Review

Teleost polarization vision: how it might work and what it might be good for

Maarten Kamermans^{1,2} and Craig Hawryshyn^{3,4,*}

¹Retinal Signal Processing, Netherlands Institute for Neuroscience, Amsterdam, The Netherlands

²Department of Neurogenetics, University of Amsterdam, Amsterdam, The Netherlands

³Department of Biology, and ⁴Centre for Neuroscience Studies, Queen's University, Kingston, Ontario, Canada

In this review, we will discuss the recent literature on fish polarization vision and we will present a model on how the retina processes polarization signals. The model is based on a general retinal-processing scheme and will be compared with the available electrophysiological data on polarization processing in the retina. The results of this model will help illustrate the functional significance of polarization vision for both feeding behaviour and navigation. First, we examine the linkage between structure and function in polarization vision in general.

Keywords: colour vision; polarization vision; modelling

1. STRUCTURE–FUNCTION RELATION IN POLARIZATION VISION

Sensory biologists are constantly challenged with linking the structure and function of sensory systems. No other example illustrates this challenge better than polarization sensitivity in animals.

(a) *Invertebrates*

For the invertebrate visual system, there are numerous examples in the literature that link the presence and orientation of microvilli in photoreceptors to polarization sensitivity (e.g. [1]). It is the orientation of light-absorbing chromophores that results in differential absorption of polarized light, with maximum absorption at an e-vector orientation parallel to the chromophore orientation and minimum at an e-vector orientation perpendicular to the chromophore orientation. This differential absorption of polarized light in two orthogonal axes is termed linear dichroism.

The dichroic ratio (maximal absorption value divided by minimum absorption) of crayfish rhabdoms can be as high as 2–3, but most invertebrate rhabdomeres have dichroic ratios vary between 1 and 2. The dichroic ratio of 2–3 for crayfish rhabdomeres is higher than can be accounted for by the tubular structure of microvilli where it was assumed that chromophores show random, rotational diffusion within microvilli [2]. Therefore, chromophore orientation in microvilli must be aligned to their long axis by some additional mechanism [3] probably related to the actin-based cytoskeleton within the membrane tubule [4,5]. When

measurements of polarization sensitivity are taken from insect visual interneurons, values as large as 10 are evident, which is much larger than the dichroic ratio of rhabdomeres [6]. This enhanced polarization sensitivity is thought to come about by synaptic inhibition or opponent interaction between receptors [7].

(b) *Vertebrates*

While polarization vision in invertebrates is well established, the diversity of vertebrates with documented polarization sensitivity has increased over the last decade, most notably among fishes. Fishes such as engraulids [8,9], pomacentrids [10,11], salmonids [12,13], cyprinids [14] and cichlids [15] have polarization sensitivity and in some cases the potential to discriminate linearly polarized light. However, a clear link between the structure of the photoreceptors and polarization sensitivity is not as evident in vertebrates as in invertebrates.

One clear exception is found in anchovy (engraulids), where the organization of disc membranes in the outer segment of vertebrate photoreceptors appears as an intuitive counterpart to invertebrate microvilli. The cone photoreceptors of some engraulids have disc membranes that are axially oriented and thus are distinct from all other vertebrate rods and cones that have disc membranes that are transversely oriented in the outer segment ([16] (bay anchovy—*Anchoa mitchilli*); [9] (northern anchovy—*Engraulis mordax*); [8] (bay anchovy—*A. mitchilli*)). This organization of disc membranes allows the anchovy cones to preferentially absorb axially presented polarized light as, similar to microvilli, the chromophore is now constrained to be oriented largely in one direction. Anchovies have two cone types, short (bifid) and long cones, both of which have a peak sensitivity, or $\lambda_{\max}$, of 540 nm. These photoreceptors are spatially arranged in the

* Author for correspondence (craig.hawryshyn@queensu.ca).

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photoreceptor layer so that the plane of orientation of their axial disc membranes is orthogonal, providing sensitivity to two polarization directions [8,9,16]. Other polarization-sensitive vertebrates that have been investigated do not show such specializations in the outer segment of photoreceptors.

(i) *Axial dichroism*

Photoreceptors in pomacentrids, cyprinids and salmonids possess disc membranes in their outer segments that are transversely oriented to the long axis of the photoreceptor, allowing random rotational and lateral diffusion [17,18]. Thus, rods and cones in these species show linear dichroism for polarized light only when it is presented transversely to the axis of the photoreceptor, with maximal absorption at an e-vector orientation parallel to the disc membrane stack. Looking at rods in the axial orientation, for example, visual pigment chromophores would be randomly oriented in the disc membrane and thus should not show axial dichroism [17,18]. Unfortunately, this logic has been used to argue that all vertebrate photoreceptors do not have polarization sensitivity [19]. However, recent optical measurements of individual photoreceptors in goldfish have shown that cones but not rods do possess axial dichroism (figure 1) [20]. The orientation of individual photoreceptors was manipulated using laser tweezing. A second laser beam was passed through the receptor's long axis to measure axial dichroism and showed that MWS cones¹ had a dichroic ratio of 1.2 [20]. Although this is well below the polarization sensitivity of goldfish cones at 7–8 [14], it was argued that the high polarization sensitivity is achieved by opponent interactions between polarization detectors [21]. Roberts & Needham [20] suggested that cone axial dichroism could be related to specializations in the outer segment of cone photoreceptors, such as disc membrane viscosity that aligns chromophores to predominately one axis of orientation and a slight tilting in the plane of absorbance of disc membrane. Together, this results in polarization sensitivity of individual cone photoreceptors [20,22].

(ii) *Dichroic mirror*

Apart from the observation of axial dichroism in cyprinid cones, a second mechanism that could generate dichroism was proposed (figure 2). Double cones in salmonids have a partitioning membrane between the two members of the double cones in the inner segment, which is tilted at the apical end of the double-cone inner segment. This membrane could behave like a dichroic mirror, reflecting polarized light onto the transverse axis of neighbouring UVS¹ cones [9]. Here the spatial organization of the square cone mosaic becomes an important consideration (figure 2). Double cones (MWS/LWS¹ cone members) surround central single cones (SWS¹ cones) and single cones (UVS cones), which occupy the corner locations in the retinal mosaic [23]. The double-cone partitioning membrane is oriented so that it faces neighbouring UVS corner cones, where the plane of the tilt of the partitioning membrane is in the direction of preferred

polarization reflected from the double-cone partition onto the transversely oriented disc membranes in single-cone outer segments of the UVS cones [9]. The central single cones (SWS cones) of a mosaic unit do not face the double-cone partitioning membrane and hence do not receive reflected light. Indeed, measurements of polarization sensitivity of SWS cones confirm this by showing that SWS cones are polarization insensitive [12,14].

In this class of polarization-detection systems in fishes, multiple cone types participate in polarization sensitivity; UVS cones and the MWS/LWS members of the double cone. Differential polarization sensitivity, in the UV-short wavelength part of the spectrum, is a product of the interaction between the α -band of the UVS cone mechanism—the vertical detector mechanism—and the β -band² of the MWS/LWS cone mechanisms—the horizontal detector mechanism [13,21].

Polarization vision or the ability to differentiate e-vector orientation occurs only in the UV-short wavelength spectrum. Polarization sensitivity in other parts of the spectrum, apart from the UV, would be limited to a uni-modal horizontal polarization detector and thus would not show polarization vision. Behavioural experiments show that when the polarized light field is limited to the visible spectrum without UV content, fishes are not capable of orienting to the e-vector [13,24] nor discriminating e-vector [11].

Hawryshyn and co-workers have shown that changes in the cone mosaic in salmonids, through a regionally specific plasticity of UVS corner cones in the ventral retina, can dictate changes in UV polarization vision. For instance, when trout lose UVS cones in the ventral retina, it abolishes polarization vision in that part of the retina [24–26], and when UVS cones regenerate, polarization vision returns [26]. Therefore, polarization vision functionality depends critically on the presence of UVS cones in the cone mosaic in a particular area of the retina.

2. FUNCTION OF POLARIZATION VISION

The question of the function of polarization vision in fishes has not received sufficient experimental attention. Research to date shows that polarization vision could be beneficial in at least three general areas of vision: (i) contrast enhancement, (ii) visual communication, and (iii) spatial orientation and navigation.

(a) *Contrast enhancement*

Behavioural studies have shown that the damselfish, green chromis (*Chromis viridis*), is capable of e-vector discrimination, independent of brightness [11]. This e-vector discrimination is critically dependent on the UV content of the polarized light field since only in the UV-short wavelength part of the spectrum do both the vertical and horizontal polarization detectors operate [10,11]. Green chromis can successfully discriminate between two polarization targets that have an angular difference (Δ e-vector) as low as 10°.

Damselfish live in shallow tropical marine waters that are characterized by high spectral complexity

Figure 1. Measurements of axial polarization in goldfish. (a) A time series of video images illustrating a 180° rotation of an axially orientated double-cone photoreceptor. The rotation is centred on the mid-wavelength sensitive (MWS) outer segment. Scale bar, 10 μm . (b) A typical set of axial absorbance measurements from an MWS outer segment indicating the axial dichroism of the cell type. (c) A time series of video images illustrating a 360° rotation of an axially orientated rod photoreceptor. Scale bar, 5 μm . (d) The corresponding constant axial absorbance measurements from a rotating rod photoreceptor. In (b) and (d), the solid symbols represent the absorbance and the open symbols show the post-bleach baseline. (e) The mean axial dichroic ratios from all measured rods and MWS cones. The mean values are significantly different between cell types ($n = 9$; $p < 0.05$; one-way ANOVA). Error bars represent mean $\pm$ 1 s.d. (figure taken from [20]).

and intensity, particularly in the UV and violet components of the spectrum. Their spectral sensitivity is based on short-wavelength-shifted cone opsins

and appears to be compressed to below 560 nm [10,27]. Pomacentrid fishes are abundant in most shallow coral reef communities and are diurnal

Figure 2. Schematic showing the cone mosaic of rainbow trout and the anisotropic transfer of linearly polarized light, assuming that the partitioning membrane acts as a dielectric mirror. Rainbow trout cone mosaic showing UVS, SWS, MWS and LWS cones. E_h , horizontal e-vector; E_v , vertical e-vector. Double-headed arrows, within the square mosaic, indicate the dominant plane of polarization. (Adapted from Flamarique *et al.* [9], which should be consulted for more details on this illustration.)

zooplanktivores. Their e-vector discrimination performance indicates that polarization contrast can be achieved with small e-vector differences (10°) between the zooplankton and the background. Furthermore, plankton can depolarize and create phase retardance of transmitted light (i.e. they are birefringent), resulting in a species-specific polarization contrast, especially in the UV spectrum, between the animal and the background; from 5 per cent in *Corycaeus* sp. to 92 per cent in *Undinula vulgaris* (Copepoda) [28]. This contrast diminishes exponentially with distance but it is well within the reactive distance (35 cm) of planktivorous fishes such as damselfish [29].

(b) Visual communication

Reflection of polarized light produced by integumental iridophores on an animal's body surface may provide communicative cues [30–33]. For instance, the dermis of pomacentrids may produce both coloration and polarization used for interspecific and/or intraspecific communication. Damselfish possess chromatophores and iridophores, which provide many combinations of body coloration and patterns. Iridophores reflect light through interference occurring in the stacks of guanine crystals [34], and light reflected from iridophore crystals can be polarized [34–36]. Both the plane and the degree of polarization produced by reflective iridophores can change dramatically depending on the movements of the fish [32,34,37]. Damselfish are very social and use visual signals/cues in intraspecific communication [38]. There is a need for a more extensive examination of polarization patterns in damselfish and other fishes.

(c) Spatial orientation

Hawryshyn and co-workers trained fish to perform a goal-oriented behaviour using polarization cues [24,39]. Fishes actively navigate during the spatial orientation response by adjusting ongoing movements in response to polarized light cues. Recent work on the spatial orientation of rainbow trout used video recording to examine the angular responses of fishes to imposed polarized light cues [39]. These recordings show that the spontaneous orientation of fishes to e-vector is highly dynamic. Trout circle and scan the overhead polarization with side-to-side head movements (up to 180°) and dynamically change their body axis relative to the polarization cue. Trout that have been trained in the laboratory and tested outdoors using natural polarization cues show very robust spatial orientation responses, illustrating that this behaviour generalizes well to natural polarization cues [39]. It has been suggested that the cues they use are polarization cues present in the celestial hemisphere [24,39,40]. These cues are produced by Rayleigh scattering and are thus most prominent in the UV part of the spectrum [41]. Polarization vision in migratory salmonids is a potentially important mechanism of navigation that permits sun compass navigation [26,39,42], an ability well known in insects [43].

3. GENERAL NEURONAL PROCESSING IN THE OUTER PLEXIFORM LAYER

Independent of the exact mechanism generating polarization sensitivity in photoreceptors, we can conclude that in many fishes, photoreceptors are responsible

Figure 3. (a) Schematic of the retina. OPL, outer plexiform layer; IPL, inner plexiform layer. (b) Schematic of the IV (current–voltage) relation of the Ca^{++} current of a cone in three conditions. (i) The cone is in the dark at its resting membrane potential. (ii) The cone is hyperpolarized by light but horizontal cell to cone feedback has not yet become active. (iii) Both cones and horizontal cells are hyperpolarized and feedback has been fully activated. (c) The light response of a horizontal cell to a 500 ms full-field flash of light. The numbers correspond to the conditions depicted in (b).

for generating a retinal signal that represents both horizontal and vertical polarization orientation and that in most fishes these signals are mediated via different spectral cone classes. Next, we will develop a model of polarization processing by the retina. However, very limited electrophysiological data are available for such an endeavour. In an effort to overcome this limitation, we will use the colour vision system as a blueprint for the polarization processing system. This approach has enabled us to establish for the first time a well-founded hypothesis for retinal polarization processing and has sparked new ideas on the possible

use of polarization cues. In addition it has induced new experimental approaches to evaluate the function of polarization sensitivity. We start by discussing the general organization of the vertebrate outer retina (figure 3).

Photoreceptors project to horizontal cells (HCs) and bipolar cells (BCs) via Ca^{++} (calcium)-dependent glutamatergic synaptic transmission. Both HCs and OFF-BCs, possess ionotropic glutamate receptors, which means that they are depolarized by glutamate [44–46]. Photoreceptors also project to ON-BCs. These cells express the metabotropic glutamate

receptor, mGluR6 [47–51]. Activation of mGluR6 by glutamate leads, via an intracellular cascade, to the closure of TrpM1 channels on the dendrites of ON-BCs [52–54]. Glutamate induces a hyperpolarization of these neurons. Light stimulation leads to hyperpolarization of photoreceptors, resulting in a reduction of their glutamate release. This induces a hyperpolarization of HCs and OFF-BCs and a depolarization in ON-BCs. HCs are strongly coupled by gap junctions. This makes their receptive fields much larger than their dendritic trees. In this way, they integrate the visual signal spatially. In other words, they sample the mean illumination falling on the retina. HCs provide negative feedback to cones. The effect of HC feedback to cones can be seen in cones as a modulation of the Ca^{++} current [55].

Figure 3*b* summarizes the events at the cone synaptic terminal during light stimulation. It shows the Ca^{++} current of a cone during various phases of the light response. Figure 3*c* indicates the resulting HC membrane potential. Cones rest at about -30 mV. This induces a Ca^{++} current of approximately 100 pA (figure 3*b*(i)), resulting in the dark resting membrane potential of the HCs (figure 3*c*(i)). Upon light stimulation, cones hyperpolarize (figure 3*b*(ii)). This leads to a reduction of the Ca^{++} influx and subsequently, to a reduction of glutamate release inducing hyperpolarization of HCs (figure 3*c*(ii)). Hyperpolarization of HCs leads to a shift of the cone Ca^{++} current to negative potentials (figure 3*b*(iii)). Such a shift leads to an increase in Ca^{++} influx in the cones and thus to an increase in neurotransmitter release that induces a small depolarization in HCs (figure 3*c*(iii)). This is a subtractive interaction and is the negative feedback pathway that generates the inhibitory surround of BCs. This mechanism is highly conserved and is used by both rods and cones [55–59].

Two hypotheses have been proposed to account for the modulation of the Ca^{++} current. One is an ephaptic or electrical mechanism involving connexin hemichannels [57,60] and the other is a pH-based mechanism [56,61]. For the present discussion, the exact nature of the feedback mechanism is not essential and will not be discussed any further in this paper.

(a) Concept of predictive coding

The organization of receptive fields into an excitatory centre and an inhibitory surround is an important principle of sensory system design and is especially prominent in the retina. A variety of functions have been ascribed to this retinal organization, including edge enhancement, image deblurring and redundancy removal. Srinivasan *et al.* [62] demonstrated that most of these functions are equivalent and can be subsumed in the idea of ‘predictive coding’. The essence of predictive coding is that the antagonistic surround, consisting of a weighted average of signals in neighbouring neurons, representing the ‘predicted value’, is subtracted from the response of the central neuron (or neurons). In this way, the central neuron only transmits information that differs from the predicted. Since this mechanism removes global features from

the image, it leads to redundancy reduction and thus to a more efficient neural code [62].

To function optimally, predictive coding needs two steps: (i) subtraction of the predicted value from the centre response and (ii) amplifying the remaining response such that it optimally uses the dynamic range of the post-synaptic neuron. Both of these transformations need to be based on estimates made in the surround. The first location in visual processing where predictive coding could occur is the photoreceptor synapse. Abundant evidence is present for the first step of predictive coding at that location: surround inhibition by HCs (see, for instance [62]). The second step, the amplification step, also occurs at that synaptic interaction and was recently described in detail by VanLeeuwen *et al.* [63] and will be addressed in the next paragraphs. Since both transformations, subtraction and amplification, have been shown to function at the cone photoreceptor synapse, one can conclude that the first coding step in the outer retina is likely to be a predictive coding step.

What is the nature of both predictive coding steps? Negative feedback from HCs to cones shifts the Ca^{++} current to negative potentials [55]. As discussed above, this is a subtractive negative feedback pathway. However, owing to the nonlinearity of the Ca^{++} current, this shift induces also a multiplicative feedback component. Let us define synaptic gain as change in cone Ca^{++} current per millivolt change in cone membrane potential. In figure 4*a*, the Ca^{++} current of a cone is indicated. Modulation of the cone membrane potential when cones are relatively depolarized leads to a large change in Ca^{++} current; the synaptic gain is high. The same modulation of the cone membrane potential will lead to a much smaller modulation of the Ca^{++} current when the cone is hyperpolarized; the synaptic gain is low. This means that direct light stimulation of a cone leads to a reduction of the synaptic gain. The system becomes less sensitive. How does feedback affect the synaptic gain? In figure 4*b*, two conditions are shown: one when HCs are at their resting membrane potential (solid line) and feedback is not active and one when HCs are hyperpolarized (dashed line) and feedback is active. Modulation of the cone membrane potential by a few millivolts around -35 mV leads to a smaller modulation of the Ca^{++} current when HCs are at their resting membrane potential compared with the condition when HCs are hyperpolarized. Feedback from HCs to cones increases the synaptic gain. The system becomes more sensitive.

In general terms, we can say that direct cone stimulation leads to a reduction of the synaptic gain and surround stimulation leads to an increase in synaptic gain. Note that the gain-increasing mechanism is spatially extensive since it is driven by HCs and, cone non-specific since HCs receive input from more than one spectral cone class. However, the gain-decreasing mechanism is cone specific and local [63].

The subtractive and multiplicative mechanisms lead to an intriguing conceptual framework. HCs integrate the visual scene spatially [64,65], spectrally [65–67] and temporally [68]. They make a time-averaged estimate of the global intensity and colour. Cones,

Figure 4. The synaptic gain changes with hyperpolarization of cones and with activation of feedback. (a) When cones are modulated slightly around its dark resting membrane potential (i), a relatively large modulation of the Ca^{++} current occurs (ii). The synaptic gain is relatively high. When the same modulation is applied at more negative potentials (iii), a much smaller modulation of the Ca^{++} current occurs (iv). The synaptic gain is low. (b) When the cone membrane potential is modulated slightly around its dark resting membrane potential, a certain modulation of the Ca^{++} current occurs (ii). When surround stimulation leads to hyperpolarization of HCs and thus induces a shift of the Ca^{++} current to negative potentials, the resulting modulation of the Ca^{++} current increases. Negative feedback increases the synaptic gain (after [63]).

on the other hand, sample the local stimulus properties with a high time resolution. For large objects, cones and HCs are stimulated similarly. However, when cones are looking at small objects, they are stimulated differently than the HCs. These differences, owing to the presence of distinct features in the visual field, are amplified by the lateral gain-enhancing mechanism [63] and are transmitted with high fidelity to BCs and the rest of the visual system. This means that objects or features that differ from the average are transmitted to higher retinal and brain areas with a higher gain than the average features. In this way, outer retinal processing strongly contributes to optimizing information flow through the retina [69–72]. Next, we will discuss whether this predictive coding step influences perception directly and proceed in discussing how predictive coding affects colour vision and presumably polarization vision.

(b) Perception

Does this processing have a perceptual counterpart? It is tempting to speculate that such a gain-enhancement step might be the first of many transformations needed for object selection. In other words, does such a change in synaptic gain at the photoreceptor level lead to changes in perception? In the accompanying movie (electronic supplementary material), a flickering spot of light with and without a surround with an equal mean luminance as the flickering spot is presented. Figure 5 gives a schematic of the movie. After viewing the movie, it will be clear that the spot seems to flicker more vigorously with the equiluminant surround than without it. This psychophysical phenomenon was first described by Kelly [73]. We have stimulated the retina with a similar stimulus and studied the responses of cones and ganglion cells (GCs). We found that the response of GCs and the output of cones to a flickering spot became larger with steady surround illumination [63]. This suggests that the psychophysical phenomenon described by Kelly could have an outer retinal origin and that it is a fundamental feature of

the vertebrate visual system. Next, we will expand the theory of predictive coding first to the spectral domain and finally we will propose how predictive coding could function in the polarization domain.

(c) Colour vision

Before we can discuss spectral processing, we need to make a clear distinction between colour and wavelength distribution of light. Colour is a psychophysical percept, whereas the wavelength distribution is a physical property of light. When looking at a scene, light reflected from coloured objects will have a specific spectral composition and will thus activate photoreceptors in a distinct ratio. The relative activity of the photoreceptors contains all the information about the spectral composition of the light reflected by an object and thus eventually of the colour it is interpreted as. If the brain had access to the activity of the various cone systems, it could calculate the absolute colour of the object. However, information pertaining to cones is not transmitted to the brain as pure cone signals. It is preprocessed in the retina by HCs and by convergence of the cone signals onto BCs, amacrine cells and GCs. The final result is that the spectral information is transmitted to the brain in spectral opponent and spectral non-opponent channels in which the pure cone signals are lost. Such division in channels correlates with the psychophysical data that suggest red–green and blue–yellow opponent colour channels and a luminosity channel [74]. The final transformation from spectrally coded activity (wavelength) to colour seems to happen for primates in V4 [75,76]. It is highly likely that for lower vertebrates a similar scheme holds and that colour will be determined in higher brain areas.

(d) Opponent coding versus non-opponent coding

The organization in opponent and non-opponent channels raises a number of questions. First of all, why do we need opponent channels? Are they the

Figure 5. Schematic of the accompanying movie illustrating that a flickering spot is better perceived in an equiluminant surround. The two images are alternated such that a flickering stimulus occurs. The graph on the bottom indicates schematically the cone output. (a) A grey spot is flickered in a dark surround. (b) a grey spot is flickered in a surround with the same mean luminance as the spot. The flickering of the spot in the grey surround (b) is perceived much more vividly than the same grey spot in a dark surround (a). The outer retinal gain control mechanism scales the cone output such that the whole scene fits the bandwidth of BCs.

first step in colour discrimination? This issue was addressed by Joselevitch & Kamermans [77], and it was concluded that retinal spectral opponency does not seem to be a specific step in colour vision, but that it is an efficient way of coding signals. As was shown by Buchsbaum, opponent–non-opponent coding leads to a reduction in redundancy in the neural representation of the signals. The logical consequence of this is that spectral coding of HCs is a highly efficient way of processing spectral information, but it is not related to colour vision *per se* [78,79]. This coding strategy seems to hold for many sensory modalities and it is therefore highly likely that a similar coding strategy is used for polarization vision as well.

The second issue concerns the function of spectral coding in HCs, and this has been extensively discussed in Kamermans *et al.* [79] and VanLeeuwen *et al.* [63]. Kraaij *et al.* [66] found that although the spectral sensitivity of HCs is opponent, their combined output to the cones is spectrally very broad and not opponent. This suggests that all HCs together estimate the mean spectral composition of the stimulus and ‘store’ this information in the HCs. This information is sent back to the cones and is used to modify the output of the cones. Thus, when discussing HC function one should consider all classes of HCs together as one functional unit. This has major consequences.

As we have discussed before, direct stimulation of a cone leads to a reduction of the synaptic gain, whereas feedback leads to an increase in synaptic gain. This means that the feedback signal from HCs to cones corrects the gain of the synapse of the various cones for the mean spectral composition of the illumination. For instance, an SWS cone in a condition with a global red illumination will have a high synaptic gain, whereas that same cone in a blue global illumination will have a low gain. We have shown that such a system will induce some form of colour constancy. The mean colour is subtracted from the scene and the representation of objects with a colour deviating from the mean is enhanced [63,79].

Is this a general mechanism? Animals with many different spectral cone types have HCs with highly complicated spectral sensitivities. However, the spectral sensitivity of the combined output of HCs is not spectrally opponent [66]. All animals tested so far with only two cone types have HCs without spectral opponency. Thus, it is highly likely that in these animals the spectral sensitivity of the feedback signal cones receive from the HCs is not spectrally opponent as well. Primates also lack spectral opponent HCs but humans have excellent colour vision. This illustrates that spectral opponency of HCs is not essential for colour vision. One might speculate that in animals without spectral coded HCs, the correction of the cone outputs by HCs and thus colour constancy will be less efficient [80].

4. WHAT CAN WE LEARN FROM COLOUR VISION THAT IS APPLICABLE TO POLARIZATION VISION?

Polarization vision is based on at least two orthogonal polarization detectors. UV cones are tuned to the vertical e-vector orientation, whereas the MWS/LWS cones are tuned to the horizontal orientation. In comparison, colour vision in trout and goldfish is based on four different detectors (LWS, MWS, SWS and UVWS cones), which is much more complicated. Next, we will simplify the colour vision scheme, and evaluate whether such simplified scheme is applicable to polarization vision. Cones project to BCs and finally, to the rest of the brain. At the BC level, spectral opponent and spectrally non-opponent BCs occur. Since the e-vector orientations are linked to spectral cone classes, it is highly likely that the same opponent/non-opponent coding will emerge for polarization vision as well.

HCs receive inputs from the cones and feed back to cones. In trichromatic and tetrachromatic animals, this results in complex opponent spectral coding of HCs. However, as discussed above, the final output of the HC system is not spectrally opponent. In dichromatic animals, opponent coding at the HC level is absent. Since e-vector processing has only two detectors, it is to be expected that HCs will not show e-vector opponency. Different HC types might have slightly different e-vector tuning curves but opponency in the polarization domain at this level is highly unlikely.

In the spectral domain, all HCs together estimate the global spectral composition of a scene. At the

cone–HC synapse, local spectral composition observed by an individual cone is compared with the spectral composition of the whole scene. When the signal sensed by a cone deviates from the signal predicted by the HCs, the difference signal is amplified and sent to the BCs. Following this scheme, we suggest that in the polarization domain, HCs estimate the global e-vector orientation in a scene. When the e-vector orientation measured by a cone looking at an object in that scene is deviating from the global e-vector orientation, the difference signal is amplified and transmitted to BCs. The outer retina is thus optimized to transmit differences in the temporal, intensity, spectral and polarization domains. In all of these domains, a predictive coding strategy is used. Note that this mechanism might be the basis for the higher polarization sensitivity values (7–8) seen in the psychophysical [14] and electrophysiological [12,13] data compared with the physical measurements of dichroism in the cones.

(a) *Physiological evidence for retinal processing of polarized light*

Is such a mechanism consistent with the available experimental data? Three datasets dealing with the processing of e-vector signals are available: electroretinogram (ERG), compound action potential (CAP) [21] and HC responses (C. Xiao, M. Kamermans & C. Hawryshyn 2008, unpublished results). Next, we will compare these three datasets with the proposed retinal processing of e-vector information. The *a*-wave activity in the ERG represents the photo-receptor activity; the *b*-wave is dominated by ON-BC activity. CAPs occur in the optic nerve and can be considered as an estimate of the retinal output. It contains both ON and OFF responses. In Ramsden *et al.* [21], only the CAP-ON responses were analysed. Finally, the HC recordings are intracellular recordings of HC polarization sensitivity in eyecup preparations. Figure 6 shows from top to bottom three levels of retinal processing; the GCs (CAP—figure 6*a*), the HC responses (figure 6*b*) and the ON-BCs (ERG *b*-wave responses—figure 6*c*). Note that HCs do not show pronounced e-vector tuning. We cannot entirely rule out the possibility that the eyecup preparation disrupted the retina to the extent that it dampened polarization sensitivity but care was taken to minimize this possibility. The ERG responses, on the other hand, show a highly unexpected behaviour. For ERG polarization sensitivity, we see peaks for the vertical and horizontal polarization detectors in addition to two other peaks, called intermediary peaks. The difference evident in the polarization sensitivity between these levels of retinal processing indicates that early retinal processing is strongly involved in e-vector processing. How can we account for these differences and what do they tell us about the retinal-processing mechanism?

5. RETINAL MODEL FOR POLARIZATION VISION

Let us assume that we have two classes of cones, one acting as a vertical polarization detector (P_v) and the other acting as a horizontal polarization detector (P_h) (figure 7*a*). The total HC activity is the sum of the

Figure 6. Polarization sensitivity measured using three recording techniques at different levels of processing in the retina. (a) Mean normalized ultraviolet polarization sensitivity (± 1 s.e.) determined by compound action potential recording from the optic nerve (GCs) in rainbow trout (solid circles, $n = 5$). The testing conditions used an UV-polarized stimulus at 360 nm on a 'white' broad-band unpolarized background. A linear subtractive model was used to generate the modelled sensitivity of the vertical polarization detector (open squares) (after [21]). (b) Mean relative ultraviolet polarization sensitivity (± 1 s.e.) determined by intracellular recording of horizontal cells in goldfish. Filled circles, monophasic horizontal cells ($n = 15$ cells). Open squares, biphasic horizontal cells ($n = 13$ cells). Open diamonds, triphasic horizontal cells ($n = 6$ cells). Note that the sensitivity of each class of cell is displaced by one log unit for purposes of clarity. The testing conditions used an UV-polarized stimulus at 380 nm on a white broad-band unpolarized background (C. Xiao, M. Kamermans & C. Hawryshyn 2008, unpublished data). (c) Mean normalized UV polarization sensitivity (± 1 s.e.) determined by electroretinogram recording in rainbow trout (solid circles, $n = 21$) (b-wave, 'ON'-BCs). The testing conditions used an UV-polarized stimulus at 360 nm on a white broad-band unpolarized background. A linear subtractive model was used to generate the modelled sensitivity of the vertical polarization detector (open squares) and the modelled sensitivity of the horizontal detector (open squares). The solid line connects the sensitivity points representing the intermediary peaks (negative feedback activity from horizontal cells) (after [21]; HC data; C. Xiao, M. Kamermans & C. Hawryshyn 2008, unpublished results).

horizontal and vertical detector inputs received from the cones. Since the input to the HCs is nonlinear, HCs will show some slight e-vector tuning (figure 7b). The output of HCs is subtracted from the cone, and this difference signal is amplified and sent to the BCs. Let us further assume that horizontal and vertical detector inputs to the various BC classes generate non-opponent and opponent pathways, just as for colour vision. These non-opponent and opponent channels arise from linear combinations of BCs with orthogonal (horizontal or vertical) e-vector orientations. But since the b-wave of the ERG contains

the global activity generated by all ON-BCs, we have not included all the different types of BCs in the model separately. The signals from the BCs are sent to the GCs. The CAP consists of integrated spike activity of the GCs. Spikes are generated by depolarization and not by hyperpolarization. Therefore, we need to rectify the BC signals. This rectification leads to ON and OFF responses. Since Ramsden *et al.* [21] analysed only the ON-CAP responses, we will ignore the OFF-CAP responses in the model. The equations and parameters used in the simulations are given in the appendix. Next, we determine the

Figure 7. The retinal model for polarization vision and the polarization tuning curves for the different components of the model. (a) Block diagram of the retinal model. P_v , photoreceptors sensitive to vertical e-vector orientation; P_h , photoreceptors sensitive to horizontal e-vector orientation; HC, horizontal cell system; BC_v, bipolar cells sensitive to vertical e-vector orientation; BC_h, bipolar cells sensitive to horizontal e-vector orientation; ERG, electroretinogram; CAP, compound action potentials of the optic nerve. For details of the model, see text. (b) Simulated polarization tuning curves for the various components of the model. (i) e-vector tuning curves for the photoreceptors (a.u., arbitrary units). Solid line, P_v ; dashed line, P_h . (ii) e-vector tuning curves of the HC system. (iii) e-vector tuning curves of the BCs. Solid line, BC_v; dashed line, BC_h. (iv) e-vector tuning curves of the ERG and CAP. Solid line, ERG; dashed line, CAP. (c) Simulated ERG and CAP e-vector tuning curves in conditions when feedback from HCs to cones has been blocked. Solid line, ERG; dashed line, CAP. In this condition, the ERG and the CAP responses show both two peaks. The intermediate peaks in the ERG have disappeared, showing that they critically depend on the HC to the cone feedback pathway.

polarization tuning curves on the different levels of the retina. The ERG *b*-wave has a four-peaked polarization tuning curve (figure 7b(iv)). The size of the

peaks fully depends on the degree of nonlinearity in HC processing. The CAP polarization tuning curve derived in this way is a double-peaked function

(figure 7b(iv)). So far, the model describes the experimental data adequately, although the HC e-vector tuning seems a bit more pronounced in the model than in the experimental data. Note, however, that this could be due to the inherent difficulty to obtain these experimental data.

Experimentally, it was found that blocking negative feedback of HCs onto cones leads to a disappearance of the intermediary peaks in the ERG polarization sensitivity curve [21]. We repeated this experiment in the model. When feedback from HCs to cones is blocked, there is no subtraction of the HC signal from the cone signal and no intermediary peaks are evident in the ERG polarization sensitivity curve, confirming the HC origin of the intermediate peaks (figure 7c).

The proposed model can account for the ERG, HC and CAP responses by following the same coding scheme as for colour vision. The only essential assumption is a nonlinearity in the HCs. It is, however, highly likely that such nonlinearity exists [81]. Since the retina performs highly specialized transformations on the incoming signals, it would be interesting to analyse how these transformations would affect polarization-guided behaviour.

6. FUNCTIONAL CONSEQUENCES OF THE RETINAL MODEL FOR POLARIZATION VISION

Based on the performance characteristics of polarization sensitivity discussed in the first part of this review, it is evident that polarization vision is particularly important for spatial orientation, contrast enhancement and intraspecific communication. The analysis of the electrophysiological signals suggests that the system enhances the response to an object when the e-vector of the light reflected or transmitted by that object differs from the mean e-vector of the scene. This means that the system mainly induces a kind of contrast enhancement. However, the contrasts will not be perceived as such. Note that the horizontal and the vertical e-vector signals are mediated by spectrally distinct photoreceptors. Therefore, differences in e-vector tuning will also be perceived as a colour difference. A transparent object that changes the e-vector orientation of the light by birefringence will be seen as a coloured object, which makes it more easily detectable. Interestingly, it seems that e-vector processing uses part of the neuronal machinery evolved for colour vision. The e-vector processing seems to 'piggy back' on the colour vision system.

For animals living in a low-contrast environment with transparent zooplankton, this might be a highly efficient way of detecting objects. For instance, it has been shown that squid can detect zooplankton at 70 per cent greater distance with polarized light than with non-polarized light [28]. Most probably, these animals make use of the difference in e-vector orientation owing to transmission and reflection of light by zooplankton [28,82]. One benefit for the animal of such an e-vector-based local 'contrast' enhancement is the better detection of transparent zooplankton, which allows more efficient feeding. This may have acted as a major evolutionary pressure on this

system to optimize e-vector discrimination. This suggests a more general conclusion that polarization vision might have been evolved first for enhancement of detection in low-contrast environments and later for spatial orientation. This mechanism of enhancing object detection, as discussed above, might also be beneficial for interspecific communication. Patterns of polarized light reflecting from the body surface will be enhanced and perceived as patterns of coloured light.

(a) Can local e-vector tuning be used for navigational purposes?

The above arguments suggest (i) that e-vector tuning is mainly a method enhancing the detection of poorly visible objects and (ii) that global e-vector orientation is filtered out. In general, the vertebrate visual system is not very good in detecting global features in a scene. It is specialized in detecting local features. Although well-developed ideas exist about the use of polarization cues in the celestial hemisphere for the purposes of spatial orientation [24,39,40], our new retinal model for polarization vision suggests that owing to predictive coding local polarization cues become enhanced. This suggests a controversy. Is polarization processing mainly tuned to local or global cues? The analogy to colour and contrast vision suggests that polarization vision is tuned to local features, whereas the present models for navigation suggest that polarization vision is mainly processing global cues. Is the use of polarized light for navigational purposes completely restricted to polarization cues in the celestial hemisphere or can local cues be used as well and what could these cues be? What is their relative contribution? Unfortunately, there is no literature about the availability of local polarization cues for navigational purposes.

The open ocean is a seemingly featureless environment. Zooplankton may reflect or transmit polarized light that has an e-vector orientation different from the background. Could such effect induce a cue for the location of the Sun and could it be used for sun compass navigation? Furthermore, often the sky will be covered by clouds, only leaving small patches of clear sky available for determining the e-vector orientation in the sky. Could these patches be considered as local features that will be enhanced by predictive coding mechanisms. Can they be used more efficiently for navigational purposes than a completely uncovered sky? Finally, could the reflection of polarized light on the bodies of other fish be used as local cues for the polarization of the light? These are just a few of the many questions that are sparked by our analysis of polarization vision in relation to colour vision.

7. HOW TO TEST THIS HYPOTHESIS?

The present discussion sparks interesting new ideas about how polarization vision can contribute to object detection and navigation. Let us look at some experimental strategies to test our hypothesis. First, because colour and e-vector are processed by common neural networks, it might be possible to

interfere with e-vector discrimination performance by compensating one e-vector orientation by an unpolarized coloured light. Furthermore, it would be very interesting to test whether salmon can use polarized light that is reflected and transmitted by transparent zooplankton or neighbouring fish to guide spatial orientation behaviour. Can a sky with clouds and small patches of blue sky be used more effectively for spatial orientation than fully blue sky? Can these local cues compete with more global cues? It is highly likely that salmonids have access to a number of cues in the natural environment and that they will choose the cue that prevails in a particular condition. Experiments as suggested above would allow us to assess which cues salmonids preferentially use for navigation and under which condition.

8. CONCLUSION

In this paper, we have proposed a retinal mechanism for the processing of e-vector information. This mechanism is fully consistent with direct measurement of e-vector tuning found on various retinal levels and in behavioural assays. This system may function similar to colour vision system. In fact, it seems to use part of the colour vision machinery. When following the analogy with colour vision, one can conclude that retinal e-vector processing is tuned to detect local deviations of e-vector orientations and translates these into colour differences, enhancing object detection. Possibly, these polarization-induced (colour) differences of objects can be used for navigational purposes as well.

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APPENDIX A

(a) Equations

Cones:

$$\left. \begin{aligned} P_v &= \log[A + \cos^2(\theta)] \\ \text{and } P_h &= \log[A + \sin^2(\theta)] \end{aligned} \right\} \quad (\text{A } 1)$$

HCS:

$$\left. \begin{aligned} I_{\text{HC}} &= P_v + P_h \\ \text{and } \text{HC} &= \frac{I_{\text{HC}}}{I_{\text{HC}} + K} + B \end{aligned} \right\} \quad (\text{A } 2)$$

BC:

$$\left. \begin{aligned} \text{BC}_v &= P_v - \text{HC} \\ \text{and } \text{BC}_h &= P_h - \text{HC} \end{aligned} \right\} \quad (\text{A } 3)$$

ERG b-wave:

$$\text{ERG}_b = \text{BC}_v + \text{BC}_h. \quad (\text{A } 4)$$

CAP:

$$\left. \begin{aligned} \text{CAP}_v &= \text{BC}_v \text{ if } \text{BC}_v > 0, \\ \text{CAP}_v &= 0 \text{ if } \text{BC}_v < 0, \\ \text{CAP}_h &= \text{BC}_h \text{ if } \text{BC}_h > 0, \\ \text{CAP}_h &= 0 \text{ if } \text{BC}_h < 0 \end{aligned} \right\} \quad (\text{A } 5)$$

and $\text{CAP}_{\text{total}} = \text{CAP}_v + \text{CAP}_h$.

θ is the e-vector orientation. A , B and C are free parameters. They indicate an offset in the cones (A), offset in the HC (B) and the feedback strength from HCs to cones (C).

(b) Parameters

parameter	values
A	0.1
B	2.13
C	0.5
K_{fb}	0.185

ENDNOTE

¹UVS, ultraviolet sensitive; SWS, short wavelength sensitive; MWS, middle wavelength sensitive; LWS, long wavelength sensitive.

²To understand α and β peak sensitivity, it is important to consider that visual pigments have three characteristic peaks in their absorption spectrum. The γ -band absorption is due to the protein absorption of photons—peaks at 280 nm and is therefore not visible. The β -band is due to absorption of photons by the chromophore resulting in partial electronic oscillations along the chromophore (11-*cis* retinal or 3-dehydroretinol bound to the opsin protein by a Schiff base linkage)—peaks at approximately 380 nm. The α -band is due to absorption of photons by the chromophore, resulting in electronic oscillations along the entire length of the chromophore (peaks between 350 and 620 nm depending on the amino acid sequence of the opsin molecule); see [19].

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