

Animal Polarization Imaging and Implications for Optical Processing

Invertebrate biology offers lessons on how to harness light for high-capacity, task-specific sensing.

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ABSTRACT | Biologically inspired solutions for modern-day sensory systems promise to deliver both higher capacity and faster, more efficient processing of information than current computational approaches. Many animals are able to perform remarkable sensing tasks despite only being able to process what would be considered modest data rates and bandwidths. The key biological innovations revolve around dedicated filter designs. By sacrificing some flexibility, specifically matched and hard-wired sensory systems, designed primarily for single roles, provide a blueprint for data and task-specific efficiency. In this paper, we examine several animal visual systems designed to use the polarization of light in spatial imaging. We investigate some implications for artificial optical processing based on models of polarization image processing in fiddler crabs, cuttlefish, octopus, and mantis shrimp.

KEYWORDS | Animals; biophotonics; image processing; optical polarization; stokes parameters

I. INTRODUCTION

Throughout the animal and plant kingdoms, specialized sensory systems provide their hosts with a remarkable diversity of information about the environment. Image and nonimage forming visual systems are no exception, and a considerable diversity of light-sensitive structures can be found in nature. Numerous visual specializations can be found within these, including multidimensional color vision [1]–[4], low-light vision [5], areas of high visual acuity [6], [7], and sensitivity to the polarization of light [8], [9].

The polarization of light is a fundamental physical property that describes how light moves through space [10]–[12]. Three quantities are used to describe the polarization: angle, percent, and ellipticity. The angle of polarization describes the average orientation of the oscillations in the electric field of light, and this has become generally referred to as the e -vector angle. The percent polarization describes the distribution of those. For example, if the light contains waves with their electric fields all-oscillating in the same plane, then the light has a percent polarization of 100%. Similarly, if the distribution of the electric fields is uniform in the plane orthogonal to the direction of propagation, the light is said to be unpolarized or has a percent polarization of 0%. The electric field can also rotate around the direction of propagation, and the ellipticity, a value between 1 and -1 ,

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describes whether the light propagates clockwise or counterclockwise, respectively.

Animals exploit this polarization information in a variety of ways. Many terrestrial insects, for example, ants [13], dung beetles [14], bees [15], or locusts [16], use the polarization pattern in the sky for navigation. Coupled to an endogenous clock, this provides any individual with a directional compass that has an advantage over a sun compass, as it can operate even in partially cloudy skies and when the sun is obscured. Aquatic invertebrates also use polarization information, but for different tasks. Stomatopod crustaceans use polarizers built into their carapace as visual signals [17], [18]. These complex signals, often coupled with color, have a high percent polarization and are either linearly or circularly polarized. In the presence of other animals that are not polarization sensitive, such signals act as a secret communication channel [19]. Cephalopod molluscs—cuttlefish, squid, and octopus—also possess differential sensitivity to different polarizations [20]–[23], and to date, cuttlefish possess the highest level of polarization discrimination, being able to behaviorally discern the difference between two linear polarizations separated by 1° in angle [24].

The aim of this paper is to bring together information on schemes that crustaceans and cephalopods use to process image-based polarization information in ways that could be applicable to modern imaging technologies. There are many papers in the literature that demonstrate how imaging polarimetry is used in areas of computer vision [25]–[31]. However, it is in this context that we want to move past the premise that anthropogenic representations of polarization information are optimal solutions for efficient image processing. It is not our aim to provide a review of animal polarization sensitivity or specific detail on the neurophysiological processing (see [8] for the most complete review). The focus here is on the merits of retinal processing architectures that have evolved for different polarization-mediated visual tasks in fiddler crabs, cuttlefish, octopus, and mantis shrimps, many of which follow the general principles of dedicated filter design.

II. MECHANISMS OF POLARIZATION DETECTION

In the examples considered in this paper, the ability to discriminate between two different forms of polarized light, either between two different angles, different percentages, different ellipticities or a combination of all three, requires four separate components of an animal's visual system to function in a coordinated fashion.

- 1) The visual pigment must be able to provide a differential response to different polarizations of light.
- 2) The visual pigments must show a degree of orientational order within the photoreceptors, to convey an overall specificity to a particular polarization for each detector cell type.

- 3) The photoreceptor array in the retina must show a degree of orientational order to provide separate input channels maximally sensitive to particular angles of polarization.
- 4) The neural processing architecture must be able to encode and sometimes integrate the polarization information with other visual channels such as color, intensity, and other sensory modalities.

Invertebrates, on which we concentrate in this paper (but see [9] for a comparative discussion of invertebrates and vertebrates), use an *R*-type rhodopsin as the visual pigment [32], which, like all known opsins, possesses an intrinsically dichroic chromophore. Inside the rhabdomeric photoreceptor, the photopigment is contained within microvilli, cylindrical lamellar membranes. If the chromophore axes are orientated randomly in the plane of the membrane, the cylindrical nature of the microvillus dictates that twice as much light polarized parallel to the length of the microvillus will be absorbed compared to light polarized across (see [33]–[35] for more detailed descriptions). However, many rhabdomeric photoreceptors exhibit cellular polarization sensitivities greater than two. This suggests that there is additional orientational ordering of the visual pigment within the microvilli membranes [36]. Fig. 1 illustrates several examples of experimentally measured dichroic ratios and photoreceptor polarization sensitivities, and how these values vary across five main animal groups (Insecta, Malacostraca, Arachnida, Cephalopoda, and Actinopterygii) [9].

The third and fourth components of the processing architecture within the retina are more species-specific. Many invertebrates display a perpendicular array of photoreceptors providing a two-channel comparative input system [58]. Such a comparative system is able to provide a measure of contrast by comparing the activity of two different photoreceptors. In studies of animal color vision, a mathematical framework often employed to provide an understanding of color discrimination returns a “color distance” based on the spectral nature of the light environment, the spectral sensitivities of the various color receptors, and the number of color input channels [59]. A similar method has been used to study the polarization discrimination abilities of animals, first by Bernard and Wehner [60] and more recently expanded upon by How and Marshall [61]. Through minimal levels of neuronal processing, the polarization information in an animal's visual environment can be interpreted as a “polarization distance.”

III. CURRENT ARTIFICIAL AND BIOINSPIRED PROCESSING ARCHITECTURES PARTICULAR TO POLARIZATION VISION TASKS

The key aim of this paper is to demonstrate that the polarization processing methods of many animals should not necessarily be thought of in the human analytical terms

of *e*-vector angle and percent polarization. The colors of our world do not appear the same to an animal with tetrachromatic color vision (e.g., a parrot or a goldfish), and the same principle applies to considerations of any animal's sensitivity to the polarization of light. While these anthropocentric mathematical frameworks provide representations that we, as humans, can visualize, the representation that other animals have of the information is entirely dependent on their neural processing and how other visual channels, such as wavelength or brightness, and other sensory modalities are fused together.

A. Stokes Parameters for Image Processing

Our current understanding of polarization in the underwater natural environment is principally based on imaging techniques that use Stokes parameter measurements to calculate the angle and percent polarization (Fig. 2). Stokes parameters mathematically relate the electric field components and relative phase between those components for any wave of light. However, man-made detectors do not measure the electric field strength of the

light, but intensity. Therefore, we tend to frame Stokes parameters in terms of measured intensity by using the assumption that an analyzer acts perfectly. We also assume that, in general, there is very little circularly polarized light in the natural environment. Therefore, we calculate the linear Stokes parameters *S*₁ and *S*₂, by making four measurements of intensity at the detector (be it photodiode or pixel array) at analyzer orientations of 0°, 45°, 90°, and 135° [Fig. 2(a)]. Normalized intensity contrasts between 0° and 90° and 45° and 135° are used to calculate *S*₁ and *S*₂, and then both *S*₁ and *S*₂ are combined to calculate the angle θ and percent polarization. Practically, to measure images through the 4-analyser orientations, two different methods are commonly used: 1) a rotatable polarizer [62] or a liquid crystal [63] device on the front of a camera lens is used with images being taken time sequentially; or 2) individual pixels on the imaging chip can be fitted with their own polarizers [64], [65], with a combined super pixel providing the basis of the Stokes calculations. The principal advantage of the on-chip technology is the simultaneous acquisition of all polarization measurements,

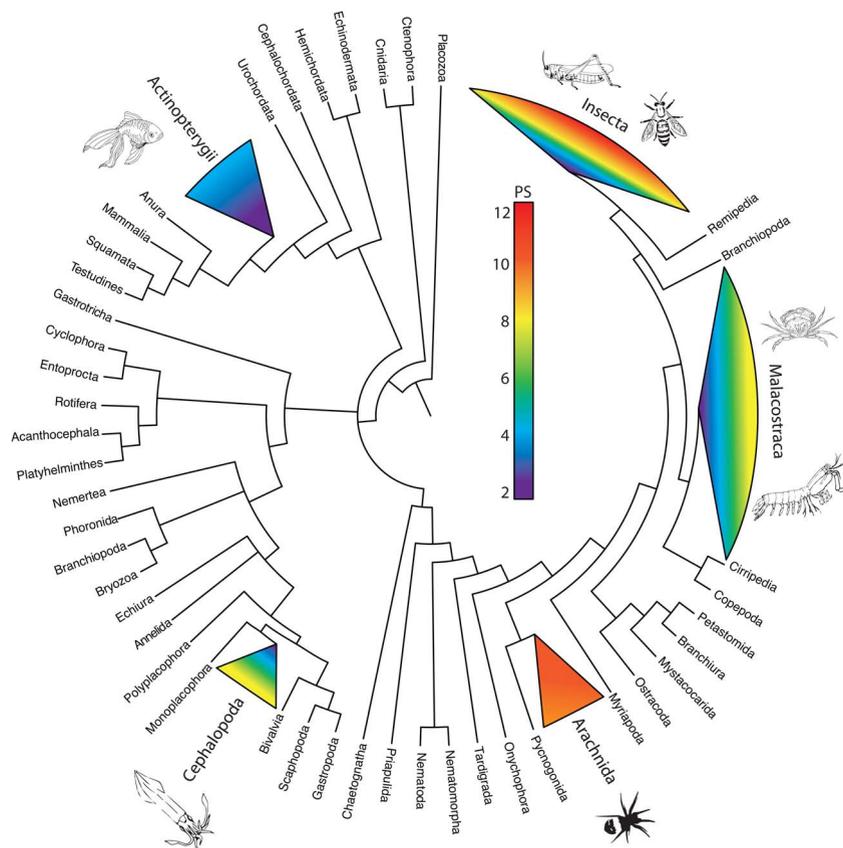


Fig. 1. Phylogeny illustrating animal classes where dichroic ratios and polarization sensitivity have been experimentally measured. The color coding represents the distribution in the varying levels of measured polarization sensitivity (see the key at the center) and is not representative of all possible polarization sensitivity (PS) values in these groups, only where direct measures are available in the literature. Relationships among major animal groups generalized from the phylogenetic studies of [37]–[41]. Examples of dichroic ratio and polarization sensitivity data from: vertebrate cones [42]–[46]; insect receptors [47]–[52]; malacostracan receptors [53]–[55]; arachnid receptors [56]; and cephalopod receptors [57].

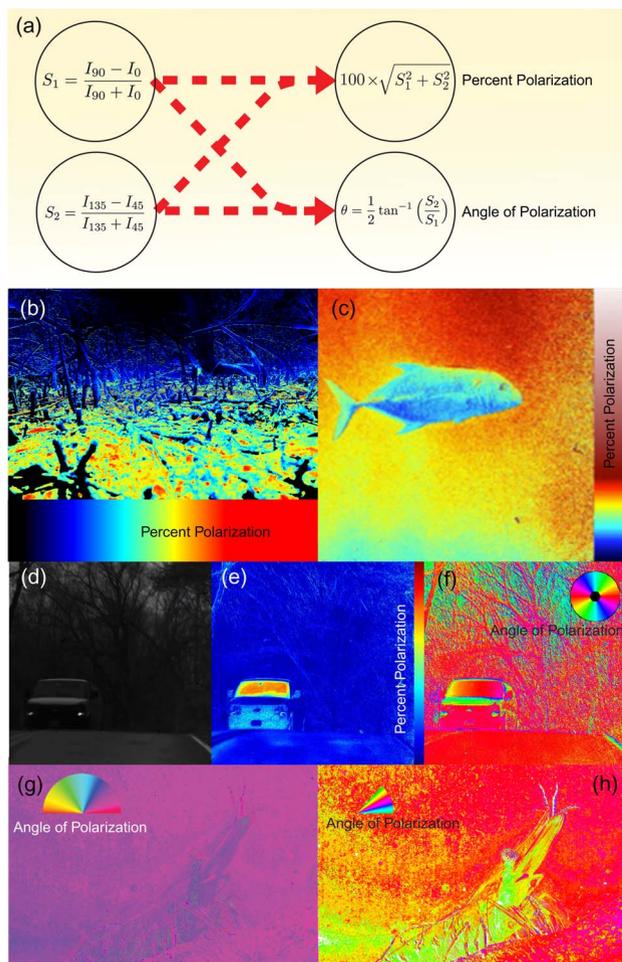


Fig. 2. Stokes parameter image processing. (a) An illustration of the method of calculating the angle and percent polarization from Stokes parameter measurements (assuming an ellipticity of zero). (b)–(f) Examples of polarization images on land and of a fish underwater. (g)–(h) Demonstration of the angle of polarization that can be visualized when the lookup table is compressed to a restricted angular range (reproduced from [24]).

thereby conveying the ability to record the polarization of moving scenes. One benefit of measuring Stokes parameters, and one that applies to both of the methods above, is the fact that Stokes parameters are coordinate-system invariant and do not rely on a known or set relationship between the polarization of the source and the angles of the polarizers in the detectors.

Both terrestrial [Fig. 2(b)] and underwater images [Fig. 2(c)] often display complex and dynamic levels of polarization information. In common, both the sky and open water present predictable background polarization patterns in the light field. In many terrestrial cases, the reflections from objects produce significant amounts of polarized light because of the refractive index contrasts between the object and air. Underwater, however, the optical properties of different materials impact considerably

their polarization response. Some materials such as animal tissue have similar refractive indices to water and, therefore, polarization by reflection can be limited. Conversely, some underwater reflecting structures, such as chitin and guanine-based reflectors, can drastically affect the polarization, either creating strongly polarized visual signals [17], [19] or polarization neutral reflections [66].

In order for humans to visualize both the percent polarization and the angle of polarization, imaging polarimetry represents this information as false-color images, typically using a spectrally based lookup table (LUT) [Fig. 2(b)–(f)]. One of the advantages that these false-color representations provide is the ability to compress color scales to highlight contrast at specific levels within the LUT. In Fig. 2(g), which represents the angle of polarization reflected from a small shrimp, it is difficult for us to detect any differences between the animal and the background. However, limiting the LUT range to 30° , rather than the full 180° , provides a method for enhancing the contrast of features of interest of an animal against the background [Fig. 2(h)] [24]. Effectively, our own limited color sensitivity overlooks the detailed information that is actually contained in the image.

B. Two-Channel Mechanisms of Polarization Sensitivity in Crustaceans and Cephalopods

Two-channel mechanisms of polarization sensitivity are common in invertebrates, and both crustaceans and cephalopods seem to have independently evolved a retinal array of two types of polarization-sensitive photoreceptors ordered perpendicularly. One channel is maximally sensitive to horizontally polarized light, and the other channel is maximally sensitive to vertically polarized light.

Fiddler crabs [Fig. 3(a)] live on tropical and semitropical intertidal mudflats. They are highly visual animals with compound eyes mounted on long stalks above their body [Fig. 3(b)], and they possess rhabdomeric photoreceptors that are polarization sensitive [Fig. 3(c)]. Mudflats are a highly polarized visual environment, influenced by the celestial polarization pattern and by the high-percent polarized reflections from the mud itself. How *et al.* [67] have demonstrated that species of fiddler crab respond to contrasting polarization information and proposed that the ability could be used for improving the detection of predators or conspecifics. Both unpolarized birds against a polarized sky, or an unpolarized land predator against the polarized reflections from the mud, provide strong contrast in the polarization domain, which can be visually informative. If the angle of polarization in the environment is constant, and only the percentage polarization varies, then S_1 provides a direct measure of that percentage [Fig. 3(d)]. Fig. 3(e) and (f) clearly illustrates the enhanced contrast between the mangrove flora and the mud flat when viewing the polarization information as might be interpreted by fiddler crab visual systems. A second possible behavioral use of polarization information is the

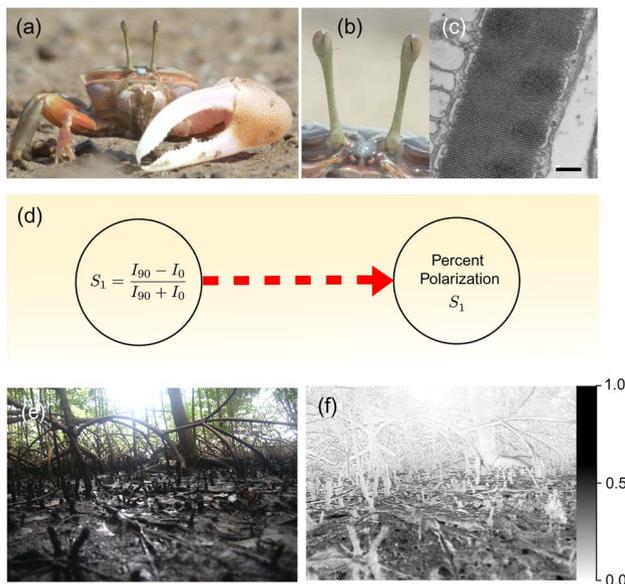


Fig. 3. Contrast processing in a two-channel polarization system. (a) A fiddler crab, *Uca elgans*, with the eyes shown in close up in (b). (c) A transmission electron micrograph illustrating the microvillar ordering of the polarization-sensitive photoreceptors in *Uca terpsichories*. Scale bar = 500 nm. (d) Processing for obtaining a measure of polarization contrast, S_1 is the equivalent of the percent polarization. (e)–(f) Examples of a color and polarization contrast image of the visual environment that is inhabited by some species of fiddler crab.

identification of conspecifics on the mudflat. Harmless neighboring crabs regularly emerge from their burrow wet, with a high-percent polarization caused by specular reflection from the carapace. Other intruding competitor crabs that do not own a burrow consequently have a much drier carapace that reflects a lower polarization of light. It is possible that visualizing the percent polarization could help discriminate harmless “damp” resident neighbors from the potentially threatening “dry” wandering competitors [68]. However, this function remains to be tested experimentally.

The level of acuity with which both fiddler crabs and some cuttlefish can discriminate between different polarizations is, in many ways, remarkable. When tested with a looming stimulus that was polarized at different angles to a background, but with zero intensity difference, both cuttlefish and fiddler crabs could discriminate between the stimulus and background when the angular differences in e -vector orientation were as little as 1° and 3° , respectively [24], [67]. This high resolution means that, despite the human need to rescale false-color images to allow us to see contrast detail, animals already have the innate ability to resolve that level of information. A key point here, however, is the fact that a two-channel system does not provide the same resolution at all angles of polarization. In the same way that a two-channel color vision system has

intrinsic confounds, a fixed two-channel polarization detector system (for example, one orientated horizontally and vertically) has the problem of a null point where a source and a background are polarized at -45° and 45° . How et al. [61], [69] have recently investigated the detail of this form of two-channel processing.

The requirement of a fixed orientational relationship between the detector array and the signal makes this architecture most relevant to cases where the polarization information to be detected has reliable properties, in the same sense as a matched filter. This would apply, for example, below the upper few meters underwater for improving visual contrast underwater in an equatorial plane when the primary source of polarization is scattering and the light tends to be horizontally polarized, above

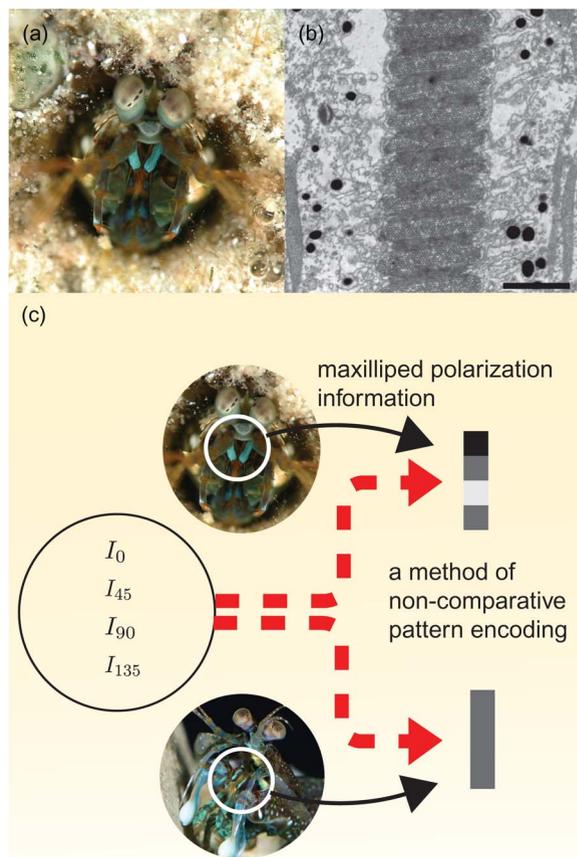


Fig. 4. Visual information recognition and not discrimination in stomatopods. (a) A *Haptosquilla trispinosa* displaying the bright blue and horizontally polarized visual signals from their first maxilliped appendages. (b) Aligned microvilli in the photoreceptors of *Pullosquilla thomasini*. Scale bar 2 μm . (c) Representation of a possible recognition scheme for pattern encoding the polarization information from the horizontally polarized blue signals from *H. trispinosa* (top) versus the unpolarized blue signals from *H. glyptocercus* (bottom).

water on a wet horizontally polarized mudflat, the detection of a horizontally polarized water surface or for detection of a known object where the polarization upon reflection provides a constant angle of polarization. The principal advantage in a man-made detector employing this sensory architecture is the processing benefit of only having two channels of information compared with three or four, as previously described. Moreover, the number of animals that employ this scheme suggests that the lower costs of processing is an advantage that outweighs any detriment of a null point confound that is intrinsic to such a system.

C. Alternative Forms of Image Acquisition and Processing

Stomatopods [Fig. 4(a)] possess some of the most complex eye designs currently known in the animal kingdom [70], [71]. Their large apposition compound eyes show remarkable degrees of translational and rotational freedom, and they have three overlapping fields of view per eye that originate from three distinct areas: two hemispheres and a midband that contain two or six rows of specialized receptors. Both hemispheres exhibit polarization sensitivity, with photoreceptors [Fig. 4(b)] maximally sensitive to 0° and 90° in the dorsal hemisphere and 45° and 135° in the ventral hemisphere. The midband is sensitive to color and elliptical polarization information, and many species of stomatopod have a 12-channel color input system, with sensitivity stretching from the deep ultraviolet to the near-infrared (300–700 nm) [72]–[74].

Recently, we have learned that this array of color channels may not be processed in the same way as is common in most other animals that have been studied [75]. Rather than using standard opponent-processing mechanisms, each channel appears to be handled independently, effectively resulting in the division of the visible spectrum into 12 color “bins.” This simple output from the anatomically complex eye could then be processed using a form of binary pattern recognition, allowing the quick discrimination of objects with little processing power [75]. While we do not know yet if analogous mechanisms ope-

rate for polarization, it is possible that man-made systems could benefit from pattern encoding for similar efficiency gains, as illustrated in Fig. 4(c). The pattern recognition of a polarization signal matched to a similar columnar organization of a neural area, in the same way the dorsal rim area maps to the proto cerebral bridge in locusts [76], may provide inspiration for a new level of efficient polarization processing.

Furthermore, the unusual configuration of the midband in the stomatopod eye does not lend itself to conventional spatial imaging; instead, the eye scans a scene of interest to build up a 2-D representation from a 1-D sensor array. This is analogous to the way that a push-broom-type imaging sensor acquires an image. Clearly, 12 color channels and two to four polarization channels produce a large amount of data input, and coupled to the fact that these animals have fast and dangerous lifestyles, there is a clear need for efficient methods of processing.

IV. SUMMARY

The common theme throughout this paper is the fact that animals do not process polarization information using the same mathematical models that humans have incorporated into sensor technology. In many species, polarization sensitivity is optimized for a specific role, be it navigation, contrast enhancement, or high-speed processing, and in any design process, this would be considered to be task-driven optimization. While it does reduce flexibility or adaptability of the sensor system to novel information and for new roles, the gains in processing efficiency and performance for those key tasks outweigh these disadvantages.

The field of imaging polarimetry is still in its infancy compared with other areas of image processing, and only a few studies have gone beyond simply displaying polarization angle images [25]–[31]. There is considerable scope for further investigations of novel ways of processing and representing polarization information, such as textural object recognition for identifying or classifying pictorial data [77]–[79], and animal models of polarization information processing should be considered in the future. ■

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