Polarization vision in bees

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A solution to the long-standing problem of how honey bees detect polarized light from the sky is presented. The mechanism involves the transformation of polarization information into modulations of perceived brightness while the bee scans the sky by rotating its field of view. Using this technique the bee needs only a very simple strategy to read compass information from the polarization patterns in the sky.

KARL VON FRISCH discovered that honey bees can detect linearly polarized light and can use this ability to derive compass information from the Sun-linked polarization patterns in the sky[1-3]. Subsequently, the basis of polarization sensitivity in the retina of bees and other invertebrates was shown to lie in the oriented arrays of pigment molecules packed in the membranes of the layered microvillar structure of the rhabdomeric photoreceptors, such that the sensitivity of the receptors is greatest when light is polarized parallel to the microvilli (see ref. 4 for review). Furthermore, it is known for bees that a small, dorsal region of the retina (the POL area) is both essential and sufficient for navigation by means of polarized sky light[5] and that this specialized retinal area contains an array of polarization-sensitive ultraviolet photoreceptors which equip it for this task[6-9]. One outstanding problem in the elucidation of polarization vision is how bees use information from the receptor array to analyse and orient by the patterns of polarized sky light.

Here we present a novel and comprehensive solution to this problem by showing how the array of receptors forms a template which the bee uses to scan and match the polarization patterns in the sky. We begin with a brief review of our recent model for the detection of polarized light and go on to report experiments designed to test the model. We conclude that the mechanisms uncovered may be generally operative in polarization-sensitive invertebrates.

Polarized light detection model

Imagine that in each eye of the bee the orientation of microvilli of polarization-sensitive photoreceptors varies in a graded manner through 180°, being horizontal in the anterior and posterior part of the eyes and oriented at all other angles between these positions (Fig. 1). Consider next what happens to the output of such an array when the bee, when presented with a small stationary patch of polarized light, rotates about its vertical body axis. The patch is positioned at 60° above the horizon and stimulates successively a ring of receptors as the bee rotates. The angle between microvilli and the *e*-vector varies gradually during the turn. As a consequence, the output of the array is a modulating signal passing through a peak as the microvilli become parallel to the *e*-vector in the patch. A similar modulation is detected by the bee when the *e*-vector direction is changed, except that the modulation now rises to a peak in a different position on the retina. Thus, we assume that for the analysis of *e*-vector directions in the sky, the bee sweeps its retinal analysers across the *e*-vectors and records which part of the retina is maximally active during the sweep.

This simple model of *e*-vector detection arose from behavioural experiments in which we analysed orientation performance of the bee to small spots of polarized sky light[10-13]. The implications of these experiments are most easily explained if we consider how the scanning mechanism might be used by bees to obtain compass bearings from the polarization patterns in the sky. Consider first a polarization pattern as it is realized

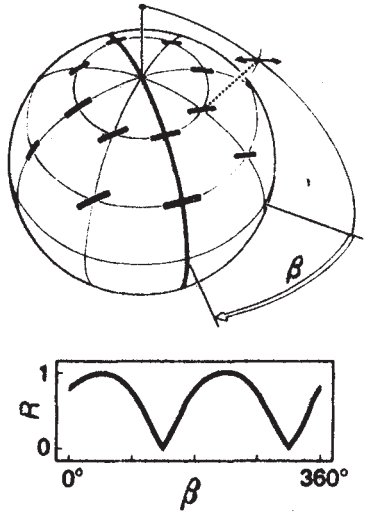

Fig. 1 Mechanism of detecting polarized light by bees. Sphere, visual fields of the left and the right eye (separated by thick continuous lines). The systematic variation of microvillar (analyser) directions of polarization-sensitive photoreceptors is shown for two elevations above the horizon (30 and 60°). Note that the dichroic visual pigments are oriented parallel to the microvilli so the sensitivity of the receptors is greatest when the *e*-vector of polarized light is parallel to the microvilli and least when it is at right angles to them. The operational principles of the model are demonstrated for a situation in which the bee views a patch of polarized light exhibiting a single *e*-vector direction (double arrow). The bee is first aligned with the patch ($\beta = 0°$) and then performs a full turn about its vertical axis ($\beta = 0$–$360°$), thus sweeping a ring of receptors with different microvilli directions across the *e*-vector. The relative output (R, log scale) of successive receptors within the ring is plotted as a function of β. A peak output is induced by the patch of polarized light when its *e*-vector direction is matched by a suitably arranged microvillar direction. The rationale behind the scanning model is that each *e*-vector direction has its own location on the retina, specified by a peak output of a corresponding photoreceptor.

at dawn and dusk (Fig. 2*a*). When the model bee is aligned with the solar and the antisolar meridian of such a pattern, the layout of polarization analysers over the eyes matches closely the distribution of *e*-vectors in the sky. Given this coincidence, the bee can rotate about its vertical body axis and assume that whenever there is a peak in the output of the *e*-vector detectors, the body is aligned with the solar and the antisolar meridian. It can then turn from this reference direction until it faces the desired compass course.

The situation changes during the day when the Sun is high in the sky (Fig. 2*b*). In this case there are substantial discrepancies between the *e*-vector pattern and the array of polarization analysers. Thus when the bee, while scanning a small patch of

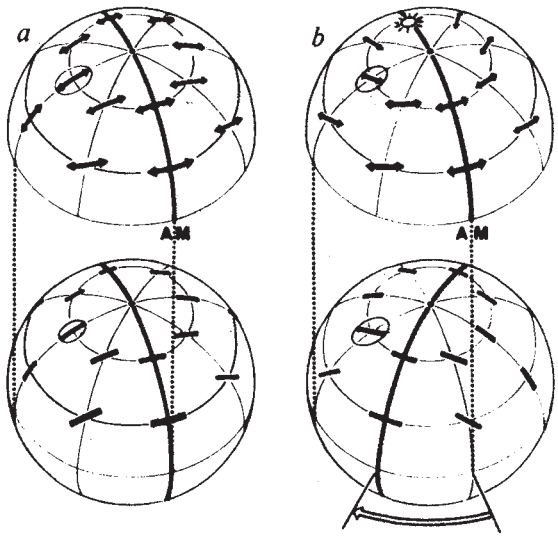

Fig. 2 Use of the scanning model in *e*-vector pattern orientation. ***a***, Upper hemisphere, distribution of *e*-vectors (arrows) across the sky when the Sun is at the horizon. The celestial sphere is viewed from the back (AM, antisolar meridian). The pattern of polarized light depends strictly on the elevation of the Sun. As a general rule the angle of polarization (*e*-vector direction) is always perpendicular to the plane containing the Sun, the patch in the sky and the observer in the centre of the celestial hemisphere. The lower sphere shows the layout of analysers within the eyes of the bee. Note that the analysers match the *e*-vectors when the bee is aligned with the solar and the antisolar meridian. Thus, to determine the position of these meridians from one or another *e*-vector in the sky (in the figure exemplified for a vertical *e*-vector) the bee sweeps its field of view across the *e*-vector and assumes that it is aligned with the reference meridians when it detects a peak output from its analyser array. ***b***, A different polarization pattern is realized in the sky when the Sun is at an elevation of 65°. When now presented with an isolated *e*-vector (examplified here by an oblique *e*-vector), the bee again assumes that it is aligned with the solar and the antisolar meridian when it perceives a peak intensity from the patch of polarized light. But, in this case, it is mistaken (open arrow) and ultimately steers an incorrect course.

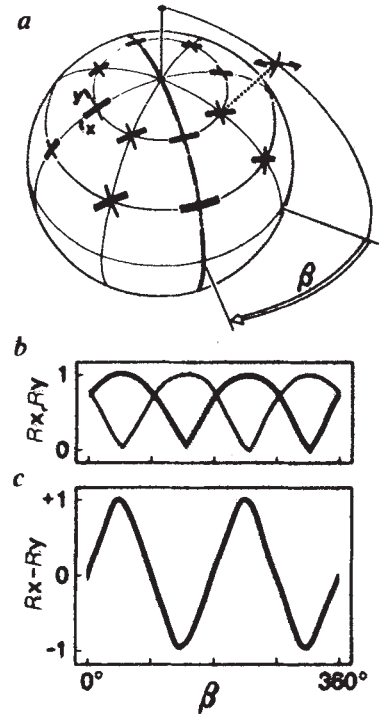

Fig. 3 Extended version of the scanning model. *a*, In addition to the array of receptors shown in Fig. 1 (here called x-type receptors) there is an array of y-type receptors with orthogonally arranged microvillar directions. Equipped with this array of crossed analysers, the bee scans a patch of polarized light displaying a single *e*-vector direction (double arrow). *b*, Output of the x- and y-type receptors (Rx and Ry, log scale) as a function of the horizontal orientation relative to the aximuthal angle β of the patch of polarized light. *c*, Output of the crossed analyser array as a function of β, when the outputs of the x- and y-type receptors are compared differentially by the visual system ($Rx - Ry$, log scale).

a daytime pattern, applies its simple method of determining the reference meridians, it may arrive at an incorrect estimate of the position of the meridians. This in turn should lead to errors of orientation expressing the discrepancy between the layout of analysers and the *e*-vector pattern. Our findings show that bees do indeed make consistent orientation errors, depending on the elevation of the Sun and the *e*-vector direction which is viewed by the bee in the sky. Therefore, the interpretation of the orientation data in terms of a scanning mechanism of *e*-vector detection allows us to infer the spatial layout of retinal analysers shown in Fig. 1.

These behavioural interferences are supported by anatomical and optical observations on the POL areas of the bees, which show that the microvillar directions of photoreceptors vary across the retina in the way predicted. However, the details of this correspondence have not been completely checked[7,9].

Finally, an important interference derives from combined anatomical and physiological studies, showing that each ommatidium of the POL area contains a set of orthogonally arranged microvillar directions[7-9]. To accommodate this, we have extended our model by adding a second array of receptors to the one already described (Fig. 3). We then suppose that the visual system compares the outputs of perpendicularly oriented receptors such that the differential response will be maximum when the microvilli of one receptor array are oriented parallel to the *e*-vector and least when the *e*-vector is parallel to the microvilli of the other[9,14]. Clearly, such antagonistic interactions of crossed analysers enhance the specificity of *e*-vector detection, but they are not essential in principle for the scanning model to work. In fact, it has already been shown theoretically that only one analyser is needed per ommatidium, if polarized light is to be analysed by a scanning method[15].

Our model can be tested by exploiting the ability of the bee to orient by means of small patches of polarized skylight. As can be deduced from Fig. 2, bees invariably treat a small patch of polarized light of a given *e*-vector as though it were at a fixed azimuthal angle relative to the solar and the antisolar meridian, although this is in fact only true of the pattern of polarization across the sky at dawn and dusk. For instance, bees orient to a patch of light with a horizontal *e*-vector as it lies along the antisolar meridian and to a patch with a vertical *e*-vector as though it is at right angles to the antisolar meridian. Thus we know both were a particular *e*-vector direction is represented within the retina and also what azimuthal angle the bee associates with a patch of light of that *e*-vector direction. The scanning model then predicts that a patch of unpolarized light arranged to evoke a peak output within a particular part of the retina will cause the bee to orient as though the light were polarized in the appropriate direction. Although this prediction is simple, a complex experiment is necessary to test it.

Experimental evidence

The standard method for analysing *e*-vector orientation is to see how polarized light influences the 'waggle dance' bees perform when they return to the hive after foraging. The orientation of this dance on the surface of the comb signals the direction

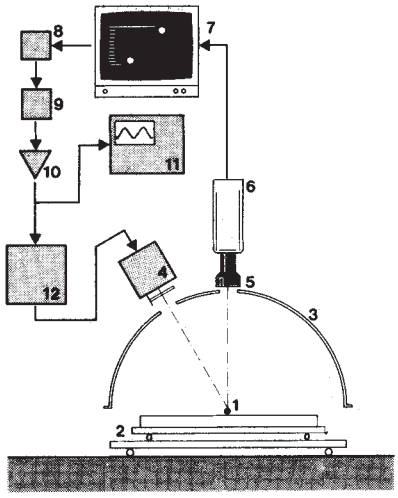

Fig. 4 Experimental device for testing the scanning model. The bee (1) performs its directional dances on horizontal combs (2) covered with a black Plexiglass hemisphere (3). Light from a Xenon arc (4), equipped with an ultraviolet filter (Schott; UG 11), is the only cue for dance orientation. The light stimulus subtends an angle of 10° and is at an elevation of 60°. The horizontal body-rotation of the dancing been controls the intensity of the Xenon arc. For this purpose two circular pieces (1 mm) of a reflecting foil (3M; 7610) are stuck onto the thorax and the abdomen of the bee, exactly 8 mm apart. The ring lamp (5), which surrounds the lens of a television camera (6), is then switched on and the aperture of the lens closed until the image on the television monitor (7) fades out completely, except for the two light spots reflected from the body of the bee. In each frame the number of lines between the first and the last image signals is counted. Because the distance between the two reflecting spots is constant, the number of lines provides a direct measure of the direction of the medial plane of the bee and hence can be used to control the intensity of the Xenon arc (8, line counter; 9, digital-to-analogue converter; 10, amplifier; 11, storage oscilloscope; 12, power supply of Xenon arc). Maximal and minimal intensities are produced when the bee is aligned either parallel or at right angles, respectively, to the vertical axis of the monitor. With respect to the medial plane of the bee, maximal intensities can be induced at any angle by rotating the camera relative to the aximuthal angle of the Xenon arc. The intensity between maximal and minimal intensity varies by a factor of three. All waggle dances are videotaped and later analysed by measuring the direction of individual waggle runs.

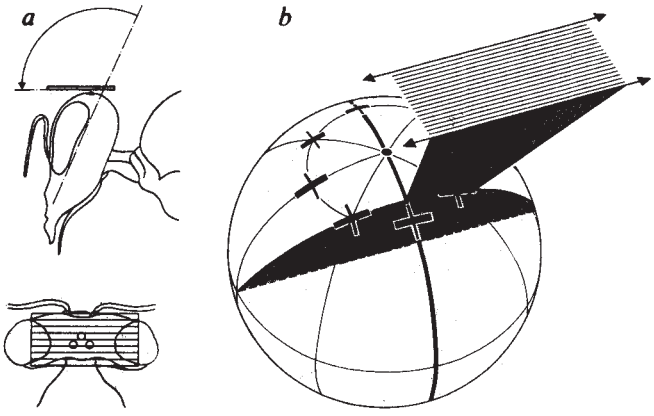

Fig. 5 Method for stimulating the receptors selectively. *a*, Side and dorsal view of the head of the bee that contains a piece of polarizing filter (Polaroid, HNP'B). The transmission axis of the filter is parallel to the transverse axis of the head. The inclination of the filter is defined relative to the back plane of the eyes. *b*, Model eyes with crossed analysers (*x*- and *y*-type receptors; Fig. 3) at an elevation of 60°, and part of the overhead filter. Throughout the array the microvillar directions of the x-type receptors are defined by the set of planes which include the transverse axis of the eyes (here one plane is shaded). In addition, these planes include the transmission axis of the filter. Therefore, light is polarized by the filter to stimulate predominantly the x-type receptors.

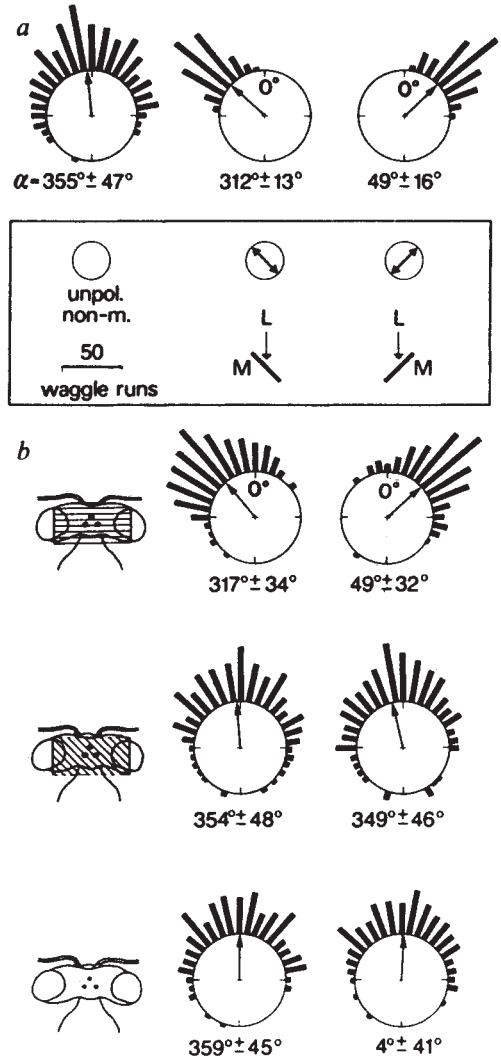

Fig. 6 a, Dance directions of bees when presented with a patch of unpolarized non-modulating ultraviolet light and a patch of polarized light with one of two oblique vectors (stimulus conditions are indicated in the upper half of the inset; *e*-vector directions are marked by double arrows). Mean dance directions (α, arrow) are calculated to indicate where the navigating bee expects the light stimulus to occur in the sky (0° marks the antisolar meridian Fig. 2). Data are based on 931 waggle runs recorded from 16 bees. *b*, Dance directions of bees when presented with a patch of unpolarized modulating ultraviolet light. The modulations are arranged to simulate the two *e*-vector directions presented to the bees in *a* (in the inset M is the orientation of the bees relative to the azimuthal angle of the light stimulus L when its intensity passes through a peak; compare with Fig. 1 for retinal positions of oblique *e*-vectors). In the upper and middle parts of *b* the dancing bees are equipped with an overhead polarization filter (the transmission axis of the filter is oriented parallel and at 45° to the transverse axis of the head). In the lower part of *b* the bees are not carrying overhead filters. Data based on 2,760 waggle runs arecorded from 24 bees.

of the foraging site from the hive. On vertical combs in the dark, bees orient with respect to the gravitational vector. On horizontal combs they will orient with respect to the Sun or the polarization patterns across the sky[3].

In the present experiments, several individually labelled bees were trained to a feeding station several hundred metres from the hive. The hive had horizontal combs and an artificial light source provided the trained bees with the only directional cue by which they could orient their dance. When given a single patch of polarized light in such a situation, the orientation of

the dance varies with the *e*-vector direction. We sought to mimic this behaviour by means of a beam of unpolarized non-modulating ultraviolet light which is modulated in intensity according to the horizontal orientation of the bee, so that the intensity of the beam peaks when it stimulates a predetermined part of the retina. Details of the servo system are given in Fig. 4.

As we described above, each ommatidium within the POL area is equipped with pairs of orthogonally oriented polarization detectors which we assume interact to give a differential output. At first sight a modulated beam of unpolarized light appears to be an inappropriate stimulus because pairs of crossed analysers will be stimulated equally, so that the differential output will be zero throughout the modulation cycle. To circumvent this effect we selectively stimulated one of the two crossed receptor arrays on its own by covering the eyes with a small piece of polarizing filter oriented to transmit *e*-vectors parallel to the transverse axis of the eyes (Fig. 5). This filter transmits the set of *e*-vector planes which contain lines that are parallel to the transverse axis. Microvilli are oriented over the retinal region of interest so that light transmitted by the filter will stimulate one of the two receptor arrays more than the other. As a control, some bees are equipped with a filter with its transmission axis oriented 45° from the transverse axis, in which case the two crossed analysers should again be stimulated equally.

The light was modulated so that the beam was of peak intensity when it fell on one of two different retinal positions which according to the model contain detectors for one of two oblique *e*-vectors. The orientation of the dances under these conditions is shown in Fig. 6. Bees indeed behave as the scanning model predicts. With the transmission axis of the filter parallel to the transverse axis of the eyes, dances orient as though the bees are presented with one of the two oblique *e*-vector directions. In contrast, with the filter oriented at 45° from the transverse axis of the eyes, the effect disappears and the bees behave as though they are stimulated by a patch of unpolarized, non-modulating ultraviolet light.

Before these results can be considered to provide conclusive evidence in support of our model, we asked whether there is an alternative mechanism of *e*-vector detection which could produce the same results. Previous accounts assumed that each individual ommatidium of the compound eyes is able to assess and report independently on the *e*-vector direction of light falling within its receptive field of view (see refs 3, 16 for review). Thus one might argue that polarization orientation in our experiments is not affected by the intensity modulations of the ultraviolet beam, but is caused by the *e*-vectors projected onto the eyes by the overhead polarization filter. This possibility, however, can be excluded. Because the direction of the *e*-vectors projecting onto the eyes varies as both the bee and filter rotate, different ommatidia would give the bee conflicting and uninterpretable information about *e*-vector directions. Similarly, we would have expected the dance directions to be the same whether the filter was parallel to the transverse axis of the eyes or oriented obliquely to it.

Conclusions

We can now explain the principles underlying polarization vision in bees in terms of the arrangement of dichroic photoreceptors, the visual cues abstracted from these receptors and the influence this processing strategy has on the orientation behaviour.

Specifically, our data show that bees have an array of retinal analysers, each of which is maximally sensitive to a different *e*-vector direction. When a patch of polarized sky light is swept across the array, the perceived direction of its *e*-vector is determined by which analysers within the array produce the largest output. We also deduce from our experiments that *e*-vector detection by the array of analysers exploits antagonistic interactions between receptors with orthogonally oriented microvilli. We believe that such interactions provide the bee with a high-contrast *e*-vector signal.

The spatial layout of retinal analysers forms the structural basis of *e*-vector detection. In addition, it matches the distribution of *e*-vectors in the sky, when the bee is aligned with the solar and the antisolar meridian (Fig. 2). Thus to determine the position of these reference meridians, the bee turns about its vertical axis and detects when the array of analysers is maximally active.

This simple strategy of reading compass information from the polarization patterns explains the orientation performance of bees whose vision of the sky is restricted to small areas containing a very small range of *e*-vector directions. At dawn and dusk there is a good match between the sky pattern and the array of detectors, but during the day substantial discrepancies occur. Thus, when the bee applies its simple compass strategy it may arrive at an incorrect course, as we have previously described[10–13]. But this shortcoming is not as serious as it might first appear. Under normal circumstances the navigating bee has large areas of the polarization patterns at its disposal. Therefore, it can benefit from the fact that *e*-vectors in each celestial half (defined by the solar and the antisolar meridian) are mirror images of each other (Fig. 2). This implies that error angles induced by *e*-vectors from the left and the right half of the sky are always opposite in sign, and thus cancel each other out[12,13]. Furthermore, during free flight the navigating bee can resort to powerful backup systems such as the Sun and landmarks[3,17].

Finally, note that the structural pecularities that characterize the array of polarization analysers within the retina of bees seem to be common in invertebrates. The retinas of cephalopds, crustacens and insects have sets of receptors with orthogonally arranged microvilli (see refs 16, 18 for review). Furthermore, there is increasing evidence that the directions of microvilli vary in fan-shaped arrays across the retina in various groups of insects[9,19,20]. It seems likely, therefore, that the principles discussed here are generally applicable to invertebrates that detect and use polarized sky light for orientation.

We thank H. Baumann, K. Feller and T. Grob for design and construction of electronic equipment, H. Baumann, K. Cheng, S. Gut and A. Rossel-Jaeckle for assistance, D. Rigoli for the drawings, T. S. Collett and S. B. Laughlin for reading and improving the manuscript. The work was supported by Swiss NSF grant 3.665-0.84.

Received 26 March; accepted 10 July 1986.

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