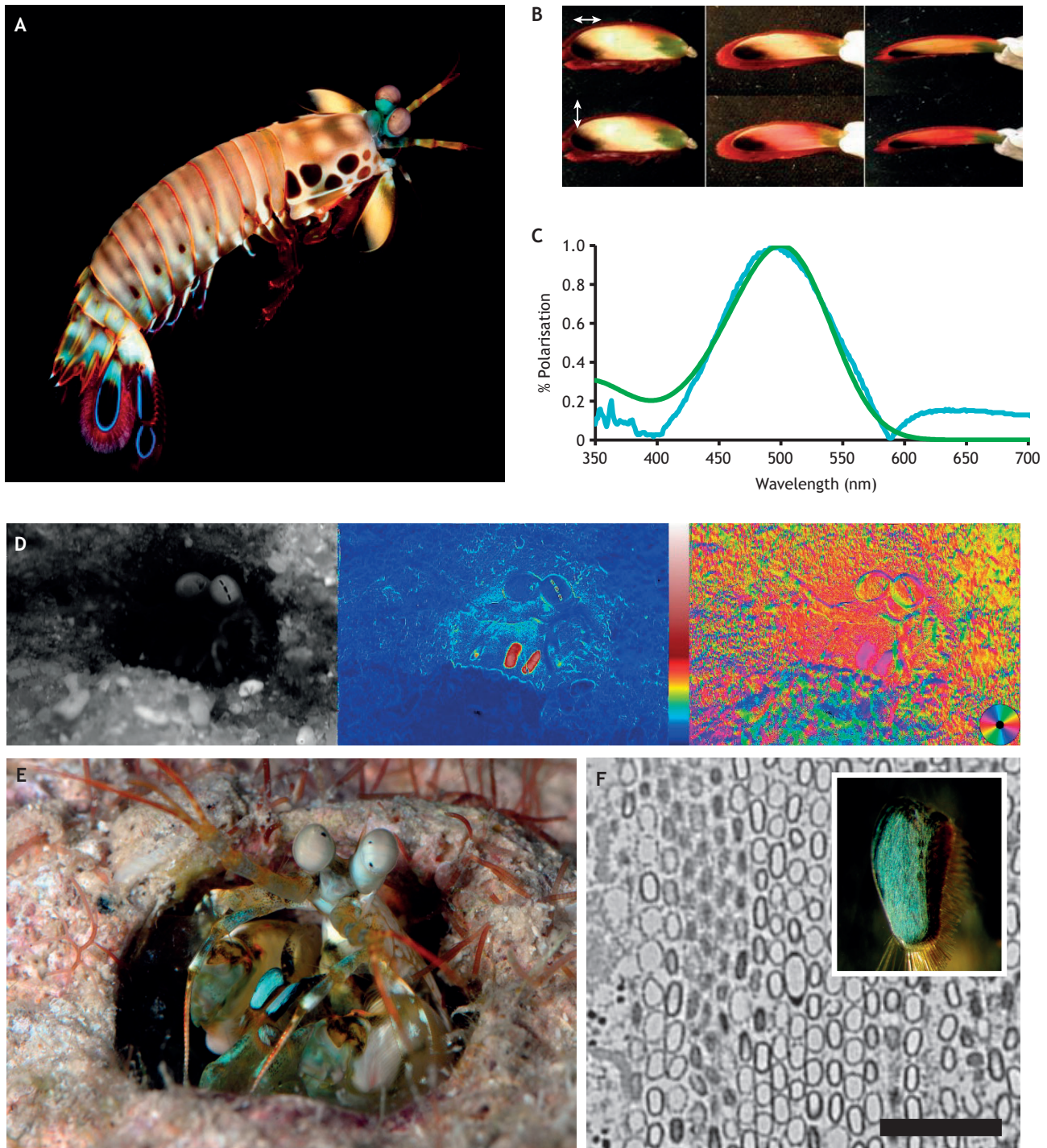


Fig. 4. Linear polarisation signals in stomatopods. (A) *Odontodactylus scyllarus* (photo courtesy of Roy Caldwell) showing polarising antennal scales (B) photographed through H and V linear polarising filters denoted by white arrows. Maximal % polarisation is reached at a ~45 deg tilt angle of the scale (far right pair and appearing dark red to the vertical analyser) and is measured in related species in C (blue line). Green line shows that linear polarisation receptor spectral sensitivity is matched to polarisation reflection spectral efficiency in many stomatopods, as in cuttlefish (Fig. 3C), with peak sensitivity close to 500 nm (Chiou et al., 2012). (D) *Haptosquilla trispinosa* polarisation images (scales as in Fig. 1) showing highly H-polarised segments of maxillipeds corresponding to blue areas in E (photo courtesy of Roy Caldwell) and F (inset). (F) TEM of the elongated vesicular structure of the blue polarised maxillipeds of *H. trispinosa*: an anisotropic, dichroic, scattering nanostructure (Jordan et al., 2016). Scale bar: 0.5 μ m.

to determine that polarisation, or indeed colour, is detected as an independent variable, this luminance difference control measure is essential (Bernard and Wehner, 1977; Foster et al., 2018), especially given the uncertainties surrounding vertebrate polarisation sensitivity (Roberts and Needham, 2007; Roberts et al., 2004; Roberts, 2014).

Both electrophysiological (Hawryshyn et al., 2003) and behavioural evidence (Mussi et al., 2005) suggest that the green chromis damselfish *Chromis viridis* responds to polarised light. The fish are able to discriminate between different angles of polarisation associated with a food reward in a two-way choice test and do so independently of

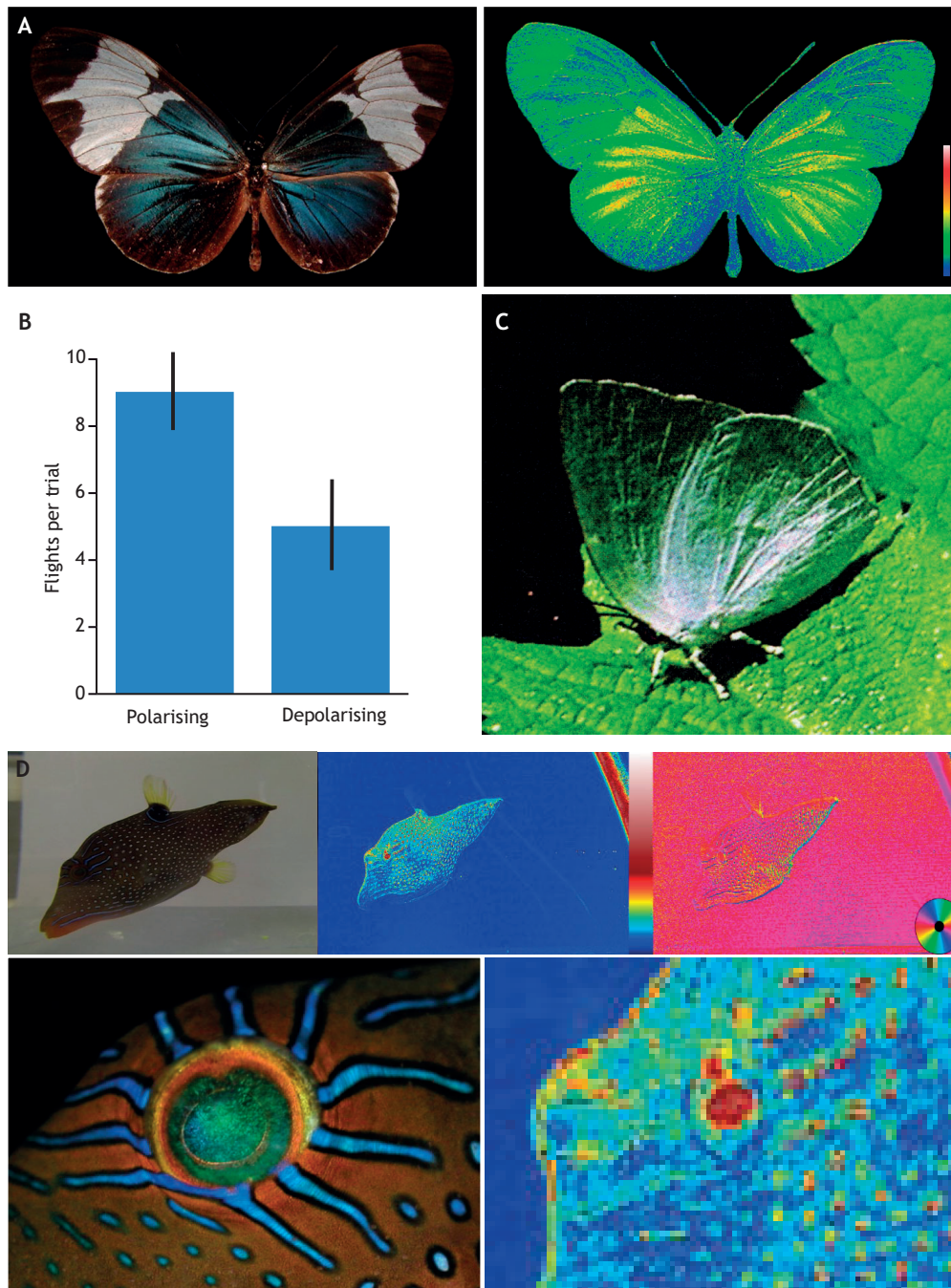


Fig. 5. Functional and probable non-functional linear polarisation signals. (A) *Heliconius cydno*, a nymphalid butterfly, in colour and % polarisation image (right, scale similar to Fig. 1). (B) Preferential mate choice frequency of males given females to interact with under normal polarising conditions and with a de-polarising filter placed over the wings (Sweeney et al., 2003). Bars indicate s.e.m. (C) The butterfly *Curetis acuta* with wings closed is thought to achieve polarisation and colour camouflage among leaves in shade by reflecting both to match the background, probably in a similar manner to that shown in Fig. 1A. (D) The toby pufferfish (*Canthigaster papua*), in common with many marine and freshwater fish, displays iridescent coloured markings that are also polarising. This includes the iridescent cornea and blue areas that, while having colour and eye-shade function (Lythgoe and Shand, 1982), are most likely non-functional polarisation signals that are not visible to this and other fish that lack polarisation vision.

brightness (to 90% variation) and down to an angle difference between 20 and 25 deg. The green structural colours of *C. viridis* also polarise light to a small degree (personal observation), so it is tempting to suggest that they may respond to the polarisation of reflections from conspecifics or indeed other species in their shallow water environment (Figs 3, 4 and 5D). There is, however, conflicting evidence for polarisation sensitivity in this fish. *C. viridis* were tested using a looming stimulus visible in polarisation contrast only (similar to that in Fig. 7) to look for escape responses. In this and three other fish species – the goldfish (*Carassius auratus*), the zebrafish (*Danio rerio*) and the ambon damselfish (*Pomacentrus ambionensis*) – no response was found, implying a lack of polarisation sensitivity. Control looms of intensity contrasts engendered strong escape reactions in all species (Pignatelli et al., 2011 and see Foster et al.,

2018). However, a large object loom (Pignatelli et al., 2011) and a small object choice (Mussi et al., 2005) represent tests of different behaviours, and more work is needed in order to determine the polarisation vision capability of these and other fish species.

Stronger evidence exists for polarisation signals in mate choice among invertebrates. Males of the stomatopod crustacean *Haptosquilla trispinosa* present polarising regions on forward-facing maxillipeds (see Glossary) to prospective mates (Fig. 4). Chiou and colleagues removed the polarisation from this signal and showed a reduction in mate preference (Chiou et al., 2005). However, the area shown in display is also an intense blue, and stomatopods have superb colour vision (Marshall and Arikawa, 2014; Marshall et al., 2007). As the manipulation also changed the colour, it was not possible to disentangle colour and polarisation components of the signal

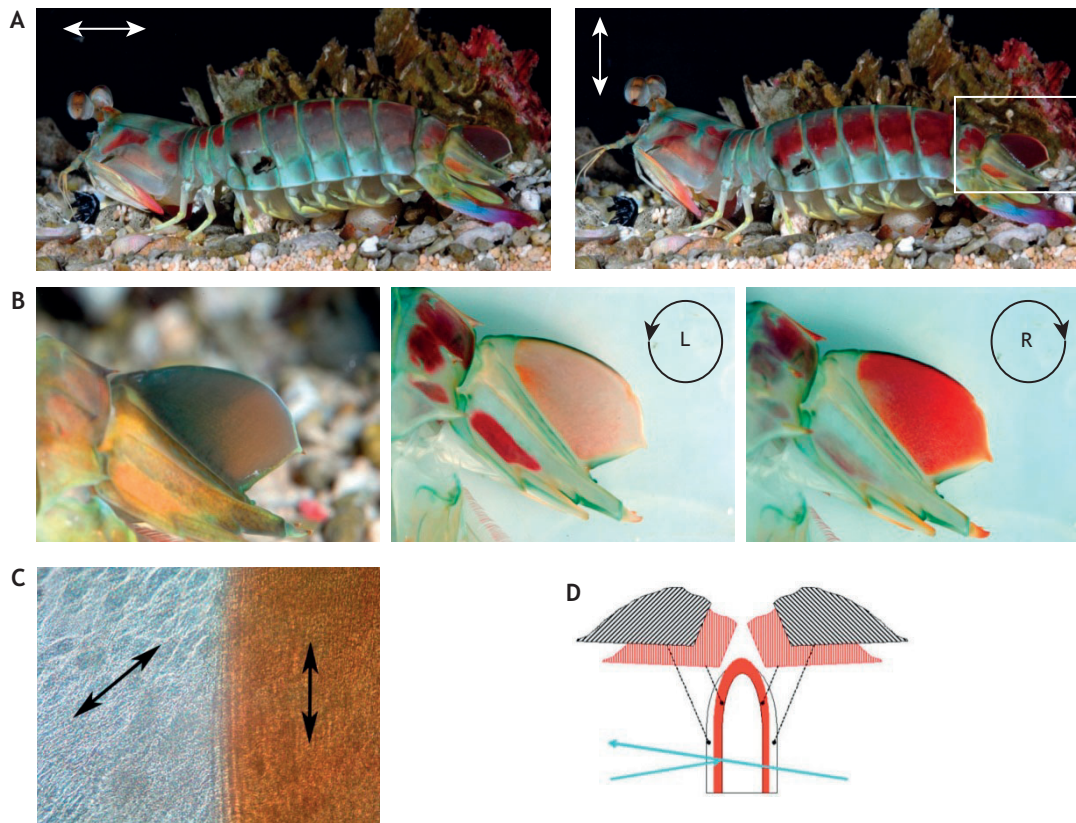


Fig. 6. Circular polarisation signals in stomatopods. *Odontodactylus cultrifer* has both linear and polarising reflections. (A) Linear reflections from abdominal and thoracic areas shown by photographing through linear H- and V-polarising filters (denoted by arrows). Note that the telson keel area does not alter reflectance (boxed area). (B) Keel from the boxed area in A shown in detail and photographed through left- and right-handed circular polarising filters. The colour change indicates circular polarising activity. (C) Section of keel showing a red-orange layer, which is presumed to be an astaxanthin linear reflector (Chiou et al., 2012), and a clear layer, which is presumed to be a quarter-wave retarder with its fast axis at 45 deg to the linear reflector underneath, resulting in circular reflection. Note that circular polarisation is not from a chiral structure as known in beetles (Vukusic and Sambles, 2004). (D) A diagram showing the currently assumed structure of the keel-reflector, in cross section (centre), that allows left-handed reflection from one side and right-handed reflection from the other.

completely. However, the comprehensive and comprehensively proven polarisation sensitivity in stomatopods (Marshall et al., 1991, 2007; Kleinlogel and Marshall, 2006), and the very high degree of polarisation of this putative signal (Fig. 4; Chiou et al., 2005) suggests polarisation as part of this communication code. Interestingly, some other *Haptosquilla* species may also combine blue and polarised reflections, while others only use blue non-polarising colouration (How et al., 2014b). Several other stomatopod species also appear to use polarisation in mate choice, and the close-range examination and display behaviours that they engage in (Figs 4 and 6 and Movie 1) suggest that judgments are being made based on the quality or content of the signal area itself.

Fiddler crabs may also use both colour and polarisation in signalling. They are probably dichromatic (with UV and green sensitivities), enabling some colour vision, but are also sensitive to H- and V-oriented polarised light (Detto, 2007; Zeil and Hemmi, 2006; Zeil and Hofmann, 2001). They are famous for their coloured claw signals, used by males to attract females and ward off rivals, and the colour and motion information content in this behavioural arena has been intensively studied (How et al., 2009; Zeil and Hemmi, 2006; Fig. 1D and Fig. 2A). A wet carapace or shiny claw also produces a polarising signal that conspecific females or rival males may attend to (Zeil and Hofmann, 2001). In this case, the polarisation is due to surface specularly (Fig. 1A) rather than an intrinsic photonic mechanism within the carapace itself as exemplified in Figs 4 and 6. Even a dry non-polarising crab

against a strongly H-polarising wet mud-flat background provides a polarised object background contrast (Fig. 1D). Fiddler crabs are known to be exquisitely sensitive to both angle and degree differences in polarised contrast in behavioural experiments (How et al., 2014a,b, 2012, 2015). This is an example where the intrinsic polarisation of the signalling object may be less important than the overall scene contrast provided by a polarised or an unpolarised object in a large-field polarising background.

Moving further into terrestrial habitats, depolarising filters were used to reduce wing polarisation in female *Heliconius cydno*, a nymphalid butterfly, lowering mate choice frequency among males (Fig. 5A–C; Sweeney et al., 2003). Polarisation-based mate choice is suggested to be more frequent in forest-dwelling species of the nymphalid butterflies. Under a forest canopy, polarised light is rare (Fig. 1B); thus, the polarised flashes of a wing are a conspicuous beacon for polarisation-sensitive eyes (Douglas et al., 2007). Efforts were made to control for intensity in the *H. cydno* experiments, and their wings are relatively dull compared with those of some butterflies. However, colour patterns are still present and, as with stomatopods, the interaction between colour, intensity and polarisation in butterfly mate choice needs further investigation, particularly given the complexity of their colour vision and complex photoreceptor distribution (Arikawa et al., 1987; Arikawa and Stavenga, 1997; Marshall and Arikawa, 2014; Stavenga et al., 2001).

Swallowtail butterflies (*Papilio aegaeus*) also combine modalities and need the correct combination of colour and polarisation to choose

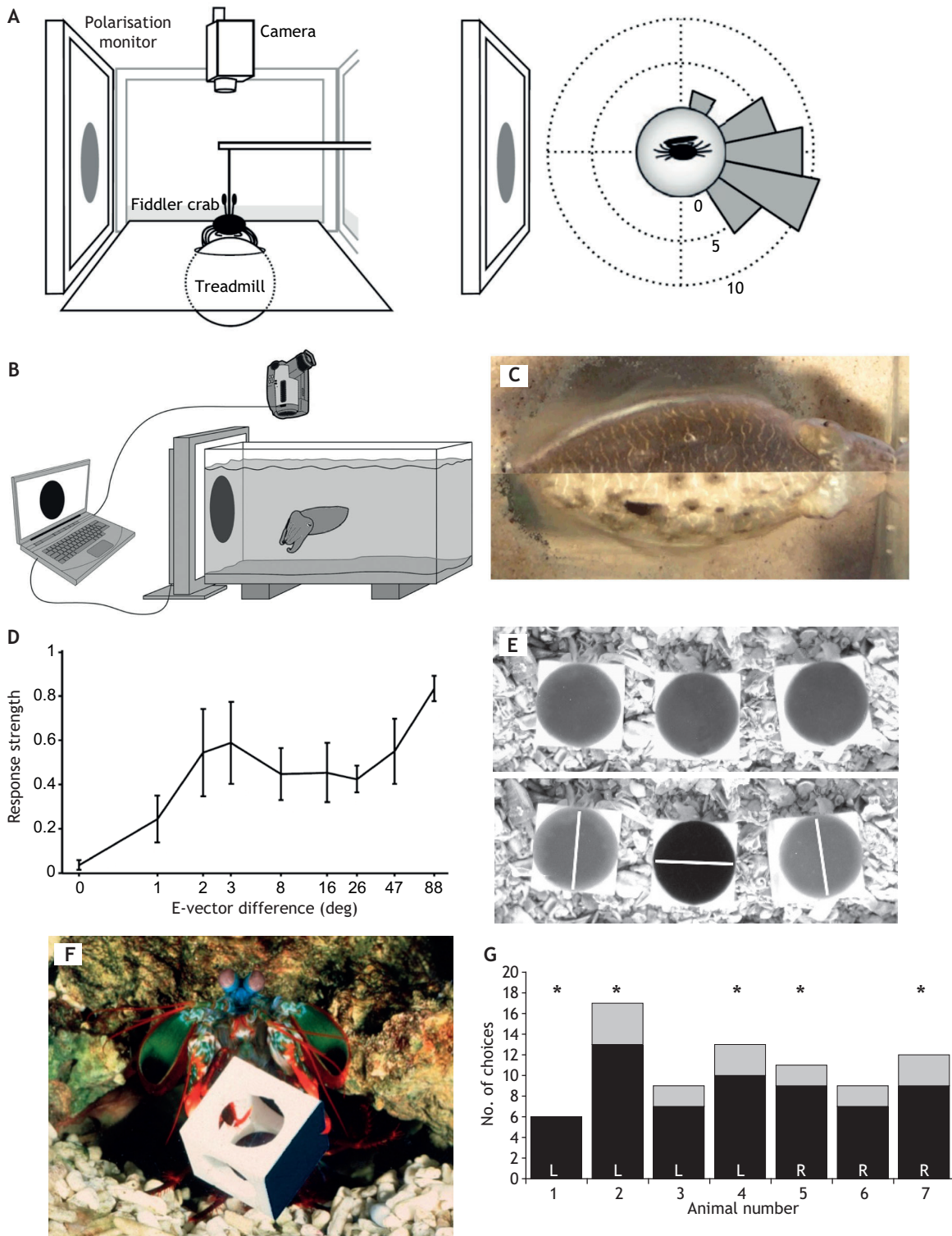


Fig. 7. Behavioural assessment of polarisation vision in the lab. (A) A fiddler crab on a floating ball treadmill and a polar-graph of the escape reaction (histogram showing the number of runs and their direction) to looming stimuli presented to the crab from a computer monitor that shows polarisation contrast only. Animals without polarisation vision see no image on the screen (Pignatelli et al., 2011; How et al., 2012). (B) The same experiment for cuttlefish; again, the looming stimulus is only visible to polarisation-sensitive animals. (C) The cuttlefish reacts to the loom shown by skin-pattern change (split-screen image of pattern before and after loom, top and bottom, respectively). (D) Graph showing high sensitivity of cuttlefish to polarisation angle difference of the stimulus down to 1.5 deg (Temple et al., 2012). Bars show s.e.m. (E) Feeding containers with linear polarising filters (top) that are invisible until photographed through a V-polarising filter (bottom). The white lines were drawn after to show the angle orientation of the filters. (F) A stomatopod handling a feeding container in a choice test where both linear polarisation e-vector angle (as in E) and circular polarisation handedness can be discriminated. (G) Results for animals trained to left- and right-handed reflecting feeding containers, as indicated by L or R. Asterisks indicate statistical significance based on a Fisher's exact test (Marshall et al., 1999a; Chiou et al., 2008b).

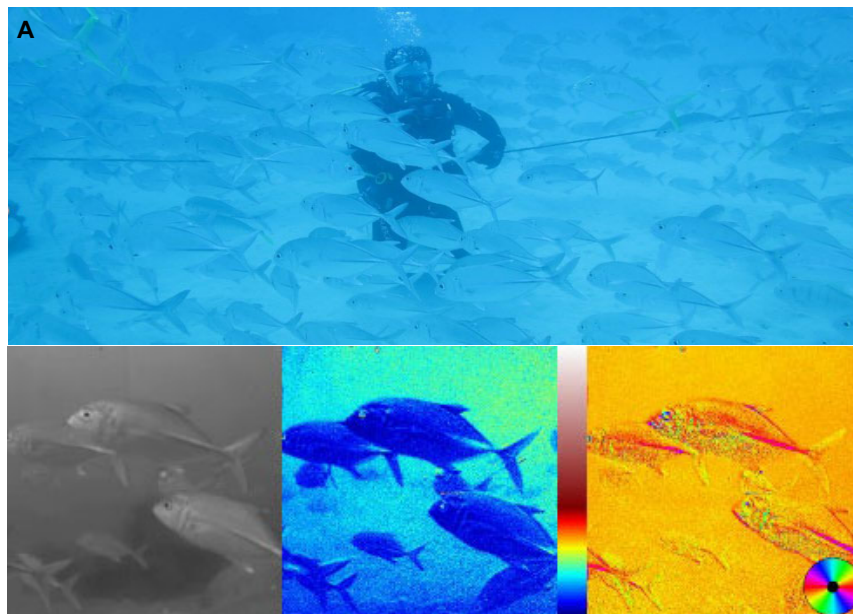
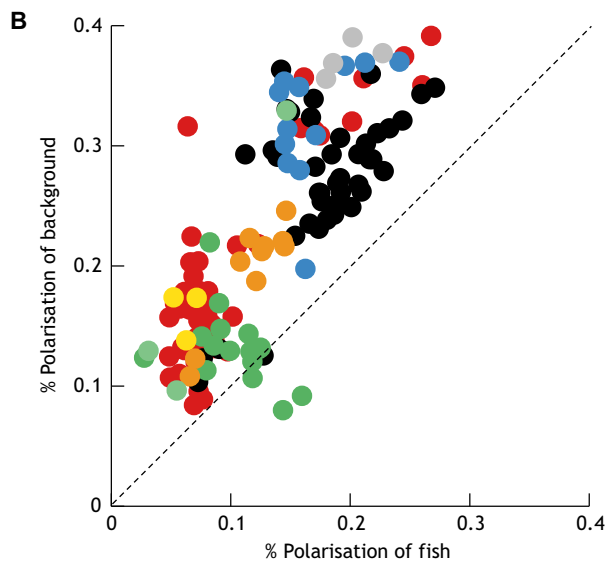


Fig. 8. Midwater camouflage and lack of polarocrypsis. (A) A diver among superbly camouflaged silvery big-eye trevally, *Caranx sexfasciatus*. The fish are also imaged using a polarising camera below (see Fig. 1 legend for explanation of scales). In intensity and colour, the reflective camouflage mechanism functions well, but it breaks down in % polarisation (Johnsen et al., 2016). (B) Ratio of % polarisation of fish and background water in 8 species of silvery fish (Johnsen et al., 2016 and see Fig. S1) showing that silvery fish do not return polarised reflections (Brady et al., 2013, 2015), as also predicted theoretically (Jordan et al., 2012). Animals with polarisation vision would therefore break this form of camouflage, suggesting that polarocrypsis, in this context, does not work. Key: red, *Caranx sexfasciatus*; black, *Sphyrna qenie*; blue, *Pseudocaranx dentex*; bright green, *Trachinotus blochii*; dark green, *Caranx melampygus*; yellow, *Gnathanodon speciosus*; grey, *Pterocaesio marri*; orange, *Fistularia commersonii*.



leaves for egg-laying. Behavioural tests indicate that they prefer to lay their eggs under green horizontal leaves that also therefore reflect H-polarisation (Kelber et al., 2001), and H-polarisation is actually prioritised over colour. A horizontal leaf may provide both the best shelter from weather and protection from the eyes of birds and other predators. This example amplifies an important difference between colour and polarisation vision. Judgements based on polarisation angle are usually (but not always, see Fig. 4B) necessarily bound to the orientation of the object, such as the leaf surface. In other words, as a leaf changes angle, so does the reflected angle and, therefore, possibly the strength of the polarisation signal to a viewer (Fig. 1A). This is examined further in the next section.

Signal orientation, confounding parameters and polarisation contrast

Colour, intensity and polarisation confounds may exist in a putative polarisation signal and may or may not be disambiguated at the neural level (Glantz, 2001). As demonstrated by the swallowtail

butterfly story, e-vector direction is often related to object surface orientation or intrinsic polarisation mechanisms in animal cuticle (Fig. 4). Even when considering polarisation alone, quality judgements based on polarisation angle and/or degree may not be easy to disambiguate, at least to the scientist observer (Bernard and Wehner, 1977; How et al., 2014a). Considerable similarities between intensity contrast sensitivity functions and polarisation contrast sensitivity functions have been found in dragonfly larvae (Sharkey et al., 2015) and in crayfish (Glantz, 1996). This means that great care is needed not to confuse what is being presented or tested when either observing nature or performing experiments (Marshall et al., 2014; Foster et al., 2018).

Examples exist where signals and/or their reception seem deliberately simplified in nature. Rhabdom or photoreceptor twist, deliberate microvillar disorganisation or cell-cell cross-talk has evolved in a number of species to reduce polarisation sensitivity in favour of another light modality such as colour (Marshall et al., 1991; Wehner and Bernard, 1993). As many waxy leaves or wet

surfaces polarise reflected light (Fig. 1) it has been suggested that this is seen as a sort of environmental noise, best removed if other cues or signals are sought. Ultimately, the apparent problem of disentangling colour and polarisation may be one of our own making, as we perhaps try too hard to neatly define modalities and signals. The ways in which polarisation is combined with colour or indeed intensity remains a challenge for the emerging ideas in polarisation signalling.

The cephalopods appear to have solved the colour–polarisation confound by ignoring colour information altogether (Marshall and Messenger, 1996). They also seem to address the potential polarisation angle–degree confound with their signals. Cuttlefish possess dynamic polarised stripes on their arms and, in common with other skin-based signals in cephalopods such as squid, the stripes can be masked or turned on and off, depending on behavioural context (Chiou et al., 2007; Mathger and Hanlon, 2006; Mathger et al., 2009a,b; Shashar et al., 2019). A de-coupling of e-vector angle from the angle of the object (the arm stripes) in space is achieved through a randomly arranged array of platelet structures or modified iridophores (see Glossary) in the arms (Fig. 3). Such independence from angle may serve to maintain polarised signal consistency from a number of viewing angles, leaving degree-only information that is relevant to the behavioural judgement underway. The actual message conveyed remains unknown in either cuttlefish or squid (Mathger et al., 2009a,b), but cuttlefish at least are known to expose the stripes during both mating and agonistic displays (Shashar et al., 1996).

Stomatopods also present signals that are independent of, or at least different to, the object surface angle. The antennal scales in the peacock mantis shrimp *Odontodactylus scyllarus* are two large paddle-shaped appendages that reflect a polarising signal best at a ~45 deg oblique angle to the paddle surface (Fig. 4; Chiou et al., 2012). This is achieved with an unusual astaxanthin-based molecular polarisation mechanism that aligns polarisation to cell membranes and the molecules' position within that membrane. The uropods (tail-fans) of this and other stomatopods from this genus also polarise light at angles unrelated to the surface plane, apparently using the same mechanism, and both these and the antennal scales are used in display to potential mates (Fig. 2 and Movie 1). *H. trispinosa*, also uses an internal photonic mechanism to produce the blue polarised signal discussed above (Fig. 4). The result is a strong horizontal signal against a non-polarising background, (Fig. 4; Chiou et al., 2005, 2008a; How et al., 2014b; Cronin, 2018).

Talbot and Marshall (2010, 2011) showed that cuttlefish and squid orient the microvilli in adjacent photoreceptors mainly H and V relative to the outside world (Fig. 2B). As noted, particularly underwater, this H–V arrangement may be important for looking into the mainly horizontal distant light field and for detecting objects against this relatively predictable polarisation curtain (Fig. 8; Fig. S1). Where known, crustaceans also tend to show an H–V arrangement in their retina relative to the outside world. Both the semi-terrestrial mud-flat and beach-dwelling fiddler crabs and ghost crabs view a horizontally reflected polarised source (Zeil and Hemmi, 2006; How et al., 2014a). Whether permanently submerged species also match an H–V array with the mostly horizontal scattered spacelight remains mostly unknown (Figs 1 and 2; Marshall et al., 1999a,b; Marshall and Cronin, 2014). The exceptional stomatopods possess four angles of linear polarisation sensitivity and are able to rotate their eyes to align photoreceptors and signals – this apparently enables them to optimise linear polarisation contrast in their environment (Land et al., 1990; Marshall et al., 2007; Marshall and Cronin, 2014; Daly et al., 2016).

Polarisation camouflage

Animals use intensity and colour for camouflage in a variety of ways, such as simple matching, disruptive camouflage and countershading (Rowland, 2009; Stevens and Merilaita, 2009; Cott, 1940; Thayer, 1909). As well as searching for polarisation signals, it is worth asking whether there are examples of polarisation reflections and patterns that camouflage or match a uniform or patterned background of polarisation. This has been termed polarocrypsis, and for a variety of reasons explained below and previously (Cronin et al., 2016) we think it unlikely, at least in some of the contexts so far imagined.

An intriguing but untested possibility concerns shiny-leafed and therefore polarising bushes (Fig. 1A). Such habitat certainly provides a disruptive polarised background into which a polarising animal might disappear. As noted already, twisted rhabdoms and other mechanisms of disrupting polarisation sensitivity remove this sort of glare and confounding information (Ribi, 1979; Wehner and Bernard, 1993; Wehner and Meyer, 1981; Marshall and Cronin, 2014). Many insects, however, do not eliminate polarisation sensitivity in their photoreceptors, and may indeed visualise colour patterns and polarisation patterns confounded together in such a background. This might benefit a polarising animal in such a bush. It has been suggested that the linearly polarised reflections from Japanese jewel beetles (*Chrysochroa fulgidissima*) may help in either camouflage or intraspecific communication in forest-edge habitat against waxy foliage (Fig. 1A; Stavenga et al., 2011).

The sunbeam butterfly, *Curetis acuta*, and the 'glass scales' of the swordtail butterfly, *Graphium sarpedon*, polarise light from their wings like the heliconids already mentioned (Fig. 5A–C; Stavenga et al., 2012; Vukusic et al., 2000). In these instances, however, it is scatter or thin film interference from the under surface of the wings that both adds polarisation and reflects colours of the local environment. The wings display a polarising signal in flight, which is presumably not visible to predators (such as birds) but is covertly visible to other butterflies. When at rest and with wings folded, a combination of their green or silvery-white colour, polarisation and local reflection from the wings may aid in camouflage in a forest edge leafy habitat. Both of these butterfly and beetle examples remain interesting ideas only, and are in need of positive behavioural and experimental verification.

The term 'polarocrypsis' in fact comes from the suggestion that a simpler background-matching camouflage exists in the marine environment. As detailed above, a background curtain of mostly horizontally polarised light exists underwater, except near dawn and dusk when it tilts substantially. In open water, there is nowhere to hide, and silvery fish possess a well-documented camouflage strategy in this habitat. Using guanine crystals as reflectors and arranging the crystals over their curved surface to be vertical, silvery fish can act as flat mirrors and reflect the local surrounding light efficiently, thus looking like water itself, both in terms of colour and intensity (Fig. 8; Denton and Land, 1971; Jordan et al., 2012). Brady and colleagues suggest that this extends to polarisation in the lookdown *Selene vomer*, a relatively large (~30 cm) semi-pelagic fish (Brady et al., 2015, 2013). That is, they claim *S. vomer* reflects polarised light as well, and would thus be less visible against a polarising background to a possible predator or any animal with polarising sensitivity.

A number of concerns about this study have previously been put forward (Cronin et al., 2016 and see counter-examples in Fig. 8 and Fig. S1). Jordan et al. (2012) also demonstrated, both theoretically and using direct measurements, that the guanine crystals of silvery fish are arranged, almost ideally, to reflect intensity and not polarisation. They conclude that for optimal camouflage, the best combination is spectrally broad-band, high-percentage and low-

polarising reflectivity. Finally, Johnsen et al. (2016) quantified and photographed many different silvery fish species at many depths using a polarisation camera specifically designed to work in water. One conclusion is that the degree of polarisation of all fish fell well below that of the background, in addition to generally having small values (Fig. 8; Fig. S1).

S. vomer may be different to other silvery fish in its mechanism (an untested possibility), but the 11 species of other silvery fish in the study (Johnsen et al., 2016) were all conspicuous against the background to a predator with polarisation sensitivity (Fig. 8; Fig. S1). Polarisation vision in large fish or their predators has yet to be shown, and while there are open-water squid species possibly large enough to tackle *S. vomer*, they typically prey upon smaller animals. It might be worthwhile to conduct a closer examination of small silvery fish in the size and distance range relevant to crustacean and cephalopod predators.

Circular polarisation and the case for covert communication

Do polarising signals, only visible to animals with polarisation sensitivity, constitute a 'secret' communication mechanism? Some animals can also see UV and other wavelength ranges that are invisible to other species. The discussion of 'secret' communication has already occurred in these contexts, and we can learn from that discussion (Bennett and Cuthill, 1994; Cuthill et al., 2000; Hausmann et al., 2003; Siebeck et al., 2006; Siebeck and Marshall, 2001). Does covert communication occur in polarisation? For example, are the exposed polarisation dances of the Odontodactyloid stomatopods (Figs 4 and 6; Fig. S2 and Movie 1) made possible and not too obvious by the 'for-your-eyes-only' nature of the event? The animals in the video, although rather well camouflaged in intensity and pattern, are moving, making them conspicuous in other ways. It is not known to what extent polarisation may be helping to keep this event 'private'. More likely, much like a displaying bird, they run the risk of detection by predators.

Stomatopods and cephalopods eat each other and probably have done for over 400 million years. Both use linear polarising signals and both possess linear polarisation sensitivity. In the marine world of these highly successful invertebrate groups is the arms race or selection for polarisation secrecy still underway? Stomatopods possess circular polarisation vision and circular polarising signals, and these are not visible to cephalopods as far as we know (Figs 2D, 6 and 7G; Chiou et al., 2005, 2007, 2008a,b). Does this indicate a step ahead in the communication arms race?

Controlled circular polarisation behavioural experiments have been conducted for stomatopods in three behavioural scenarios. In one, *O. scyllarus* was trained to discriminate left- from right-handed circular polarisation in a food-rewarded binary choice test (Fig. 7G; Chiou et al., 2008b), while *H. trispinosa* discriminated linear from circular polarisation under similar circumstances but could not discriminate left from right circular polarisation (Templin, 2017). The reef-dwelling stomatopod *Gonodactylus falcatus* shows innate avoidance of burrow entrances containing circular polarisation, suggesting that this species may use circular polarisation in interspecific communication (Gagnon et al., 2015). Further to behavioural evidence, the optical mechanism (quarter-wave retarder) required for circular polarisation sensitivity has been identified in a specific set of stomatopod photoreceptors, direct optical measurements of the quarter-wave components have been made, electrophysiology has shown circular polarisation sensitivity in several species and a partially understood photonic mechanism to produce the reflection has been documented (Chiou et al., 2008b; Roberts et al., 2009).

Despite these multiple lines of evidence, several holes also exist in the stomatopod story, including the fact that many of the species that appear to have circular polarisation sensitivity lack the relevant body reflections. As noted already, the food-based experiments indicate that they can discriminate different forms of linear and circular polarisation, and can transfer this conditioning to a feeding scenario that they apparently never meet in the real world (Chiou et al., 2008a,b). That is, we are yet to discover potential stomatopod food that selectively reflects circular or indeed linear polarisation.

Scarabs, some other beetles and a few other insects also reflect circular polarisation, and their metallic beauty tempts us to believe this could be a signal perceived by their own species (Pye, 2010). Many are bright green and well camouflaged in a green bush, and it is easy to imagine they rely on their circular polarised reflections for 'secret' communication. The photonic mechanism has been known for some time (Neville and Caveney, 1969; Vukusic and Sambles, 2004; Jewell et al., 2007), and recent behavioural evidence was cited to suggest that scarabs might also see circular polarisation (Brady and Cummings, 2010). This idea, based on phototaxis rather than signal recognition, has since been comprehensively countered, with several different species of scarab (Blahó et al., 2012; Horváth et al., 2014). There is also no evidence at the retinal, optical or neural level for circular polarisation sensitivity in beetles.

A guide to studying polarisation signalling Behaviour

Investigations of polarisation signalling are usually triggered by the observation of a behaviour relative to a small object that is suspected to reflect polarised light (Fig. 7). These behaviours are distinct from navigational or polarotactic behaviours that cue on large- or medium-sized fields of view such as sky or water. However, a signal may also include a small unpolarised object against a large polarised field. When investigating behavioural responses to polarised signals, appropriate control measures to avoid unintentional presentation of polarisation or intensity confounds are essential and difficult (Foster et al., 2018). If, as is often the case, the polarised region of reflectance coincides with a colour, some attempt to disambiguate or discount colour and intensity is worthwhile. It is also valid to recognise and quantify mixed signals (Kelber et al., 2001).

In experimental manipulation, is the test relevant to the animal's natural behavioural repertoire? Large, looming polarised objects and polarised food are rare in nature but a response to such stimuli does indicate polarisation sensitivity and may be used to quantify angle or degree sensitivity. Polarisation sensitivity that can be transferred onto tasks that do not usually involve polarisation is indicative of higher-level polarisation vision, including signalling. Mate choice has a direct association with polarisation, so behavioural manipulations around this task may be most productive (Sweeney et al., 2003; Marshall and Cronin, 2011; Chiou et al., 2011).

Retinal substrates, electrophysiological recordings and polarisation-specific pathways

It is both instructive for experimental design and a key element of our understanding to demonstrate a receptor mechanism, or at least a subsequent neuronal signal, that responds to polarised light and that might drive the relevant behaviour (Flamarique and Harosi, 2002; Kondrashev et al., 2012; Roberts, 2014). In invertebrates, microvillar direction and regularity provide an easy-to-quantify proxy for e-vector angle sensitivity. The mechanism for detection of polarisation by vertebrates is less well defined, and animals such as fish and birds probably do not see object-based (or indeed any) polarisation (Marshall et al., 1991; Horváth, 2014; Mussi et al.,

2005; Coemans et al., 1994). Neuronal responses to polarisation variation, such as angle rotation or varying degree, are indicative of polarisation sensitivity but not necessarily polarisation vision. Electrophysiological data are hard to obtain, compared with indicative photoreceptor structures, but are instructive at every level, from receptors through to processing, to brain and motor output (Labhart and Meyer, 2002; Heinze and Homberg, 2007; Doujak, 1984; Shaw, 1966; Chiou et al., 2008b; Kleinlogel and Marshall, 2006; Moody and Parriss, 1961; Glantz, 1996, 2008).

Quantification of polarisation properties

When investigating polarisation signalling, the polarised reflection, its area and location, should at the very least be photographed to qualitatively detail its altered appearance through changing linear and/or circular polarising filters (Douglas et al., 2007; and Gagnon and Marshall, 2016; Cronin and Marshall, 2011; Cronin et al., 2003). This can be taken further with relatively simple polarisation photography to quantify angle, intensity and degree (Foster et al., 2018). Small area polarimetry using simple filters is easy with portable spectrophotometers (Cronin et al., 2009). Quantification may extend to photonic characterisation and molecular nanostructure, using electron microscopy, x-ray diffraction and ellipsometry. As with colour, the efficacy of polarisation signals is defined through the evolution of these structures by natural or sexual selection (Chiou et al., 2005, 2012; Jewell et al., 2007; How et al., 2014b).

In situ observation and natural history

One of the least attended to but most necessary set of observations in any potential signalling scenario comes from observing the animal *in situ* and thinking through its biology and behavioural repertoire. The alternating behaviours of revealing and covering up polarised arm stripes on cuttlefish or the polarised wings and carapace in butterflies and stomatopods, respectively, are good examples of this sort of desirable data (Sweeney et al., 2003; Chiou et al., 2008a; Mathger et al., 2009a,b). Quantification of the polarised light environment and, in particular, polarised background is particularly worthy of attention, and it is relatively straightforward with the now frequently used portable spectrophotometers and appropriate filters. Such measurements allow estimates of polarisation contrast in the real world (Fig. 1 and Shashar et al., 1995).

Conclusions

Multifaceted evidence for polarisation signalling exists in butterflies, cephalopods and stomatopods, but not yet in fish, beetles and flowers. While we generally agree with Labhart's view that polarisation vision is not designed to extract angle information per se [aside from some exceptional behaviours in butterflies (Kelber et al., 2001) and possibly stomatopods (Cronin, 2018)], we propose that polarisation signals contain specific information. These signals, unlike large-field cues, may be subject to evolutionary pressures, and, in common with colour, may become in some way optimised or matched to specific receivers. Some evidence suggests that degree might be more reliable than angle in polarisation signals, and mixed modalities of colour and polarisation also exist.

In signalling systems where both a colour and polarisation are present and a colour vision system exists that can see the colour, studies must address whether there is an advantage to the additional polarisation information. It is convenient for us to divide polarisation and colour or, indeed, to divide each into components (e.g. hue and saturation for colour, and degree, angle and ellipticity for polarisation). However, both behaviourally and evolutionarily,

these distinctions are possibly misleading. While it is important to measure and parameterise as much as possible, especially when dealing with a form of light we don't see, considering the perspective of the animal in its natural environment may lead to more likely conclusions. What this requires is a return to the careful observations and time spent in the field by the likes of Lorenz and von Frisch, who have strongly influenced our thoughts on behaviour and polarisation (e.g. von Frisch, 1949; Lorenz, 1962).

Competing interests

The authors declare no competing or financial interests.

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.134213.supplemental>

References

- Alkaladi, A., How, M. J. and Zeil, J. (2013). Systematic variations in microvilli banding patterns along fiddler crab rhabdoms. *J. Comp. Physiol. A* **199**, 99-113.
- Arikawa, K. and Stavenga, D. G. (1997). Random array of colour filters in the eyes of butterflies. *J. Exp. Biol.* **200**, 2501-2506.
- Arikawa, K., Inokuma, K. and Eguchi, E. (1987). Pentochromatic visual system in a butterfly. *Naturwissenschaften* **74**, 297-298.
- Bennett, A. T. D. and Cuthill, I. C. (1994). Ultraviolet vision in birds: what is its function? *Vision Res.* **34**, 1471-1478.
- Bernard, G. D. and Wehner, R. (1977). Functional similarities between polarization vision and color vision. *Vision Res.* **17**, 1019-1028.
- Blahó, M., Egri, A., Hegedüs, R., Jósvali, J., Tóth, M., Kertész, K., Biró, L. P., Kriska, G. and Horváth, G. (2012). No evidence for behavioral responses to circularly polarized light in four scarab beetle species with circularly polarizing exocuticle. *Physiol. Behav.* **105**, 1067-1075.
- Boyer, J., Keresztes, J. C., Saeys, W., Koshel, J. (2016). An automated imaging BRDF polarimeter for fruit quality inspection. In *SPIE Optical Engineering +Applications*, Vol. 9948, pp. 9. SPIE.
- Brady, P. C. and Cummings, M. E. (2010). Differential response to circularly polarized light by the jewel scarab beetle *Chrysina gloriosa*. *Am. Nat.* **175**, 614-620.
- Brady, P. C., Travis, K. A., Maginnis, T. and Cummings, M. E. (2013). Polarocryptic mirror of the lookdown as a biological model for open ocean camouflage. *Proc. Natl Acad. Sci. USA* **110**, 9764-9769.
- Brady, P. C., Gilerson, A. A., Kattawar, G. W., Sullivan, J. M., Twardowski, M. S., Dierssen, H. M., Gao, M., Travis, K., Etheredge, R. I., Tonizzo, A. N. et al. (2015). Open-ocean fish reveal an omnidirectional solution to camouflage in polarized environments. *Science* **350**, 965-969.
- Buschbeck, E., Sbita, S. and Morgan, R. (2007). Scanning behavior by larvae of the predaceous diving beetle, *Thermonectus marmoratus* (Coleoptera: Dytiscidae) enlarges visual field prior to prey capture. *J. Comp. Physiol. A* **193**, 973-982.
- Calabrese, G. M., Brady, P. C., Gruev, V. and Cummings, M. E. (2014). Polarization signaling in swordtails alters female mate preference. *Proc. Natl Acad. Sci. USA* **111**, 13397-13402.
- Chiou, T.-H., Cronin, T. W., Caldwell, R. L. and Marshall, N. J. (2005). Biological polarized light reflectors in stomatopod crustaceans. In *Optics & Photonics 2005*, pp. 58881B-58881B-9. International Society for Optics and Photonics.
- Chiou, T.-H., Mäthger, L. M., Hanlon, R. T. and Cronin, T. W. (2007). Spectral and spatial properties of polarized light reflections from the arms of squid (*Loligo pealeii*) and cuttlefish (*Sepia officinalis* L.). *J. Exp. Biol.* **210**, 3624-3635.
- Chiou, T.-H., Caldwell, R. L., Hanlon, R. T. and Cronin, T. W. (2008a). Fine structure and optical properties of biological polarizers in crustaceans and cephalopods. *Proc. SPIE* **6972**, 1-10.
- Chiou, T.-H., Kleinlogel, S., Cronin, T. W., Caldwell, R. L., Loeffler, B., Siddiqi, A., Goldizen, A. and Marshall, N. J. (2008b). Circular polarization vision in a stomatopod crustacean. *Curr. Biol.* **18**, 429-434.
- Chiou, T.-H., Marshall, N. J., Caldwell, R. L. and Cronin, T. W. (2011). Changes in light-reflecting properties of signalling appendages alter mate choice behaviour in a stomatopod crustacean *Haptosquilla trispinosa*. *Mar. Freshwater Behav. Physiol.* **44**, 1-11.
- Chiou, T.-H., Place, A. R., Caldwell, R. L., Marshall, N. J. and Cronin, T. W. (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.
- Coemans, M., Hzn, J. and Nuboer, J. (1994). The orientation of the e-vector of linearly polarized light does not affect the behaviour of the pigeon *Columba livia*. *J. Exp. Biol.* **191**, 107-123.
- Cott, H. B. (1940). *Adaptive Coloration in Animals*. London: Methuen & Co. Ltd.
- Cronin, T. W. (2018). A different view: sensory Drive in the polarized-light realm. *Curr. Zool.* **64**, 513-523.

- Cronin, T. W. and Marshall, N. J.** (2011). Patterns and properties of polarized light in air and water. *Phil. Trans. R. Soc. B* **366**, 619-626.
- Cronin, T. W. and Shashar, N.** (2001). The linearly polarized light field in clear, tropical marine waters: spatial and temporal variation of light intensity, degree of polarization and e-vector angle. *J. Exp. Biol.* **204**, 2461-2467.
- Cronin, T. W., Shashar, N., Caldwell, R. L., Marshall, N. J., Cheroske, A. G. and Chiou, T.-H.** (2003). Polarization vision and its role in biological signaling. *Integr. Comp. Biol.* **43**, 549-558.
- Cronin, T. W., Chiou, T.-H., Caldwell, R. L., Roberts, N. W. and Marshall, N. J.** (2009). Polarization signals in mantis shrimps. In *Polarization Science and Remote Sensing IV*, Vol. 7461 (ed. J. A. Shaw and J. S. Tyo), pp. 74610C-10. San Diego, CA, USA: SPIE.
- Cronin, T. W., Johnsen, S., Marshall, N. J. and Warrant, E. J.** (2014). *Visual Ecology*. Woodstock: Princeton University Press.
- Cronin, T. W., Gagnon, Y. L., Johnsen, S., Marshall, N. J. and Roberts, N. W.** (2016). Comment on 'Open-ocean fish reveal an omnidirectional solution to camouflage in polarized environments'. *Science* **353**, 552-552.
- Cuthill, I. C., Partridge, J. C., Bennett, A. T. D., Church, S. C., Hart, N. S. and Hunt, S.** (2000). Ultraviolet vision in birds. *Adv. Study Behav.* **29**, 159-214.
- Dacke, M., Doan, T. A. and O'Carroll, D. C.** (2001). Polarized light detection in spiders. *J. Exp. Biol.* **204**, 2481-2490.
- Dacke, M., Nordstrom, P., Scholtz, C. H. and Warrant, E. J.** (2002). A specialized dorsal rim area for polarized light detection in the compound eye of the scarab beetle *Pachysoma striatum*. *J. Comp. Physiol. A* **188**, 211-216.
- Daly, I. M., How, M. J., Partridge, J. C., Temple, S. E., Marshall, N. J., Cronin, T. W. and Roberts, N. W.** (2016). Dynamic polarization vision in mantis shrimps. *Nat. Commun.* **7**, 12140.
- Denton, E. J. and Land, M. F.** (1971). Mechanism of reflexion in silvery layers of fish and cephalopods. *Proc. R. Soc. Lond. Series B* **178**, 43-61.
- Detto, T.** (2007). The fiddler crab *Uca mjoebergi* uses colour vision in mate choice. *Proc. R. Soc. B* **274**, 2785-2790.
- Douglas, J. M., Cronin, T. W., Chiou, T.-H. and Dominy, N. J.** (2007). Light habitats and the role of polarized iridescence in the sensory ecology of neotropical nymphalid butterflies (Lepidoptera: Nymphalidae). *J. Exp. Biol.* **210**, 788-799.
- Doujak, F. E.** (1984). Electrophysiological measurement of photoreceptor membrane dichroism and polarization sensitivity in a Grapsid crab. *J. Comp. Physiol. A* **154**, 597-605.
- Flamarique, I. N. and Harosi, F. I.** (2002). Visual pigments and dichroism of anchovy cones: a model system for polarization detection. *Vis. Neurosci.* **19**, 467-473.
- Foster, J. J., Sharkey, C. R., Gaworska, A. V. A., Roberts, N. W., Whitney, H. M. and Partridge, J. C.** (2014). Bumblebees learn polarization patterns. *Curr. Biol.* **24**, 1415-1420.
- Foster, J. J., Temple, S. E., How, M. J., Daly, I. M., Sharkey, C. R., Wilby, D. and Roberts, N. W.** (2018). Polarisation vision: overcoming challenges of working with a property of light we barely see. *Naturwissenschaften* **105**, 27.
- Gagnon, Y. L. and Marshall, N. J.** (2016). Intuitive representation of photopolarimetric data using the polarization ellipse. *J. Exp. Biol.* **219**, 2430-2434.
- Gagnon, Y. L., Templin, R. M., How, M. J. and Marshall, N. J.** (2015). Circularly polarized light as a communication signal in mantis shrimps. *Curr. Biol.* **25**, 3074-3078.
- Glantz, R. M.** (1996). Polarization sensitivity in crayfish lamina monopolar neurons. *J. Comp. Physiol.* **178**, 413-425.
- Glantz, R. M.** (2001). Polarization analysis in the crayfish visual system. *J. Exp. Biol.* **204**, 2383-2390.
- Glantz, R. M.** (2008). Polarization vision in crayfish motion detectors. *J. Comp. Physiol. A* **194**, 565-575.
- Goldstein, D. H.** (2010). *Polarised Light*. CRC Press.
- Gruev, V., Perkins, R. and York, T.** (2010). CCD polarization imaging sensor with aluminum nanowire optical filters. *Opt. Express* **18**, 19087-19094.
- Hausmann, F., Arnold, K. E., Marshall, N. J. and Owens, I. P.** (2003). Ultraviolet signals in birds are special. *Proc. R. Soc. Lond. Series B* **270**, 61-67.
- Hawryshyn, C. W.** (1992). Polarization vision in fish. *Am. Sci.* **80**, 164-175.
- Hawryshyn, C. W.** (2000). Ultraviolet polarization vision in fishes: possible mechanisms for coding e-vector. *Phil. Trans. R. Soc. Lond. Series B* **355**, 1187-1190.
- Hawryshyn, C. W., Moyer, H. D., Allison, W. T., Haimberger, T. J. and McFarland, W. N.** (2003). Multidimensional polarization sensitivity in damselfishes. *J. Comp. Physiol.* **189**, 213-220.
- Hecht, E.** (2017). *Optics*. Harlow: Pearson Education Limited.
- Heinloth, T., Uhlhorn, J. and Wernet, M. F.** (2018). Insect responses to linearly polarized reflections: orphan behaviors without neural circuits. *Front. Cell. Neurosci.* **12**, 50.
- Heinze, S. and Homberg, U.** (2007). Map-like representation of celestial e-vector orientations in the brain of an insect. *Science* **315**, 995-997.
- Horváth, G.** (2014). Polarised light and polarisation vision in animal sciences. In *Springer Series in Vision Research* (ed. N. J. Marshall and S. P. Collin). New York: Springer.
- Horváth, G. and Varju, D.** (1997). Polarization pattern of freshwater habitats recorded by video polarimetry in red, green and blue spectral ranges and its relevance for water detection by aquatic insects. *J. Exp. Biol.* **200**, 1155-1163.
- Horváth, G., Blahó, M., Egri, A., Hegedüs, R. and Széll, G.** (2014). Circular polarization vision of scarab beetles. In *Polarised Light and Polarisation Vision in Animal Sciences. Springer Series in Vision Research* (ed. N. J. Marshall and S. P. Collin), pp. 147-170. New York: Springer.
- How, M. J. and Marshall, N. J.** (2014). Polarization distance: a framework for modelling object detection by polarization vision systems. *Proc. R. Soc. B* **281**, 20131632.
- How, M. J., Zeil, J. and Hemmi, J. M.** (2009). Variability of a dynamic visual signal: the fiddler crab claw-waving display. *J. Comp. Physiol. A* **195**, 55-67.
- How, M. J., Pignatelli, V., Temple, S. E., Marshall, N. J. and Hemmi, J. M.** (2012). High e-vector acuity in the polarisation vision system of the fiddler crab *Uca vomeris*. *J. Exp. Biol.* **215**, 2128-2134.
- How, M. J., Christy, J., Roberts, N. W. and Marshall, N. J.** (2014a). Null point of discrimination in crustacean polarisation vision. *J. Exp. Biol.* **217**, 2462-2467.
- How, M. J., Porter, M. L., Radford, A. N., Feller, K. D., Temple, S. E., Caldwell, R. L., Marshall, N. J., Cronin, T. W. and Roberts, N. W.** (2014b). Out of the blue: the evolution of horizontally polarized signals in *Haptosquilla* (Crustacea, Stomatopoda, Protosquillidae). *J. Exp. Biol.* **217**, 3425-3431.
- Ivanoff, A. and Waterman, T. H.** (1958). Factors, mainly depth and wavelength, affecting the degree of underwater light polarization. *J. Mar. Res.* **16**, 283-307.
- Jewell, S. A., Vukusic, P. and Roberts, N. W.** (2007). Circularly polarized colour reflection from helicoidal structures in the beetle *Plusiotis boucardi*. *New J. Phys.* **9**, 99.
- Johnsen, S.** (2012). *The Optics of Life: a Biologists Guide to Light in Nature*. Princeton: Princeton University Press.
- Johnsen, S., Gagnon, Y. L., Marshall, N. J., Cronin, T. W., Gruev, V. and Powell, S. B.** (2016). Polarization vision seldom increases the sighting distance of silvery fish. *Curr. Biol.* **26**, R752-R754.
- Jordan, T. M., Partridge, J. C. and Roberts, N. W.** (2012). Non-polarizing broadband multilayer reflectors in fish. *Nat. Photonics* **6**, 759-763.
- Jordan, T. M., Wilby, D., Chiou, T.-H., Feller, K. D., Caldwell, R. L., Cronin, T. W. and Roberts, N. W.** (2016). A shape-anisotropic reflective polarizer in a stomatopod crustacean. *Sci. Rep.* **6**, 21744.
- Kelber, A. and Osorio, D.** (2010). From spectral information to animal colour vision: experiments and concepts. *Proc. R. Soc. B* **277**, 1617-1625.
- Kelber, A., Thunell, C. and Arikawa, K.** (2001). Polarisation-dependent colour vision in Papilio butterflies. *J. Exp. Biol.* **204**, 2469-2480.
- Kirschfeld, K.** (1973). Vision of polarised light. In *International Biophysics Congress*, Vol. 4, pp. 289-296. Moscow.
- Kleinlogel, S. and Marshall, N. J.** (2006). Electrophysiological evidence for linear polarization sensitivity in the compound eyes of the stomatopod crustacean *Gonodactylus chiragra*. *J. Exp. Biol.* **209**, 4262-4272.
- Kondrashev, S. L., Gnyubkina, V. P. and Zueva, L. V.** (2012). Structure and spectral sensitivity of photoreceptors of two anchovy species: *Engraulis japonicus* and *Engraulis encrasicolus*. *Vision Res.* **68**, 19-27.
- Labhart, T.** (1988). Polarization-opponent interneurons in the insect visual-system. *Nature* **331**, 435-437.
- Labhart, T.** (1999). How polarization-sensitive interneurons of crickets see the polarization pattern of the sky: a field study with an optoelectronic model neuron. *J. Exp. Biol.* **202**, 757-770.
- Labhart, T.** (2016). Can invertebrates see the e-vector of polarization as a separate modality of light? *J. Exp. Biol.* **219**, 3844-3856.
- Labhart, T. and Meyer, E. P.** (2002). Neural mechanisms in insect navigation: polarization compass and odometer. *Curr. Opin. Neurobiol.* **12**, 707-714.
- Land, M., Marshall, J., Brownless, D. and Cronin, T.** (1990). The eye-movements of the mantis shrimp *Odontodactylus scyllarus* (Crustacea: Stomatopoda). *J. Comp. Physiol. A* **167**, 155-166.
- Lorenz, K.** (1962). The function of colour in coral reef fishes. *Proc. R. Inst. Great Britain* **39**, 282-296.
- Lythgoe, J. N. and Shand, J.** (1982). Changes in spectral reflections from the iridophores of the neon tetra. *J. Physiol. Lond.* **325**, 23.
- Marshall, N. J.** (1988). A unique color and polarization vision system in mantis shrimps. *Nature* **333**, 557-560.
- Marshall, N. J. and Arikawa, K.** (2014). Unconventional colour vision. *Curr. Biol.* **24**, R1150-R1154.
- Marshall, N. J. and Cronin, T. W.** (2011). Polarisation vision. *Curr. Biol.* **21**, R101-R105.
- Marshall, N. J. and Cronin, T. W.** (2014). Polarisation vision of crustaceans. In *Polarised Light and Polarisation Vision in Animal Sciences* (ed. G. Horváth), pp. 171-216. New York: Springer.
- Marshall, N. J. and Johnsen, S.** (2017). Fluorescence as a means of colour signal enhancement. *Philos. Trans. R. Soc. B* **372**, 20160335.
- Marshall, N. J. and Messenger, J. B.** (1996). Colour blind camouflage. *Nature* **382**, 408-409.
- Marshall, N. J., Land, M. F., King, C. A. and Cronin, T. W.** (1991). The compound eyes of mantis shrimps (Crustacea, Hoplocarida, Stomatopoda). 1. Compound

- eye structure—the detection of polarized light. *Philos. Trans. R. Soc. Lond. Series B* **334**, 33–56.
- Marshall, J., Cronin, T. W., Shashar, N. and Land, M.** (1999a). Behavioural evidence for polarisation vision in stomatopods reveals a potential channel for communication. *Curr. Biol.* **9**, 755–758.
- Marshall, J., Kent, J. and Cronin, T.** (1999b). Visual adaptations in crustaceans: spectral sensitivity in diverse habitats. In *Adaptive Mechanisms in the Ecology of Vision* (ed. S. Archer, M. Djamgoz, E. Lowe, J. Partridge and S. Vallerga), pp. 285–328. London: Kluwer.
- Marshall, J., Cronin, T. W. and Kleinlogel, S.** (2007). Stomatopod eye structure and function: a review. *Arthropod. Struct. Dev.* **36**, 420–448.
- Marshall, N. J., Roberts, N. W., Cronin, T. W.** (2014). Polarisation signals. In *Polarised light and Polarisation Vision in Animal Sciences* (ed. G. Horváth), pp. 407–442. New York: Springer.
- Mathejczyk, T. F. and Wernet, M. F.** (2017). Sensing polarized light in insects. *Oxford Res. Ency. Neurosci.*
- Mathger, L. M. and Hanlon, R. T.** (2006). Anatomical basis for camouflaged polarized light communication in squid. *Biol. Lett.* **2**, 494–496.
- Mathger, L. M., Denton, E. J., Marshall, N. J. and Hanlon, R. T.** (2009a). Mechanisms and behavioural functions of structural coloration in cephalopods. *J. R. Soc. Interface* **6**, S149–S163.
- Mathger, L. M., Shashar, N. and Hanlon, R. T.** (2009b). Do cephalopods communicate using polarized light reflections from their skin? *J. Exp. Biol.* **212**, 2133–2140.
- Moody, M. F. and Parriss, J. R.** (1961). The discrimination of polarized light by octopus—a behavioural and morphological study. *Zeitschrift Fur Vergleichende Physiologie* **44**, 268–291.
- Mussi, M., Haimberger, T. J. and Hawryshyn, C. W.** (2005). Behavioural discrimination of polarized light in the damselfish *Chromis viridis* (family Pomacentridae). *J. Exp. Biol.* **208**, 3037–3046.
- Neville, A. C. and Caveney, S.** (1969). Scarabaeid beetle exocuticle as an optical analogue of cholesteric liquid crystals. *Biol. Rev. Camb. Philos. Soc.* **44**, 531–562.
- Pignatelli, V., Temple, S. E., Chiou, T.-H., Roberts, N. W., Collin, S. P. and Marshall, N. J.** (2011). Behavioural relevance of polarization sensitivity as a target detection mechanism in cephalopods and fishes. *Phil. Trans. R. Soc. B* **366**, 734–741.
- Powell, S. B., Garnett, R., Marshall, J., Rizk, C. and Gruev, V.** (2018). Bioinspired polarization vision enables underwater geolocalization. *Sci. Adv.* **4**, 6841.
- Pye, J. D.** (2010). The distribution of circularly polarized light reflection in the Scarabaeoidea (Coleoptera). *Biol. J. Linn. Soc.* **100**, 585–596.
- Ribi, W. A.** (1979). Do the rhabdomeric structures in bees and flies really twist. *J. Comp. Physiol.* **134**, 109–112.
- Roberts, N. W.** (2014). Polarization vision in fishes. In *Polarised light and Polarisation Vision in Animal Sciences* (G. Horváth), pp. 171–216. New York: Springer.
- Roberts, N. W. and Needham, M. G.** (2007). A mechanism of polarized light sensitivity in cone photoreceptors of the goldfish *Carassius auratus*. *Biophys. J.* **93**, 3241–3248.
- Roberts, N. W., Gleeson, H. F., Temple, S. E., Haimberger, T. J. and Hawryshyn, C. W.** (2004). Differences in the optical properties of vertebrate photoreceptor classes leading to axial polarization sensitivity. *J. Opt. Soc. Am. A* **21**, 335–345.
- Roberts, N. W., Chiou, T.-H., Marshall, N. J. and Cronin, T. W.** (2009). A biological quarter-wave retarder with excellent achromaticity in the visible wavelength region. *Nat. Photonics* **3**, 641–644.
- Rosenthal, G. G. and Lobel, P.** (2006). Communication. In *Behaviour and Physiology of Fish*, Vol. 24 (ed. K. Sloman, S. Balshine and R. Wilson), pp. 39–78. Academic Press.
- Rowland, H. M.** (2009). From Abbott Thayer to the present day: what have we learned about the function of countershading? *Phil. Trans. R. Soc. B Biol. Sci.* **364**, 519–527.
- Schwind, R.** (1983a). A polarization-sensitive response of the flying water bug *Notonecta-glauca* to UV-light. *J. Comp. Physiol. A* **150**, 87–91.
- Schwind, R.** (1983b). Zonation of the optical environment and zonation in the rhabdom structure within the eye of the backswimmer, *Notonecta-glauca*. *Cell Tissue Res.* **232**, 53–63.
- Schwind, R.** (1984). Evidence for true polarization vision based on a 2-channel analyzer system in the eye of the water bug, *Notonecta glauca*. *J. Comp. Physiol. A* **154**, 53–57.
- Sharkey, C. R., Partridge, J. C. and Roberts, N. W.** (2015). Polarization sensitivity as a visual contrast enhancer in the Emperor dragonfly larva, *Anax imperator*. *J. Exp. Biol.* **218**, 3399–3405.
- Shashar, N. and Cronin, T. W.** (1996). Polarization contrast vision in Octopus. *J. Exp. Biol.* **199**, 999–1004.
- Shashar, N., Addessi, L. and Cronin, T. W.** (1995). Polarization vision as a mechanism for detection of transparent objects. In *Ultraviolet Radiation and Coral Reefs* (ed. D. Gulko and P. L. Jokiel), pp. 207–211. Honolulu, HI: University of Hawai'i.
- Shashar, N., Rutledge, P. S. and Cronin, T. W.** (1996). Polarization vision in cuttlefish—A concealed communication channel? *J. Exp. Biol.* **199**, 2077–2084.
- Shashar, N., Hanlon, R. T. and Petz, A. D.** (1998). Polarization vision helps detect transparent prey. *Nature* **393**, 222–223.
- Shashar, N., Hagan, R., Boal, J. G. and Hanlon, R. T.** (2000). Cuttlefish use polarization sensitivity in predation on silvery fish. *Vision Res.* **40**, 71–75.
- Shashar, N., Sabbah, S. and Cronin, T. W.** (2004). Transmission of linearly polarized light in seawater: implications for polarization signaling. *J. Exp. Biol.* **207**, 3619–3628.
- Shaw, S. R.** (1966). Polarized light responses from crab retina cells. *Nature* **211**, 92–93.
- Siebeck, U. E. and Marshall, N. J.** (2001). Ocular media transmission of coral reef fish—can coral reef fish see ultraviolet light? *Vision Res.* **41**, 133–149.
- Siebeck, U. E., Losey, G. S. and Marshall, J.** (2006). UV communication in Fish. In *Communication in Fishes*, Vol. 2 (ed. F. Laddich, S. P. Collin, P. Moller and B. G. Kapoor), pp. 423–455. Plymouth, UK: Science Publications Inc.
- Stavenga, D. G., Kinoshita, M., Yang, E. C. and Arikawa, K.** (2001). Retinal regionalization and heterogeneity of butterfly eyes. *Naturwissenschaften* **88**, 477–481.
- Stavenga, D. G., Matsushita, A., Arikawa, K., Leertouwer, H. L. and Wilts, B. D.** (2012). Glass scales on the wing of the swordtail butterfly *Graphium sarpedon* act as thin film polarizing reflectors. *J. Exp. Biol.* **215**, 657–662.
- Stavenga, D. G., Wilts, B. D., Leertouwer, H. L. and Hariyama, T.** (2011). Polarized iridescence of the multilayered elytra of the Japanese jewel beetle, *Chrysochroa fulgidissima*. *Phil. Trans. R. Soc. B* **366**, 709–723.
- Stevens, M. and Merilaita, S.** (2009). Animal camouflage: current issues and new perspectives. *Phil. Trans. R. Soc. B* **364**, 423–427.
- Stowe, S.** (1983). A theoretical explanation of intensity-independent variation of polarisation sensitivity in crustacean retinal cells. *J. Comp. Physiol.* **153**, 435–441.
- Sweeney, A., Jiggins, C. and Johnsen, S.** (2003). Insect communication: polarized light as a butterfly mating signal. *Nature* **423**, 31–32.
- Talbot, C. M. and Marshall, J.** (2010). Polarization sensitivity and retinal topography of the striped pyjama squid (*Sepioloidea lineolata*—Quoy/Gaimard 1832). *J. Exp. Biol.* **213**, 3371–3377.
- Talbot, C. M. and Marshall, J. N.** (2011). The retinal topography of three species of coleoid cephalopod: significance for perception of polarized light. *Phil. Trans. R. Soc. B* **366**, 724–733.
- Temple, S. E., Pignatelli, V., Cook, T., How, M. J., Chiou, T.-H., Roberts, N. W. and Marshall, N. J.** (2012). High-resolution polarisation vision in a cuttlefish. *Curr. Biol.* **22**, R121–R122.
- Temple, S. E., McGregor, J. E., Miles, C., Graham, L., Miller, J., Buck, J., Scott-Samuel, N. E. and Roberts, N. W.** (2015). Perceiving polarization with the naked eye. *Proc. R. Soc. B* **282**, 20150338.
- Templin, R.** (2017). Circular Polarisation Vision in Stomatopod Crustaceans. *PhD Thesis*. University of Queensland.
- Thayer, G. H.** (1909). *Concealing-Coloration in the Animal Kingdom: An Exposition of the Laws of Disguise Through Color and Pattern: Being a Summary of Abbott H. Thayer's Discoveries*. New York: Macmillan.
- von Frisch, K. R.** (1949). Die Polarisation des Himmelslichtes als orientierender Faktor bei den Tänzchen der Bienen. *Experientia* **5**, 142–148.
- Vukusic, P. and Sambles, J. R.** (2004). Photonic structures in biology. *Nature* **429**, 680–680.
- Vukusic, P., Sambles, J. R. and Lawrence, C. R.** (2000). Structural colour - Colour mixing in wing scales of a butterfly. *Nature* **404**, 457–457.
- Waterman, T. H.** (1954). Polarization patterns in submarine illumination. *Science* **120**, 927–932.
- Waterman, T. H. and Westell, W. E.** (1956). Quantitative effect of the sun's position on submarine light polarization. *J. Mar. Res.* **15**, 149–169.
- Wehner, R.** (2001). Polarization vision—a uniform sensory capacity? *J. Exp. Biol.* **204**, 2589–2596.
- Wehner, R. and Bernard, G. D.** (1993). Photoreceptor twist: a solution to the false-color problem. *Proc. Natl Acad. Sci. USA* **90**, 4132–4135.
- Wehner, R. and Meyer, E.** (1981). Rhabdomeric twist in bees - artefact or in vivo structure? *J. Comp. Physiol.* **142**, 1–17.
- Wehner, R. and Rossel, S.** (1985). The bees celestial compass - a case study in behavioural neurobiology. *Fortschr. Zool.* **31**, 11–53.
- Zeil, J. and Hemmi, J. M.** (2006). The visual ecology of fiddler crabs. *J. Comp. Physiol. A* **192**, 1–25.
- Zeil, J. and Hofmann, M.** (2001). Signals from 'crabworld': cuticular reflections in a fiddler crab colony. *J. Exp. Biol.* **204**, 2561–2569.

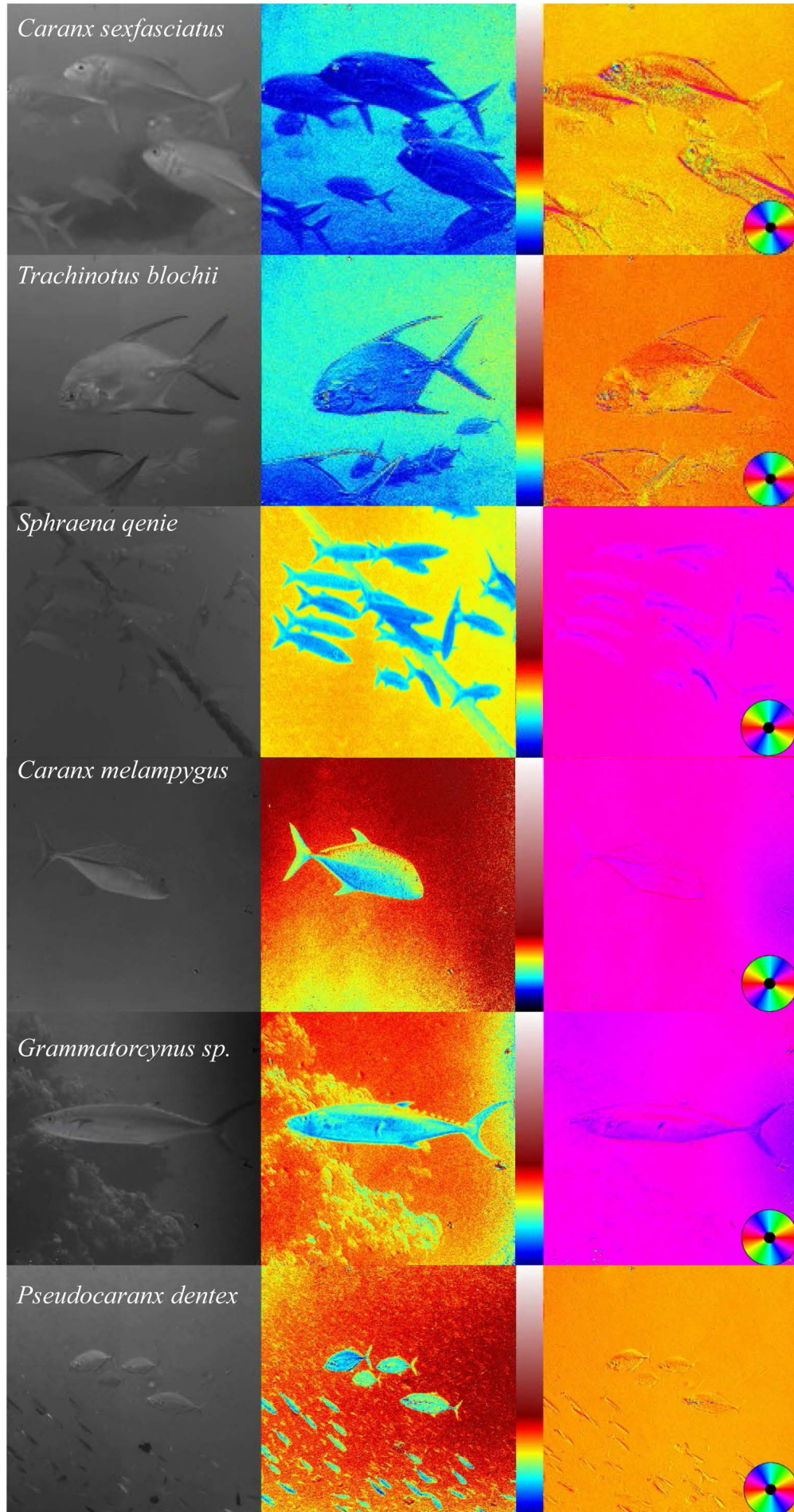
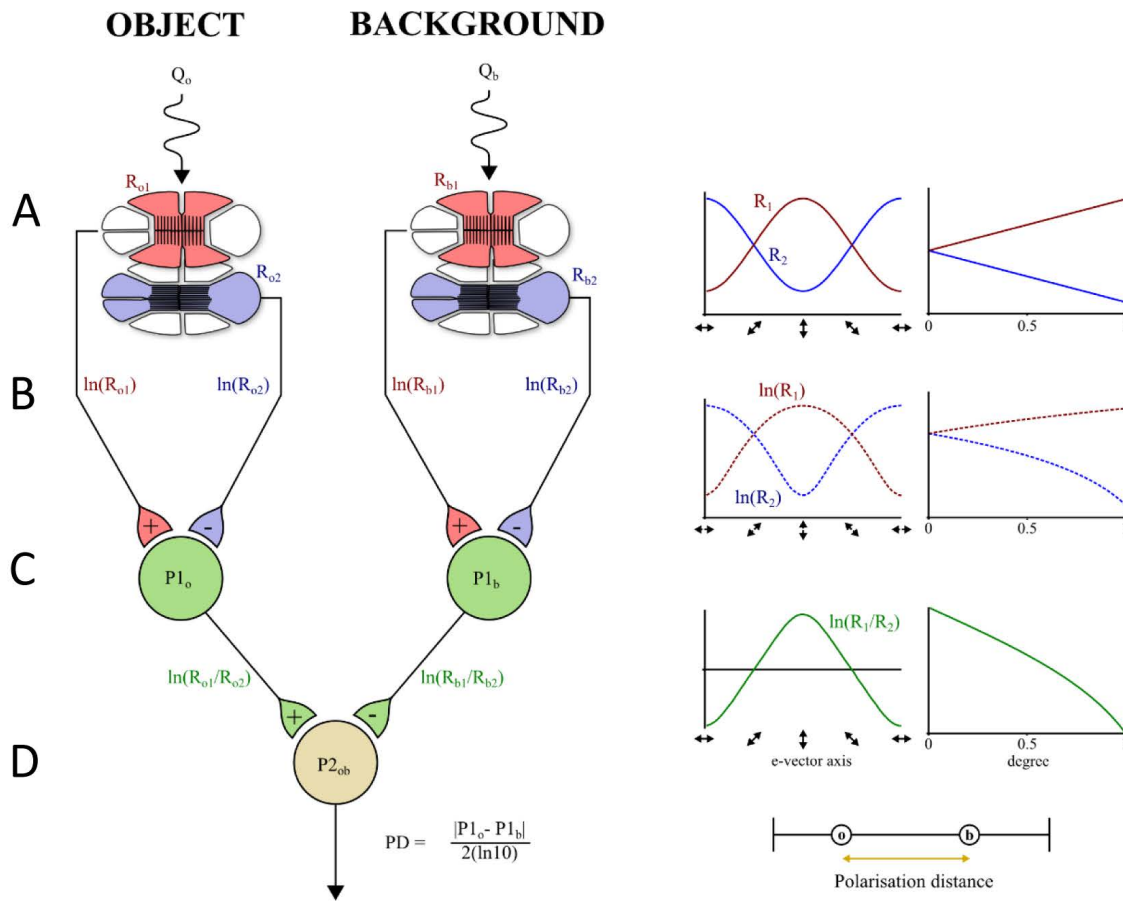
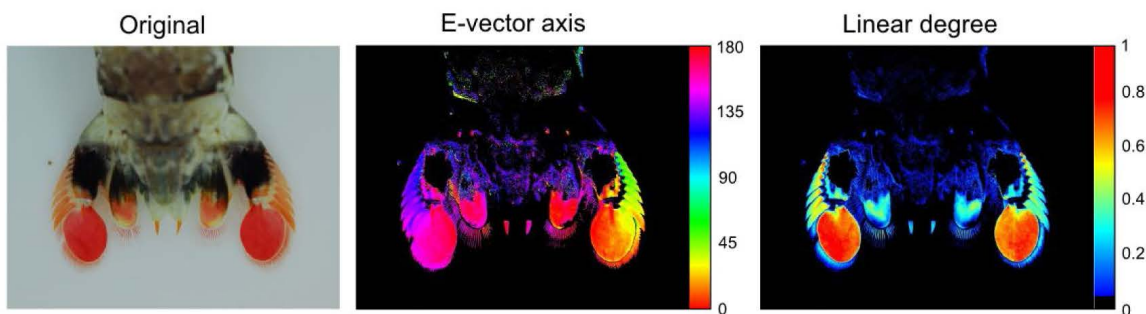


Figure S1 – Polarisation camera images of 6 of the 11 silvery fish species examined by Johnsen et al., 2016 and in Fig. 8 main text (with images and degree(%) and angle scales explained in main text Fig. 1). Note that against a variety of background water % polarisations, the silvery fish skin never reflects polarisation (above very low levels of polarisation) while being more effective at matching intensity (Denton and Land, 1971; Jordan et al., 2012).



Polarimetry of stomatopod tail, similar to Figures throughout text.



Polarisation distance from above images using equation below

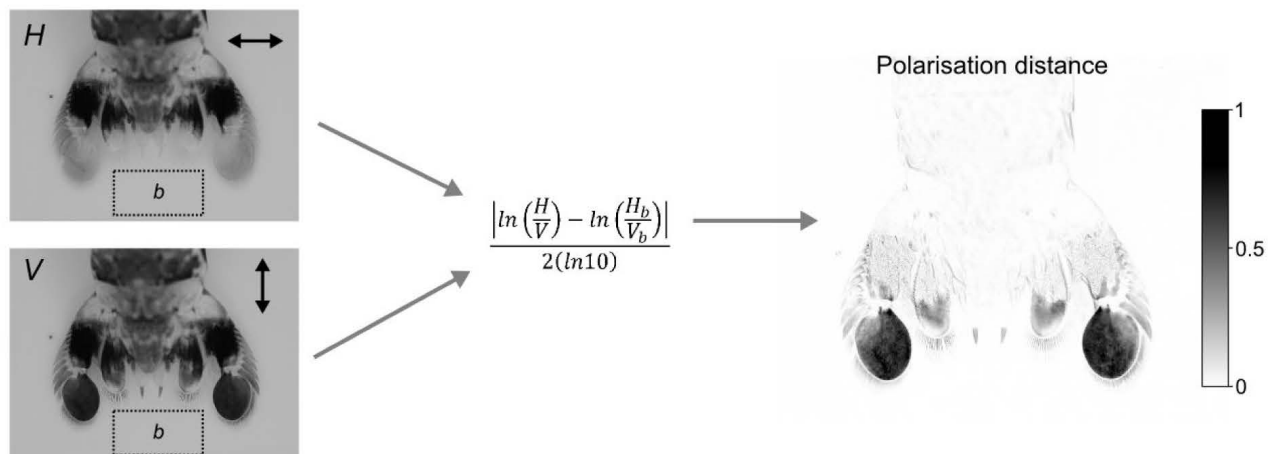


Figure S2 - Details of hypothetical neuronal processing of polarisation in a 2D, H-V polarisation system and from this how polarisation distance, similar to colour distance, might be determined (modified from How and Marshall, 2014). Top – A schematic view of a two-channel crustacean-like polarisation vision system. (A) Polarised light from background and object detected by receptors in different eye regions. As often found in crustaceans or cephalopods and insects, each receptor contains two cell populations with orthogonally arranged angle sensitivity (Fig. 2 main text), V – red, H – blue. Receptor response modulation to changes in e-vector axis (0-180°) and normalised % polarisation or degree (0-1) are shown in graphs to the right. (B) Opponent interneurons pass inhibitory and excitatory signals on to secondary interneuron at (C), equivalent to the lamina ganglionaris neuropil in arthropods (e.g. Glantz, 1996). At this level, polarisation distance as defined by How and Marshall is calculated by next level P2 interneuron as a normalised measure of activity in the interneurons P1. Graphs on right show schematised activity at each level.

Bottom – Polarimetry of stomatopod (*Odontodactylus latirostris*) tail region – similar to that shown in Supplementary Video. Here still photographs through V and H linear polarising filters have been used to estimate e-vector axis and degree or % polarisation and are then used to calculate a polarisation distance image according to parameters defined in How and Marshall (2014). The discriminability of polarised objects is based on a just-noticeable-differences (JNDs) scale (similar to colour – Vorobyev and Osorio, 1998) and converted to a greyscale from 0-1.

One conclusion is that horizontal and vertical arrays are ideal for detecting differences in degree and not e-vector axis. One corollary of this prediction is that polarisation vision of small objects rarely needs to step beyond a two-channel (dichromatic equivalent), especially if background polarisation is predictable or if there are ways of optimising channel differences through eye or body movement (Daly et al., 2016). Even stomatopods appear to employ multiple two-channel systems rather than combining their full set of eight sensitivities over two wavelength ranges to analyse polarisation from every angle.



Movie 1 – A female and a male (in burrow) mantis shrimp (*Odontodactylus havanensis*) display to each other with polarisation reflections from antennal scales and uropod region of tail. The flashing regions indicate areas of polarisation shown through a polarised switch-plate filter that alternates vertical and horizontal filter conditions at alternate video frames. As a result any area in the scene that polarised is seen flickering. The male appears either to court or to drive away the female; however, the information content of the signals in either direction is unknown. (Video by Alex Cheroske).