POLARIZATION VISION – A UNIFORM SENSORY CAPACITY?

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Summary

In this concept paper, three scenarios are described in which animals make use of polarized light: the underwater world, the water surface and the terrestrial habitat vaulted by the pattern of polarized light in the sky. Within these various visual environments, polarized light is used in a number of ways that make quite different demands on the neural circuitries mediating these different types of behaviour. Apart from some common receptor and pre-processing mechanisms, the underlying neural mechanisms may differ accordingly. Often, information about χ (the angle of polarization), d (the degree of polarization) and λ (the spectral content) might not – and need not – be disentangled. Hence, the hypothesis entertained in this account is that polarization vision comes in various guises, and that the answer to the question posed in the title is most probably no.

Introduction

There is an abundance of polarized light in natural environments, but there are only two main sources from which such light arises: the scattering of sunlight within the atmosphere (Fig. 1) and hydrosphere, and the reflection of light by water surfaces (Fig. 2) and other shiny, non-metallic, dielectric surfaces such as soil, rocks and vegetation.

Recently, it has become apparent that animals can make use of these rich sources of information in a multitude of ways. Hence, it seems pertinent to ask whether all these ways of exploiting polarized-light information are based on one common neural polarization-vision system designed to process information about polarized light and employed by different animal species. For example, does such a common neural polarization-vision channel unambiguously determine, in a first step, the angle of polarization (the orientation of the plane in which the electric vector, or e-vector, of light oscillates) in any particular point of the animal's polarized visual world, and is it this unambiguous e-vector information that is later, in a second step, used to fulfil whatever the particular ecological situation requires? Of course, any system using polarized light as a source of environmental information must have some kind of sensor that is differentially activated by different states of polarization, but it might be at this peripheral stage that the common characteristics of such systems end, let alone the possibility that even the sensory devices – the polarization analyzers – might differ depending on the particular task the animal must accomplish and also on the animal's evolutionary history.

What is the behavioural task that the animal must accomplish by using polarized-light information? It is

manifold. A large number of behavioural studies have been performed by various authors under various conditions and experimental paradigms in various groups of animals. These studies have led to a variety of results and, in turn, to considerable debate about how to define 'polarization vision'. These definitions range widely from any general ability to respond to polarized light to what could be called the most sophisticated e-vector-detecting system, namely one that is able to determine the angle of polarization (the e-vector orientation, χ) independently of variations in intensity (I), degree of polarization (d) and spectral content (λ). The conditions such a 'true polarization-vision system' (*sensu* Nilsson and Warrant, 1999) must meet were outlined nearly a quarter of a century ago (Bernard and Wehner, 1977), but whether the polarization-sensitive systems of any animal species obey these theoretical requirements has not been shown yet. Hence, let us move from definitions to observations, and consider three stimulus situations.

Stimulus situation I: water/air interface

Stimulus situation I is characterized by a rather simple set of polarization cues: light reflected from water surfaces is linearly polarized (Fig. 2). In reflection polarization, the degree of polarization varies with the angle of incidence, the elevation of the sun and the properties of the dielectric interface (e.g. air/water or air/glass), but for all practical purposes light polarized by reflection from water (and other shiny) surfaces is polarized predominantly parallel to the reflecting surface. As Rudolf Schwind has shown in a number
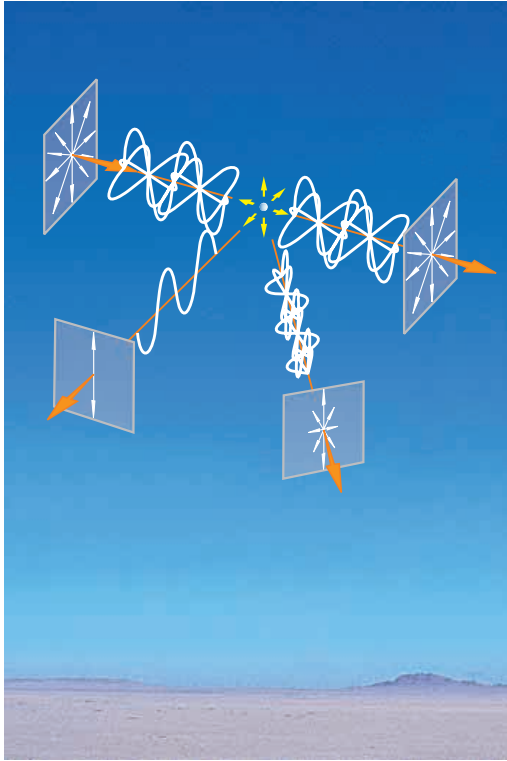
Fig. 1. Polarization arising from light scattering within the earth's atmosphere. Unpolarized sunlight (upper left panel) remains unpolarized if it reaches the observer directly (scattering angle 0°, right panel), but is linearly polarized if it is scattered by atmospheric O_2 and N_2 molecules. Within a theoretical (Rayleigh) atmosphere, the degree of polarization reaches 100%, if the scattering angle is 90° (lower left panel). Other scattering angles yield smaller degrees of polarization (lower right panel). The light is then said to be partially linearly polarized. In the real atmosphere, the degree of polarization – even in full blue skies – is almost always less than 70% (see Horvath and Wehner, 1999). Background landscape: Naukluft gravel plain desert, north of Gobabeb, Namibia.

of painstaking studies (e.g. Schwind, 1984; Schwind, 1991; see also Kriska et al., 1998), many water beetles and bugs flying on dispersal in search of bodies of water are attracted by horizontally polarized reflections from the ground. Unpolarized light is ineffective, even if its intensity is several times higher.

Note, however, that polarized reflections can also give rise to incoherent and erratic polarization cues, which can invade, so to speak, any colour vision system if the latter receives its input from photoreceptors that – as in arthropods – are inherently sensitive to polarized light. This problem is avoided by destroying the polarization sensitivity of photoreceptors in those parts of the eye that are involved in colour vision (Wehner and Bernard, 1993). Butterflies, however, at least the Australian orchid butterflies of the species *Papilio aegeus*, do not seem to disentangle the ambiguity between colour and polarization (Kelber, 1999; Kelber et al., 2001). Rather than being a failure, the use of polarization-induced 'false' colours

might help the butterflies to detect appropriate oviposition sites, horizontally oriented green leaves.

It appears that, whenever the polarized reflections create predictable arrays of stimuli indicative of biologically meaningful parts of the environment, some species of animal have evolved sensory filters that are matched to perceive them. The backswimmer *Notonecta glauca* is a prime example. It possesses a set of specialized photoreceptors that are most sensitive to horizontally polarized light. Let us term the part of the eye that contains these specialized photoreceptors the POL area of the eye. Each visual unit (ommatidium) of this POL area contains two sets of photoreceptors that have their e-vector tuning axes oriented in mutually perpendicular ways: one axis horizontal, the other vertical (Schwind, 1983). As we shall see below, such an orthogonal arrangement of polarization analyzers enhances polarization contrast if appropriately combined and renders the resulting signal invariant against fluctuations in radiant intensity. Thus, the structural peculiarities of the waterbug's POL channel are adapted to the stimulus characteristics prevailing at the surface of its aquatic world.

Stimulus situation II: water

Let us now move right into the aquatic world. Of course, there is the polarization pattern of the sky (see stimulus situation III) that can be seen within Snell's window just above the observer, especially if the observer is close to the water surface. However, outside this aerial window, light is polarized by scattering within the water itself. The angle of this water-induced polarization is almost always horizontal, but the degree of polarization increases the further one moves away from the shore towards the open water. Again, these consistent environmental stimulus characteristics have been exploited by polarization-sensitive animals. Small branchiopod crustaceans such as *Daphnia* species swim consistently towards the light with a higher degree of polarization if the e-vector is oriented horizontally and do so regardless of light intensity (Schwind, 1999). Outdoors in a pond, this behaviour will lead to the well-known ecological phenomenon of 'shore flight', i.e. the horizontal swimming movements of small pelagic crustaceans away from the shoreline towards deeper waters, where the density of predators is lower than in shoreline regions.

However, there is more to polarization vision under water than just using it for swimming away from the shore. Note that, in underwater vision, the scattering of light largely degrades contrast by interposing a 'veil of light' between the observer and any object observed (Lythgoe and Hemmings, 1967; Lythgoe, 1971; Nilsson, 1996). As a result of the prevailing horizontal polarization, a vertical analyzer would reduce the amount of scattered light perceived and, hence, increase contrast. This is analogous to the effect of polaroid sunglasses, but for scattered rather than reflected light (or to the use of yellow glasses when skiing in fog). More particularly, there is much more scatter in the background spacelight than between

Fig. 2. Polarization arising from the reflection of light by a water surface. Unpolarized sunlight (left panel) becomes linearly polarized when it is reflected by water surfaces. The reflected light is horizontally polarized (right panel). Maximum polarization is reached at a particular angle of incidence (Brewster's angle; 53 ° for the air/water interface). Background landscape: Sabkhat al Muh, south-east of Tadmur, Syria.
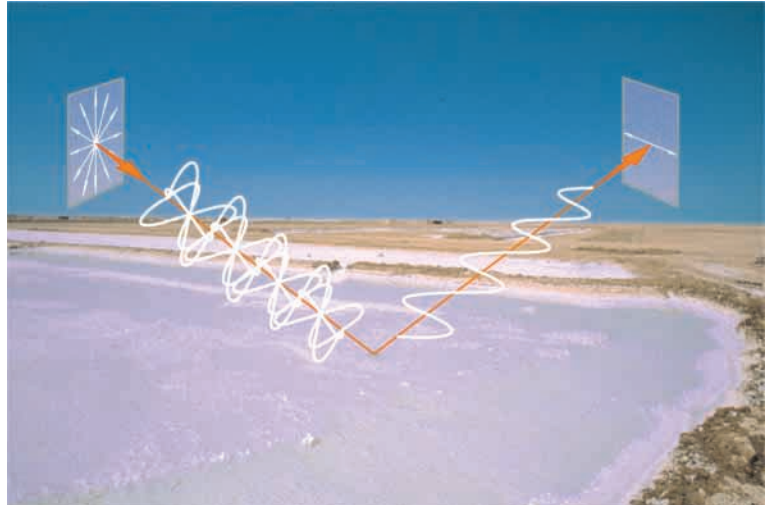
the object and the observer, so polarization sensitivity helps to enhance the contrast between any object and its surroundings. In principle, a single class of polarization-sensitive photoreceptor might provide the animal with such a contrast-enhancing, haze-reducing device, but again a set of orthogonally arranged analyzers is the superior solution if the entire spectrum of intensity differences between light and dark objects and dark and light backgrounds is considered. The widespread occurrence of such mutually perpendicular analyzers in the eyes of cephalopods (first described by Moody and Parriss, 1961) and crustaceans (first described by Eguchi, 1965) supports this point.

Even though cutting through the 'veiling brightness' of underwater spacelight might be the most general function of polarization vision in aquatic animals, individual targets can also be detected by their intrinsic polarization properties. Nadav Shashar and colleagues have shown that polarization sensitivity can help to detect transparent prey, i.e. to break camouflages. This is because various tissues of planktonic animals exhibit strong birefringent retardances of up to one-quarter of the wavelength. Hence, the mostly transparent but polarization-active pelagic organisms become conspicuous when viewed by a polarization-sensitive system. Furthermore, some animals, such as cuttlefish (Shashar et al., 1996) and stomatopod crustaceans (Marshall et al., 1999), possess polarized body patterns which, like colour signals, might be used in interspecific communication.

It is in the latter group of animals, especially in the visually advanced mantis shrimps, that true polarization vision as defined above has been proposed on the basis of behavioural experiments. On the sensory side, there seems to be a special POL area (mid-band ommatidial rows 5 and 6 of the stomatopod's compound eyes) that is specifically designed for the analysis of polarized light (Marshall, 1988; Marshall et al., 1991). This streak-like area fulfils the theoretical requirements for two distinct two-dimensional polarization-vision systems, one receiving its input from short-wavelength (ultraviolet) receptors, the other from long-wavelength (blue/green) receptors. In addition, stomatopod eyes show frequent scanning movements (Land et al., 1990), so that time-modulated polarization signals might also be used. Strong indications that gonodactyloid stomatopods, which are equipped with large-sized mid-band ommatidia, might actually exhibit true polarization vision have been deduced from neatly designed behavioural experiments (Marshall et al., 1999). In these experiments, the animals were successfully trained to choose objects characterized by a particular angle of polarization, but they failed to discriminate between objects that differed only in brightness cues. Even though the effects of intensity (I) and e-vector orientation (χ) were tested in separate experimental series, rather than by varying I and χ independently in the same stimulus, the results are highly suggestive of the shrimp's ability to discriminate two light stimuli on the basis of polarization alone.

However, before fully acknowledging such a 'true polarization-vision system', one would like to demonstrate the intensity-invariance of its χ-detecting capabilities. For example, one would like to use e-vector stimuli that can be varied in radiant intensity, then select pairs of such stimuli (χ_1 and χ_2) that are equally bright to the animal (for an experimental paradigm, see Fig. 3) and, finally, test whether these equally bright e-vector stimuli χ_1 and χ_2 can be discriminated. Furthermore, in a similar χ_1 *versus* χ_2 paradigm, one could test for intensity-invariance by changing the intensity of, say, the training stimulus (e.g. χ_1) and observe whether or not the animal's responses can be described as a trade-off between χ and I. I agree that such parametric test paradigms might seem a bit academic, but it is only by entertaining such a systematic approach that we can learn something about the potentials and constraints of an animal's polarization-vision system, e.g. about the degree of I invariance, $\Delta\chi$ thresholds and those values of χ to which the system is most sensitive. This is what we are looking for. The range between 'true' and what then might be dubbed 'spurious' polarization-vision systems is certainly wide.

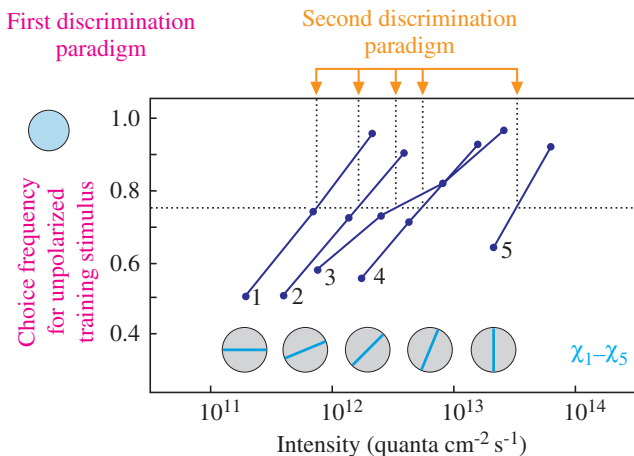Obtaining the information mentioned above is important for

Fig. 3. Experimental paradigm to test an animal's ability to detect the angle of polarization (e-vector orientation, χ) independently of radiant intensity (I) and to determine the animal's sensitivity to different values of χ. In the first discrimination paradigm, the animal is trained to an unpolarized stimulus, which it later has to discriminate from linearly polarized stimuli (χ_1–χ_5) that are varied in intensity (abscissa). The resulting family of response curves (choice frequency *versus* log$I$; one for each value of χ) allows one to define combinations of χ/I that are discriminated equally well, e.g. by 75 % responses, from the unpolarized training stimulus. Hence, the animal perceives them as equally bright. If, in a second training and discrimination paradigm, the animals are able to discriminate these χ/I combinations from each other, this ability must be due exclusively to the stimulus differences in χ. In addition, the family of response/log$I$ characteristics allows one to compute the animal's sensitivity to various values of χ. This is because the sensitivity to χ is proportional to the reciprocal of the intensity values that elicit equal responses for all values of χ (see orange arrowheads and black dotted lines in the upper part of the graph). [Actually the response/log$I$ functions have been taken from an analogous study on colour vision in fish. The latter data can be restored by replacing the unpolarized stimulus by an uncoloured (grey) stimulus, and the χ_1–χ_5 values by λ_1=461 nm, λ_2=555 nm, λ_3=434 nm, λ_4=599 nm and λ_5=719 nm (Neumeyer, 1986).] Note that the rationale behind the experimental paradigm described for detecting different values of χ is strictly valid only for a stationary (rather than scanning) detector system. Such restrictions are not necessary in tests on colour vision.

understanding the functional significance of the observed behaviour. Is the stomatopod's polarization-vision system simply used in the context of prey detection – a possible function discussed earlier in this account – or is it (also) employed in intraspecific communication and/or interspecific encounters? The latter is conceivable because, in several stomatopod species, imaging polarimetry has revealed some quite strong polarization activities in certain parts of the body (Marshall et al., 1999).

Stimulus situation III: air

Finally, let us deal with e-vector patterns in the sky. These patterns cover the entire celestial hemisphere, so they present us with one of the most conspicuous polarization cues present in terrestrial environments. Bees, ants and most probably many other insects that routinely return to the points of departure of their foraging journeys use these patterns as an external compass. In fact, they can infer any particular compass direction from any particular sector of the pattern encountered at any particular time of day.

This striking behaviour led to the early assumption that the insect comes programmed with detailed map-like knowledge of all possible e-vector patterns in the sky or that it is endowed with some abstract geometrical means of deducing, say, the position of the solar meridian from individual pixels of the skylight patterns (von Frisch, 1965; Kirschfeld et al., 1975; Brines and Gould, 1982). However, this does not seem to be the case. Present investigations in which bees and ants were presented with individual e-vectors (Rossel and Wehner, 1984; Wehner and Rossel, 1985; Fent, 1986; for a review, see Wehner, 1994) have shown that, under certain experimental conditions, systematic navigational errors occur. It is most likely that the insect acquires and uses global rather than local skylight information. For example, if *Cataglyphis* ants are trained to walk in a particular direction while they are presented with a partial e-vector pattern (a strip-like aerial window) and later tested under the full skylight pattern, they make systematic mistakes (Fig. 4). The sign and size of these error angles depend on the particular parts of the sky that the animal has seen during training. Such systematic errors should not occur if the animal were endowed with precise knowledge of the celestial e-vector patterns or if it were capable of performing spherical geometrical constructions of one kind or another. However, the experimental errors immediately vanish when the insect is exposed to the same patch of sky during both the training and the testing phase (see green data point in the upper graph of Fig. 4).

What is it that the animal has seen? Neuroanatomical and behavioural studies performed in our laboratory have led to the conclusion that bees and ants (Wehner et al., 1975; Räber, 1979; Wehner, 1982; Wehner and Strasser, 1985), and many other insects as well (Labhart and Meyer, 1999), are equipped with a special polarization channel. Our present hypothesis, based on neurophysiological data obtained in crickets and ants (Labhart and Petzold, 1993; Labhart et al., 2001; Petzold, 2001), is that polarization-sensitive photoreceptors in a specialized dorsal rim area of the eye – a different kind of POL area from the one described above – converge onto sets of (at least) three large-field polarization-sensitive interneurons, so-called POL neurons, located within a restricted area of the second visual neuropil, the medulla (for details of polarization-sensitive interneurons in the central complex of the locust brain, see Vitzthum, 1997). Antagonistic interactions between pairs of orthogonally arranged photoreceptors render the interneuron signals independent of fluctuations in radiant intensity and, in addition, enhance polarization contrast. The e-vector tuning axes of the three large-field interneurons vary by approximately 60 °, so they are equally spaced across all points of the compass.

Taken together, the behavioural and neurophysiological data lead to the following hypothesis: some ambiguities notwithstanding (for their possible solution, see Wehner, 1997), each point of the compass is characterized by a particular response ratio of three POL neurons. We do not know yet how these response ratios are neurally encoded, but there must be some kind of neural network translating the broad-band compass responses of the POL neurons into narrowly tuned responses of particular 'compass neurons'. A particular compass neuron should be activated whenever the animal is heading in a particular compass direction (see also Hartmann and Wehner, 1995). Whatever this translation

system actually might be (one can imagine several possibilities), the behavioural data (e.g. Fig. 4) are compatible with the hypothesis that the POL/compass neuron system is recalibrated anew every time the animal sets out for a foraging journey. The calibration could occur during rotatory (yaw) body movements performed fully or partially by the ants when leaving their nest (Wehner et al., 1992).

Computer simulations and robotics implementations (Lambrinos et al., 1997) have shown that a system consisting of a few (three) large-field polarization analyzers (polarization-opponent units, POL-OP units, analogous to the POL neurons of the insect's visual system) is sufficient to yield compass

Fig. 4. Experimental paradigm in which desert ants, *Cataglyphis fortis*, were trained to walk in a particular compass direction while a partial e-vector pattern (a strip-like aerial window) was displayed to them. Examples are given for three earthbound orientations of the slit-like window (α_w) shown in training. The training directions were 180°, 210° and 270° (blue arrowheads in inset figures). During the course of the day, the sun (yellow disc) and concomitantly the entire e-vector pattern (blue bars) moved across the sky (see abscissa, which is calibrated linearly with respect to time of day). In the subsequent tests performed immediately after training, the ants were presented either with a full e-vector pattern (paradigm A) or, in one case, with the same aerial window that they had seen during training (paradigm B). Systematic navigation errors, α_e, occur in the former case (paradigm A; black data points, means ± S.D., N=433), but not in the latter (paradigm B; green data point, mean ± S.D., N=34). Technically, it is much more difficult to carry out paradigm B tests rather than paradigm A tests. Therefore, the former tests are represented by only one series of experiments. The orange lines depict the errors to be expected theoretically (the mean of the errors induced in paradigm A tests by the presentation of individual e-vectors in isolated pixels of sky). The open arrowheads in the upper parts of the figures mark the zero crossings of the theoretical curves. Paradigm A tests are based on Wehner (Wehner, 1997).
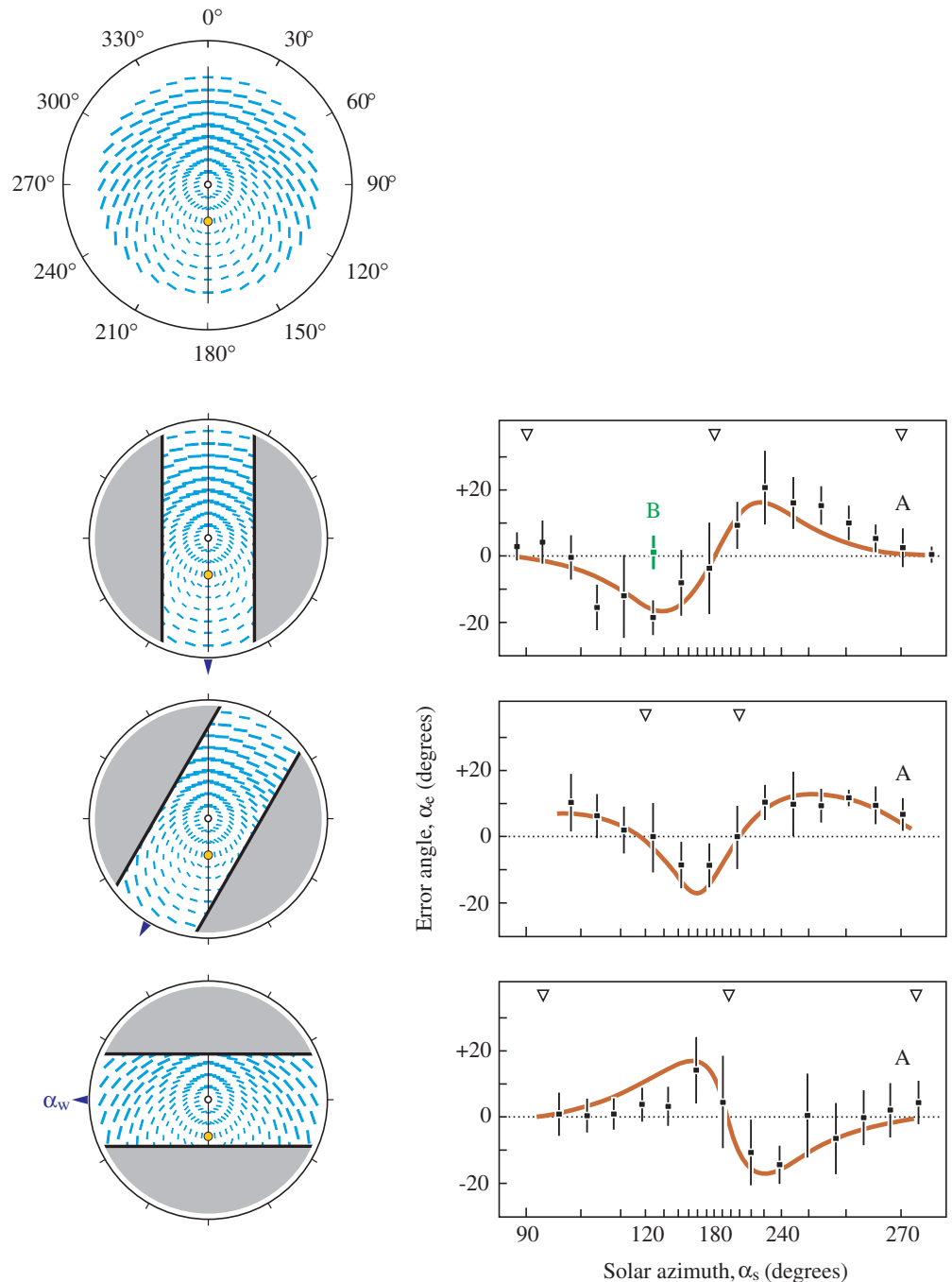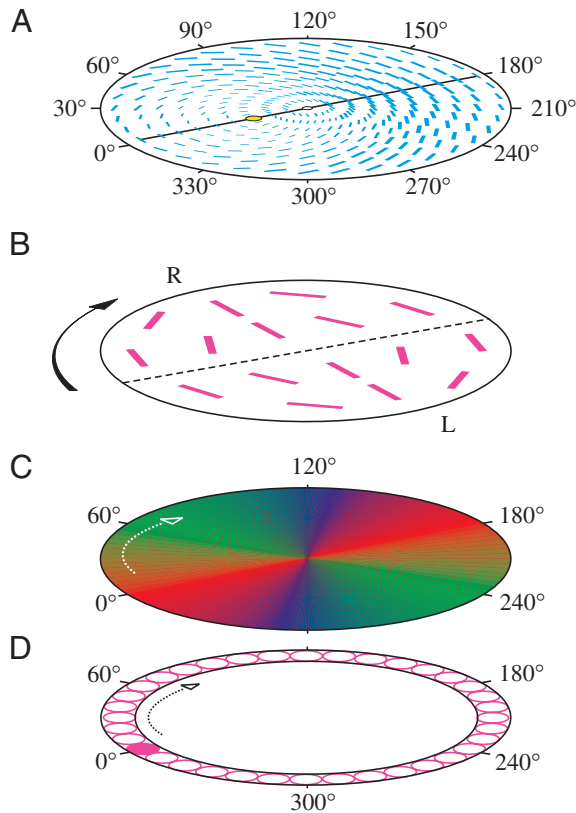
Fig. 5. The insect's polarization channel for the e-vector compass. Hypothetical scheme based on neurophysiological data. (A) The e-vector pattern in the sky. The orientation and size of the blue bars indicate the angle and degree of polarization, respectively. 0°, azimuthal position of the sun; open disc, zenith. In the particular case shown here, the elevation of the sun (yellow disc) is 60°. (B) Array of polarization detectors (L and R, left and right visual field, respectively). The e-vector tuning axes of only a few of the total of 55–75 polarization (POL) detectors per eye (in *Cataglyphis bicolor*) are shown. Each detector consists of a pair of orthogonally arranged analyzers (photoreceptors), which interact antagonistically. The dashed line depicts the animal's longitudinal body axis. To simplify matters, the array of detectors shown here is symmetrical with respect not only to the animal's longitudinal but also to its transverse (L–R) body axis and, thus, introduces a 180° ambiguity in the compass responses. The latter symmetry does not hold in the animal. (C) Response ratios of three large-field POL neurons. The response ratios are schematically translated into false colours. If the animal rotates relative to the skylight pattern (see filled arrow in B), different false colours show up (see white arrow in C). (D) Circular array of hypothetical compass neurons. Each fine-tuned compass neuron encodes a particular response ratio of the broadly tuned POL neurons. The compass neuron marked by the filled red circle is maximally excited when the animal faces the solar azimuth. (Owing to the 180° ambiguity mentioned above, in this artificial case the 180° circle should be coloured red, too).

responses that are as precise as those exhibited by the foraging ants. Each time the robot is told, by a wireless command, to choose a particular compass course, e.g. 30° to the left of the solar meridian, it first performs a 360° turn to generate a look-up table, correlating the current outputs of the POL-OP units with the compass scale, and then moves in the desired direction.

In summary, Fig. 5 provides a hypothetical flow-chart of the insect's e-vector compass. In Fig. 5C, the various response ratios of the three broad-band POL neurons are encoded by false colours. This illustrative false-colour representation is chosen on purpose because the algorithmic task of encoding polarization information from the response ratios of three POL neurons is analogous to the task of encoding hues of colour from the response ratios of three broad-band colour receptors. Similarly, particular response ratios of the three POL neurons could define particular values of χ. Note, however, that in the insect's skylight compass, it is not the χ-scale *per se*, but the e-vector compass scale, to which the response ratios of the POL neurons are related. For technical reasons, in electrophysiological studies, the POL neurons have been presented only with individual e-vectors in particular points of their visual fields, but in real life they are stimulated by wide-field e-vector patterns, and it is the integrated response to these patterns that the POL neurons transmit.

Of course, in an exclusively large-field system, information about individual e-vectors in individual pixels of sky is buried in the integrated overall responses. But this need not be disadvantageous. For example, if skylight conditions vary on a short-term basis, e.g. as a result of changes in the cloud cover, a large-field system will immediately be able to balance the effects of such local variations caused by cloud disturbances (see Labhart, 1999; for the first full-sky video-polarimetric demonstration that the e-vector pattern can continue underneath clouds, see Pomozi et al., 2001).

The accuracy of the insect's skylight compass depends on how distinctly the response ratios of the POL neurons vary as the animal rotates about its vertical body axis, i.e. faces different points of the compass. Hence, selection should have favoured an array of e-vector detectors that maximizes the differences in the response ratios of the POL neurons for different points of the compass. Attempts to design such an optimal detector array, at least for certain skylight conditions, are under way (G. D. Bernard and R. Wehner, in preparation; for a preliminary result, see Wehner, 1996).

Recently, a polarization-vision system that could be dubbed a one- (rather than three-) POL-unit device has been described in a spider, the gnaphosid *Drassodes cupreus* (Dacke et al., 1999). Here, the POL unit consists of a pair of upward-pointing (postero-median) eyes, which are lensless and hence do not form images within their large (125° wide) visual fields. The e-vector tuning axes of the polarization-sensitive photoreceptors coincide within each eye, but differ by 90° between the left and the right eye. It has not yet been shown whether antagonistic interactions occur between the eyes, but this is a likely hypothesis. Of course, if precise and unambiguous compass orientation is at stake, a one-POL-unit system would be inferior to a three-POL-unit system, but the potentials and constraints of such a system have not yet been tested in behavioural experiments.

Concluding remarks

A comparison of the sensory tasks accomplished under stimulus conditions I–III reveals the obvious: the answer to the question posed at the beginning, and in the title of this account, is most probably no. Even though it is only in the insect's skylight compass that the neural hardware has been unravelled in quite some detail, behavioural studies have shown that the tasks to be accomplished by different species in different environmental contexts are quite different. As described above, contrast enhancement and haze reduction, breaking camouflage, optical signalling, detecting particular (horizontal) e-vectors or using entire e-vector gradients as compass cues are mediated by polarization-sensitive visual systems of one kind or another. In arthropods, rhabdomeric photoreceptors are the common input stage, but additional structures such as tapetum layers may act as polarization enhancers (e.g. in spiders; Dacke et al., 1999). In vertebrates, in which the use of polarized skylight for navigation has been proposed from fish (e.g. Hawryshyn, 1992) to birds (e.g. Helbig, 1990; Munro and Wiltschko, 1995), no one has yet been able to record polarization-sensitive signals from any photoreceptor (for theories of analyzer mechanisms, see, for example, Rowe et al., 1994; Novales-Flamarique et al., 1998). In cephalopods, insects and crustaceans, the antagonistic interaction between photoreceptors endowed with orthogonally arranged e-vector tuning axes seems to provide a first step in neural preprocessing that is common to most, if not all, polarization-vision systems, but network conformities are not known to occur further upstream nor are they necessarily to be expected.

Of course, the latter assumption is provocative. It is especially important to emphasize that 'true polarization vision', in which the orientation of individual e-vectors can be detected unambiguously (independently of, say, d and λ; see above) in any point of the animal's environment, might not be what polarization-vision systems are designed for. One of the most elaborate and best-studied polarization-vision systems, the insect's skylight compass, is a case in point. The information this system provides is not about individual e-vectors; it is about compass courses, which are derived from the (most probably) global processing of e-vector gradients in the sky. If, within this system, calibration works as described above, one could envisage a network in which information about χ and information about d are not processed independently. Another example is provided by the oviposition behaviour of certain butterflies. In this behavioural context, polarization and colour are not processed separately (Kelber, 1999; Kelber et al., 2001). In *Papilio aegeus*, for instance, the most attractive oviposition sites are horizontally oriented shiny green leaves. Such leaves preferentially stimulate polarization-sensitive green receptors equipped with horizontal e-vector tuning axes.

In conclusion, experimental paradigms such as that outlined in Fig. 3, as attractive and consistent as they certainly are, might often prevent us from appreciating the real task that a given polarization-vision system must accomplish. If we consider such a paradigm the *experimentum crucis* for polarization vision, time and again we might fall victim to an ill-posed question and might miss most of the exciting ways in which animals make use of the various forms of polarized light prevailing in their visual worlds.

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