

How bees analyse the polarization patterns in the sky

Experiments and model

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Summary. Polarized light from the blue sky exhibits an extensive pattern which in terms of both direction and degree of polarization is linked to the position of the sun (Fig. 1). Honeybees, among other animal species, are able to perceive skylight polarization and to use it as compass in both foraging flights and communication dances.

1. From our previous work it is known that bees orient by means of a simplified e-vector map when their view of the sky is restricted to single e-vector directions (Fig. 2). Nothing is known, however, regarding how navigating bees analyse the polarization pattern as a whole.

2. To study this, dancing bees were presented large parts of the natural e-vector patterns, and their orientation performance with respect to known feeding stations was analysed (Fig. 4A, 5A, 6A).

3. The results show that bees make mistakes, and these are consistent with the hypothesis that they invariably apply their simplified e-vector map to any polarization pattern they are exposed to (Figs. 3, 4B, 5B, 6B).

4. Based on these findings it is suggested that information processing in the bee's visual system does not elaborate a detailed image of the polarization patterns. Rather, it is hypothesized, a simplified version of the pattern, as the one deduced experimentally (Fig. 2), is determined and mimicked by the spatial layout of polarization analysers in the bee's retina (Fig. 7). For the model to work, the insect then has to rotate about its vertical body axis and in doing so perceives celestial polarization in the form of temporal brightness and/or colour modulations (Fig. 8).

5. It is explained how the bee could use these modulations to derive the orientation of the celestial sphere and subsequently the direction of the intended compass course.

Introduction

In his fundamental experiments on polarization sensitivity in bees, von Frisch showed that a 10° – 15° spot of polarized skylight is sufficient to allow a dancing bee to indicate the direction of its food source (von Frisch 1949). Essentially on the basis of these results, it has generally been assumed that bees come equipped with a detailed knowledge of the geometry and the dynamics of the e-vector pattern in the sky (for the principles of skylight polarization see Fig. 1 and Wehner 1983).

Recently, however, we have challenged this view by demonstrating that bees use approximate rules and rely on a simplified e-vector map when reading compass information from small spots of polarized light (Rossel et al. 1978; Rossel and Wehner 1982). This has been proven by exposing dancing bees to single e-vector directions and by analysing the resulting orientation performance during extensive periods of the day. It turned out that bees make consistent orientation errors depending on the direction of the e-vector and its azimuth angle from the sun. Thus, the position assumed by the bee for a particular e-vector does not necessarily correspond to its actual position in the sky, but deviates from the latter by an angle which equals the orientation error made by the bee. Based on these findings we were then able to reconstruct the bee's version of the e-vector patterns (Fig. 2A), and to provide an explanation as to how it can be derived from the real e-vector patterns in the sky (Fig. 2B).

In the present paper we now examine the significance of this map concept when the navigating bees analyse large areas of clear sky with different angles and degrees of polarization. Theoretically, there are at least three possible ways in which bees might behave when exposed to such patterns:

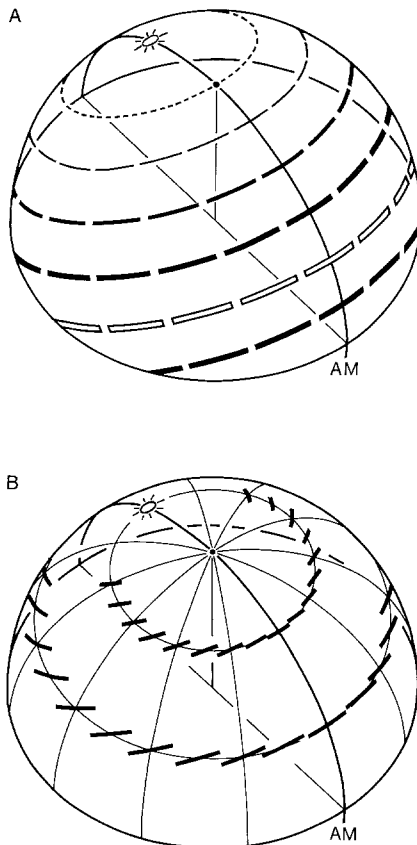


Fig. 1. **A** The celestial polarization pattern. Predominant vibration directions (e-vector directions) of polarized skylight are concentrically arranged around the sun or its opposite, the anti-sun. Within a range of approximately 30° from the sun and the antipode (marked by dashed line), the percentage of polarization is less than 10%, i.e. polarization is below the perceptual threshold of bees (von Frisch 1967). The maximum polarization occurs along the great circle 90° away from the sun and the antipode (marked by white bars). This circle thus represents a prominent intrinsic line of symmetry of the polarization pattern. *AM* antipolar meridian. **B** Polarization pattern in a horizon system of coordinates given by the meridians converging towards the zenith. E-vector directions are shown for two elevations (30° and 60°) with the sun at 60° . Note that within this system of coordinates a second line of symmetry is given by the solar meridian and the antipolar meridian (*AM*). Along these meridians, light is always horizontally polarized. For all other celestial points e-vector directions vary with the elevation of the sun (for full details see Wehner 1983)

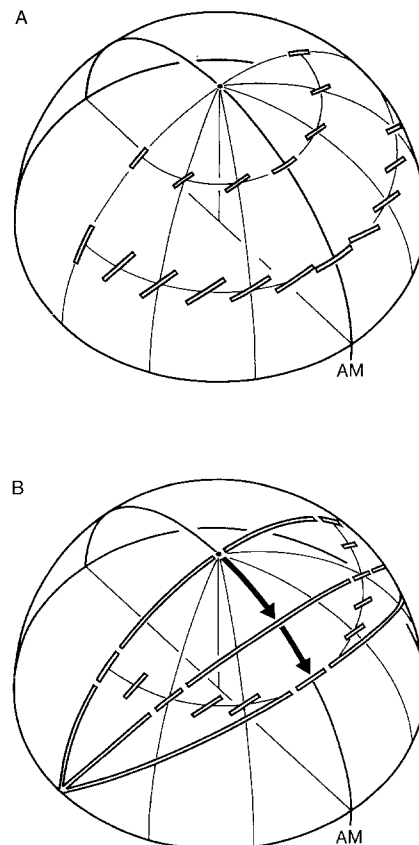


Fig. 2. **A** The bee's e-vector map. When navigating by means of isolated spots of polarized light, bees use the same e-vector map throughout the day. In this map all e-vector directions which occur in the sky are concentrated within one half of the celestial sphere (the one which is centered about the antipolar meridian, *AM*). Furthermore, the e-vector distributions are identical for all elevations as shown here for 30° and 60° . As a rule for the daytime sky, the goodness of fit between the bee's map and actual e-vector patterns in the sky decreases as one moves away from the antipolar meridian towards the solar meridian (compare the map with Fig. 1B). **B** The bee's map can be derived theoretically from the real polarization patterns in the sky by referring to the line of maximum polarization. When the sun moves up, the line of maximum polarization tilts down (according to the rule that the maximally polarized e-vectors are always 90° from the sun, see Fig. 1A). The resulting distribution of the maximally polarized e-vectors are very similar for all elevations above the horizon, and the distribution at approximately 45° corresponds to the distribution which is realized in the bee's map (for full details see Rossel and Wehner 1982)

First, they could invariably apply their simplified map to any of the e-vectors perceived regardless of their percentage of polarization. Since the map does not exactly match the e-vector distribution in the sky, each e-vector would induce an orientation error and the arithmetical mean of these errors would be expressed by a deviation from the correct compass course (see Fig. 3). Second, the bees could assign e-vector positions according to the map, but

with the more strongly polarized e-vectors weighted more heavily. Because the map closely reflects the e-vector positions in the highly polarized part of the sky, orientation errors would still occur, but they would be smaller than expected from the first prediction. Third, the bees may no longer use their approximate e-vector map. Large celestial patterns with different angles and degrees of polarization could provide them with sufficient

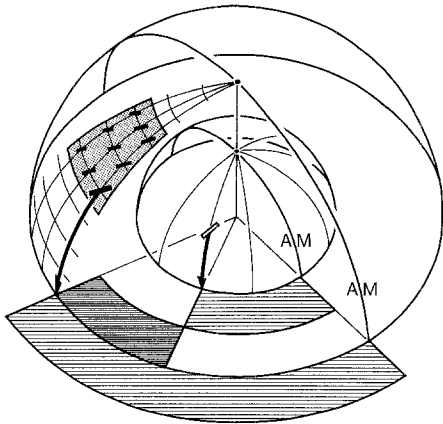


Fig. 3. Diagram of the celestial sphere (outer sphere) and the bee's map (inner sphere) to show the method of estimating expected orientation errors. Within the sky region viewed by the bee (grey area), the e-vector directions were determined for the intersection points of a 10° coordinate system, using the tables of Coulson et al. (1960). Next, the azimuth of each e-vector relative to AM was compared with the azimuth of the corresponding e-vector (i.e. the e-vector with the same direction) in the bee's map. In the figure the procedure is illustrated for one e-vector (light hatching marks the azimuth angles of the e-vector in the sky and in the bee's map; dark hatching illustrates the difference between the two azimuth angles). Finally, the mean of the resulting azimuth differences of all e-vectors considered was calculated. The error angle, so determined, is then expected to correspond to the orientation error which must occur when the bee tries to match its simplified e-vector map as closely as possible with any e-vector in the sky area observed

information that they can recognize the pattern as part of the actual e-vector pattern in the sky. In this case no orientation errors would occur.

The results described below strongly support the first hypothesis. It is shown that bees have no other knowledge of the polarization patterns in the sky than that expressed by their simplified e-vector map. In the Discussion an attempt is made to elaborate the physiological basis of these findings. It is hypothesized that the map is determined by the peripheral arrangement of polarization analysers and that a successive mechanism is involved in e-vector discrimination.

Material and methods

Individually labelled bees (*Apis mellifera mellifera*) were foraging at feeding stations 400 m NNE and 200 m S from the hive. Upon their return from the food source the bees performed their waggle dances on a horizontal comb. To control the celestial cues the observation hive was covered with a translucent Plexiglass hemisphere (see Rossel and Wehner 1982). The hemisphere depolarized skylight completely and closely matched the radiance field of a fully overcast sky. Under these conditions the waggle dances were oriented randomly unless the bees could view clear sky through one of the windows which could be opened in the hemisphere. To avoid any distortion of the natu-

ral e-vector pattern displayed through the window, the glass which covered the comb was removed during all experiments. The waggle dances were recorded from above with a video camera, and later the direction of each waggle run was measured from the monitor. Finally, the mean direction of each waggle dance was calculated and compared with both the azimuth of the food source and the error angle which one expects to occur when the bees apply their map to any one e-vector they were exposed to. How this error angle has been estimated is shown in Fig. 3.

Most experiments were performed between local noon and 3 pm during the summer months, with the sun having an elevation between 58° and 63°. For these high sun elevations large orientation errors must be expected because the polarization patterns in the sky are poorly matched by the bee's simplified e-vector map (compare Figs. 1 and 2).

Apart from the orientation errors which must occur when bees use their map, there are several other sources which possibly might induce mistakes, e.g. when the bees do not properly compensate for the movement of the sun, or when they are deflected from the correct compass course by inhomogeneities in the physical environment. Several precautions have been taken to reveal such sources of error and to separate them from the errors which arise from the use of the map. For example, two groups of bees were tested, each visiting a different food source (see above). Furthermore, each experimental situation was repeatedly tested for different azimuth angles of the sun. Finally, each e-vector pattern was presented alternately to the left and to the right of the antisolar meridian. (Note that the antisolar meridian represents a line of symmetry of the e-vector patterns; Fig. 1). This experimental strategy is particularly effective in detecting the orientation errors which arise from the bee's map because the difference between the dance directions induced by the two patterns is always twice as large as the error angle relative to the food source. Thus any successive presentation of symmetrical patterns makes the orientation errors immediately apparent, and no reference must be taken to the accurate directions of the food source.

Results

To investigate to what extent the concept of the bee's simplified e-vector map can be applied, the dancing bees were exposed to increasingly larger areas of clear sky.

To begin with, horizontal stripes of blue sky were shown (Fig. 4A). The stripes originated from the antisolar meridian and were presented either at 30° or at 60° above the horizon. They had a constant height of 10° but varied in length between 60° and 150°. The orientation performance displayed by dancing bees with respect to each celestial stripe is illustrated in Fig. 4B. It shows that bees make mistakes and these mistakes increase with the length of the stripe. This result is perplexing at first because large stripes provide more e-vector information than small ones. However, if one refers to the bee's e-vector map, this apparent paradox can readily be resolved. Since the stripes were extended towards the sun, they included sky regions which were poorly matched by the bee's map (compare Fig. 1B with Fig. 2A). In other

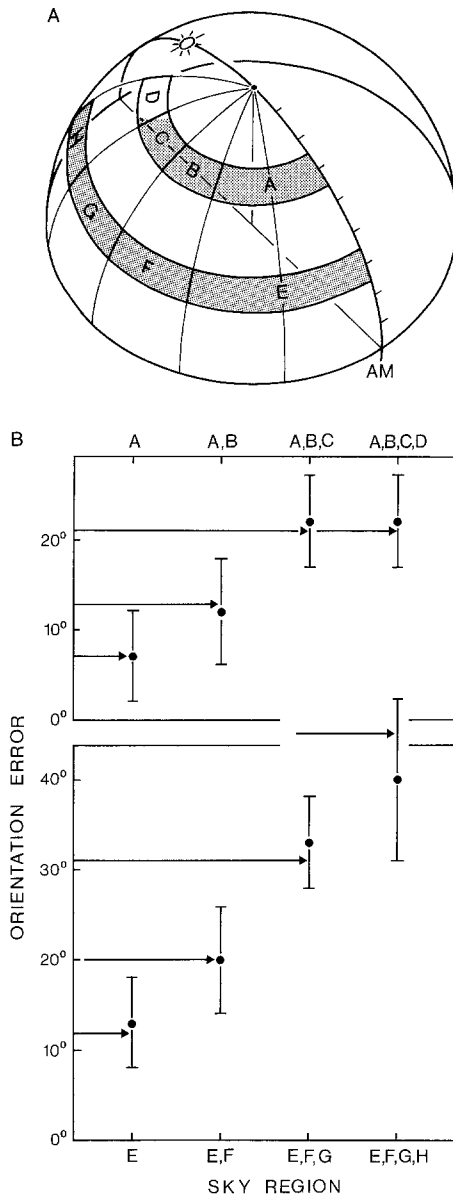


Fig. 4. **A** Celestial sphere with the sky regions shown to the bees (A–D, E–H; for details see text). According to Rayleigh theory the degree of polarization is less than 10% in region D. **B** Orientation errors in relation to the sky regions shown. Each data point is the mean of a number of waggle dances. Taken together, 221 waggle dances comprising 2491 waggle runs have been recorded from 64 individuals. Arrows mark orientation errors predicted from the bee's map. A comparison between observed and predicted orientation errors shows a close correspondence for all sky regions tested

words, the mean difference between e-vector positions in the sky and the corresponding e-vector positions in the bee's map increase with the length of the stripe and so do the dance errors made by the bees. How precisely the experimental data correspond to the predictions which can be made from the map is also shown in Fig. 4B.

The striking correspondence between predicted and observed dance errors further suggests that all e-vectors are treated as being equally important regardless of their percentage of polarization. This can be deduced most convincingly from the experiments which included large stripes because then the degree of polarization varied through almost the full range that was realized in the sky (compare Fig. 4 with Fig. 1). The only limitation is that e-vectors with a degree of polarization of less than 10% are no longer perceived by the bees (von Frisch 1967). The corresponding sky regions are then ignored and have no effect on orientation (see window D in Fig. 4).

In this context it should be noted that in the real sky the percentage of polarization is generally lower than expected by Rayleigh theory. This discrepancy depends on many factors and haze is but one that needs to be considered (Sekera 1956; Waterman 1981; Brines and Gould 1982). Thus, the sky regions for which polarization is below the perceptual threshold of bees may be larger than theoretically expected. As a consequence, the orientation errors may saturate at a lower level than theoretically predicted when the celestial stripes shown to the bees are extended towards the sun. Obviously, in the experiments above this effect did hardly show up because they were performed on days at which the sky was exceptionally clear. Yet under less favourable atmospheric conditions the bees often ignored nearly the half of the sky that was opposite to the antisolar meridian (see also Fig. 5).

The conclusions derived from Fig. 4 also hold when almost half of the e-vector pattern in the sky is shown to the bees (Fig. 5). Here the celestial windows extended 50° in the vertical direction and up to 135° in the horizontal direction (Fig. 5A). Yet even in this case the bees were not able to indicate the direction of the food source correctly, but they made mistakes which closely followed the predictions from the map (Fig. 5B).

So how do bees orient themselves when viewing the whole polarization pattern in the sky? Clearly there is no simple answer to this question because in this case no orientation errors occur. Nonetheless, from the results described so far, there are only two hypotheses which deserve a closer consideration. One, of course, is that the bees invariably use their simplified map. A precise compass course would then result, because errors induced by the left and right part of the pattern would cancel each other out. The other hypothesis suggests that the bees recognize the antisolar meridian as a symmetry line of the polarization pattern and use it as

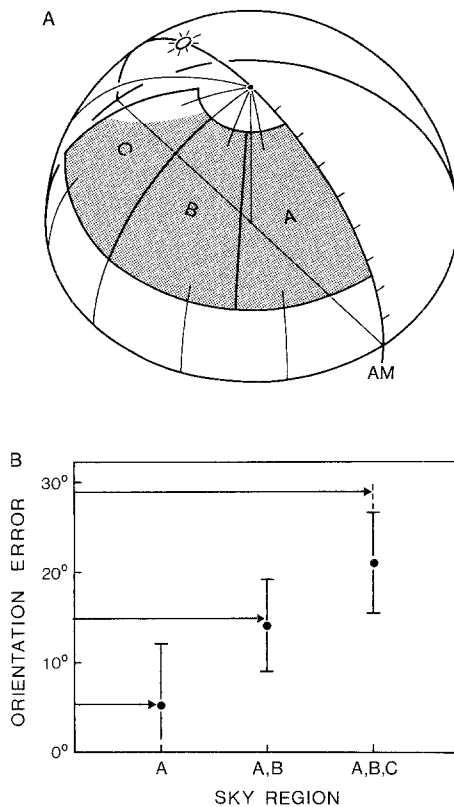


Fig. 5. **A** Celestial sphere with sky regions shown to the bees (A–C). Within the white area of region C the theoretical degree of polarization is less than 10%. **B** Orientation errors in relation to sky regions shown. Data are based on 154 waggle dances (1910 waggle runs) from 77 individuals. Arrows mark orientation errors predicted from the bee's map. There is no significant difference between observed and predicted errors except when the sky area viewed by the bee included region C. The most likely reason for this discrepancy is that light in a region larger than indicated in A was not sufficiently polarized to be perceived by the bees, due to the hazy conditions that were prevalent during the course of the experiments

the only directional cue for orientation. To orient the waggle dances toward the food source the bees then only would have to know that this meridian is always opposite to the sun. The experimental evidence, however, makes this hypothesis very unlikely as is documented in Fig. 6. From the data it is clear that accurate orientation occurs only when polarization patterns which are equal in size are symmetrically arranged about the antisolar meridian, as is the case when the whole pattern is shown. Yet if parts of the pattern that are on one side of the antisolar meridian are increased in size relative to parts on the other side, the bees make mistakes even though the antisolar meridian is visible to them, and these mistakes are consistent with the rule that the bees apply their map to all e-vectors which they can see. This finding has been confirmed by many additional experiments in

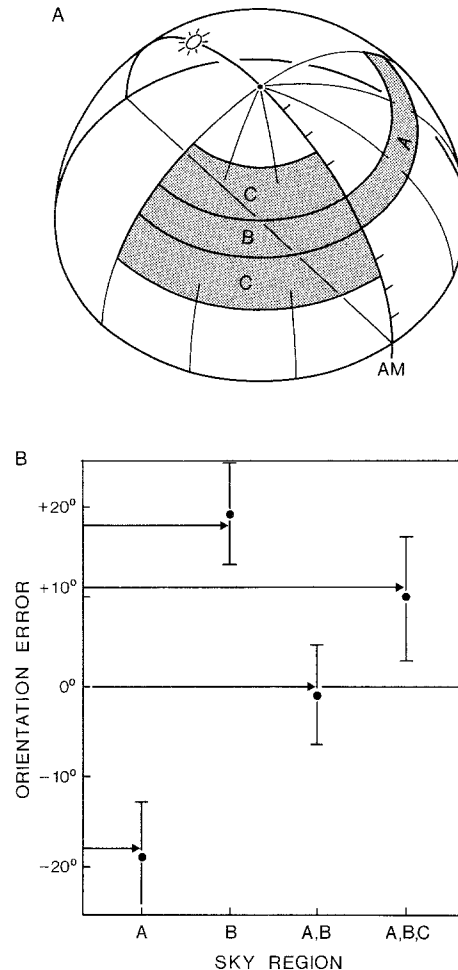


Fig. 6. **A** Celestial sphere with sky regions displayed to the bees (A–C) being arranged about the antisolar meridian (AM). For the terrestrial observer this meridian forms a prominent symmetry line of the polarization pattern (Fig. 1). **B** Orientation performance shown by the bees. Dance directions deviate from correct course to the left or to the right according to whether A or B is shown. No orientation errors occur when A and B are shown simultaneously. When B is extended by C, errors arise, even though the symmetry of the pattern is still inherent in A and B. For all situations the bee's behaviour is in accord with the predictions derived from its map (predictions marked by arrows). Data are based on 150 waggle dances (1270 waggle runs) from 22 individuals

which different pattern constellations including the antisolar meridian were shown. All in all, we were never able to find any indication that bees can use more information from the polarization patterns than that expressed by their simplified map.

One final point should be noted. When two celestial stripes, one at an elevation of 30° and the other at 60° are shown simultaneously, the upper stripe is weighted by the bees more heavily than the lower stripe. This effect does not show up when both stripes have the same azimuthal position, because in this case the errors induced by

either stripe are not that different. The same is true with respect to large celestial patterns as the ones tested in Figs. 5 and 6. Yet the weighting of the elevation readily shows up when the lower stripe is arranged to the left (right) and the upper stripe to the right (left) of the antisolar meridian, so that the errors induced by either stripe differ by substantial amounts. The weighting factor given by the expression

$$|E_{30} - E_{30+60}| / |E_{60} - E_{30+60}|^1$$

can then be calculated. On the average it is about 2 in favour of the upper stripe.

Further experiments will be necessary to reveal how other celestial elevations (and in particular the zenith) are weighted. At present the only data available in this respect refer to the situation in which single e-vectors are presented simultaneously in the zenith and at 60° above the horizon. In this case both e-vectors are equally attractive (Wehner and Rossel 1983).

Discussion

The conclusions to be drawn from the experiments described here is that bees rely on a polarization compass which is confined, in every respect, to an approximate e-vector map. This finding opens the way to a new thinking of the mechanisms which underly polarization pattern analysis in these and probably other arthropods as well.

A new model for e-vector pattern analysis and orientation

The basic principle of the model. Imagine that each ommatidium of the compound eyes contains only one polarization sensitive photoreceptor. Clearly, a single receptor cannot unambiguously determine the angle of an e-vector (Kirschfeld 1972), but an array of receptors each having a different direction of maximum sensitivity to polarized light (Φ_{\max}) can do so when it swept through the e-vector and when the peak of the sequential response pattern is detected and associated with the receptor involved.

In fact, when this is the mechanism of e-vector discrimination in bees, the simplified map and the way it is used can be explained very simply. What one has to assume is that in each horizontal array of polarization sensitive receptors, the Φ_{\max} values rotate in the same fashion through 180° as do the

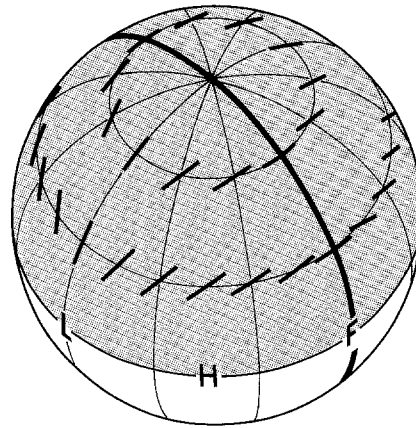


Fig. 7. Model eyes showing hypothetical arrays of polarization analyzers (bars indicate direction of maximum polarization sensitivity (Φ_{\max}) of photoreceptors). Note that the Φ_{\max} 's rotate in the same fashion as do the e-vectors in the bee's map (Fig. 2). Thick line separates the left and the right eye. *F* frontal; *L* lateral; *H* horizon

e-vectors in the map, where Φ_{\max} is horizontal in the anterior and the posterior parts of the eye with all other directions in between (compare Fig. 7 with Fig. 2A). In other words, when the bee is aligned with the solar or the antisolar meridian, the Φ_{\max} 's are arranged to match closely the maximally polarized e-vectors as they occur during the course of the day (compare Fig. 7 with Fig. 2B).

The appropriate action by the bee in estimating the direction of the solar or the antisolar meridian from a single e-vector would then be to rotate about the dorsoventral axis and to assume that the body is aligned with these reference meridians when a peak response is induced by the celestial point observed. The solar or the antisolar meridian are then correctly indicated when the e-vector involved is in its position of maximum polarization, but errors must occur for all other possible positions of the e-vectors in the sky (Fig. 8). These errors, of course, are exactly as large as the orientation errors which have been observed in the first place (Rossel et al. 1978; Rossel and Wehner 1982).

Next it should be noted that all Φ_{\max} 's are realized twice (diametrically opposite to each other in the left and in the right eye) and hence two peak responses are induced during a full body rotation. However, this does not confuse the bees because they assume that they face in the direction of the solar meridian or the antisolar meridian according to whether the peak is perceived in the posterior or the anterior part of the eyes, respectively. This rule holds for all e-vectors except for the vertical ones which are matched by the lateral eye regions. In this case, therefore, no distinction

¹ E_{30} and E_{60} , orientation errors with respect to the lower and the upper stripe, respectively; E_{30+60} , orientation error when both stripes are shown simultaneously

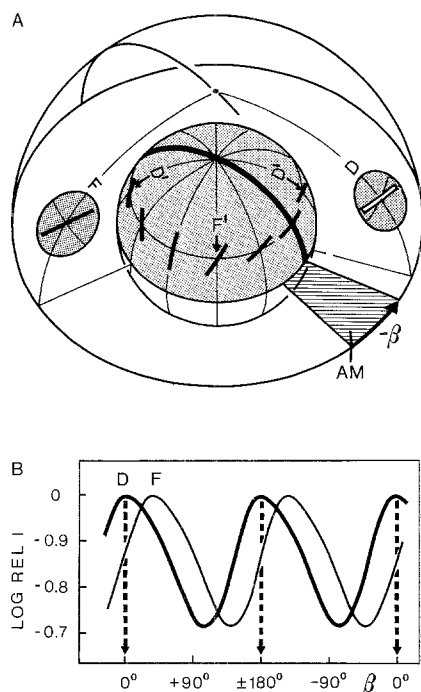


Fig. 8A, B. The model in operation. **A** Outer sphere: celestial sphere with two e-vectors (D and F). D, but not F, lies on the line of maximum polarization. Inner sphere: model eyes with receptor arrays at same elevation as e-vectors. D' and F' represent the matching receptors for e-vectors D and F, respectively (i.e. Φ_{\max} values of the receptors correspond to the directions of the e-vectors). β is the forward direction of the eyes relative to the antisolar meridian (AM); $\beta = 0^\circ$ and $\pm 180^\circ$ means that the insect faces into the direction of the antisolar and the solar meridian, respectively. When the bee rotates – here it is assumed to rotate clockwise – polarization is perceived in the form of a temporal intensity modulation (log rel I), where peak responses occur when D and F are matched by D' and F', respectively (**B**). These peaks inform the bee that it is aligned with the antisolar or the solar meridian. Yet the peaks allow a correct estimate of the antisolar or the solar meridian only when the e-vector observed is in its position of maximum polarisation, as is the case for e-vector D but not for e-vector F (compare the peaks induced by D and F with β ; B). Thus e-vector F induces an error which ultimately is manifested as a navigational error. Note that modulation curves are not exactly sinusoidal. This is because the Φ_{\max} values within the receptor array are assumed to rotate in a non-linear fashion, according to the non-linear distribution of the positions of the maximally polarized e-vectors

between the solar and the antisolar meridian can be made and the bees display a bimodal dance orientation with preferred directions 180° to each other (Rossel and Wehner 1982).

A somewhat more complicated situation is met when the bee views large areas of clear sky as in Figs. 4, 5 and 6. In this case the Φ_{\max} 's of the receptor arrays do not simultaneously match all e-vectors available. Rather, there is some angular range of rotation during which peak responses are

perceived, and as a consequence the bee arrives at a range of different directions for the solar or the antisolar meridian (compare Fig. 7 with Fig. 1B). Thus to account for the orientation errors described in this study, we assume that the bee takes the mean of the solar or antisolar meridians induced by any point of the celestial pattern shown.

The last point that needs to be settled is how the bee, once it has determined the direction of the solar or the antisolar meridian, sets the appropriate compass course. In fact, this task could be solved in just the same way as when the sun is used as a reference cue. There the bee rotates until the longitudinal axis of the body relative to the bearing of the sun corresponds to the intended flight path. Accordingly, any landmark or isolated areas of blue skylight or clouds could be used as a reference to set the compass course. Note, however, that once this course is steered, the model allows no further directional information to be deduced from the e-vector patterns. Nonetheless, celestial polarization would still be useful to maintain a straight course because any disturbance that results in body rotations is immediately indicated by brightness modulations in the sky.

An extended version of the model. The basic idea behind the model is that the spatial arrangement of retinal analysers mimicks a simplified version of the polarization patterns in the sky and that polarization is perceived in the form of temporal modulations. Without altering this basic principle there are two ways of improving the model's performance in extracting e-vector information from the sky. The first is to equip each ommatidium with a second analyser, oriented at right angles to the one already described in the basic version of the model (see Fig. 7). Then, when the bee rotates, the visual system differentially compares the responses of the two crossed analysers in each ommatidium and thus achieves a greater sensitivity to contrast modulations than when only one analyser were available per ommatidium. Secondly, the retinal analysers – which according to behavioural and electrophysiological investigations are UV receptors (von Helversen and Edrich 1974; Labhart 1980) – could be plugged into the colour coding network, where their response is compared with those of polarization insensitive blue and green receptors. Thus when the bee rotates, not only the brightness, but also the perceived colour hue is modulated and the highest UV content is registered when the Φ_{\max} of a UV receptor matches the e-vector direction in the celestial point ob-

served. This in turn would inform the bee about the direction of the solar or the antisolar meridian.

Experimental evidence

At present it is not possible to decide conclusively whether the scheme outlined above has really been adopted by the bee but much of the data available actually support the hypothesis.

From behavioural investigations it is known that the analysis of polarized light is mediated by a small dorsal region of the compound eyes (Wehner 1982; Wehner and Strasser, in prep.; Rossel and Wehner, in prep.). Within this specialized area each retinula is equipped with a set of orthogonally arranged polarization-sensitive UV receptors (Labhart 1980). While this arrangement of polarization analysers is well suited for discriminating contrast of temporal modulations (see above), it does not allow e-vector angles to be discriminated instantaneously (Kirschfeld 1972; Wehner et al. 1975). Thus for this reason alone a successive analysis of e-vector information seems more likely to be true. This hypothesis is substantiated when we consider the microvillar directions of the polarization sensitive receptors projected into visual space. In fact it turns out that the arrangement of receptor orientations in various retinulae is similar to that in the model eye (compare Fig. 7 with the data given by Wehner 1982). Also it should be noted that the specialized dorsal region of each eye is composed of not more than 140 ommatidia. Actually, the lower parts of the sky can be analysed only because the visual fields of the dorsal receptors are extremely large (Labhart 1980). Clearly, with such a limited number of sampling units a precise localisation of e-vectors in space is not possible. This is, however, much less of a disadvantage for a successive method of e-vector discrimination in which it is more important *when*, rather than *where*, polarization information is sampled.

The possibility that e-vector perception is based on a colour discrimination mechanism has first been raised by van der Glas (1975, 1976, 1980). His hypothesis is that e-vector patterns are converted into colour patterns by means of orthogonally arranged blue and UV receptors. Yet, contrary to our proposal, van der Glas suggests that throughout the retina the analysers have fixed angles relative to the horizon. This implies that a stable colour pattern is induced which is not subject to temporal modulations when the bee rotates about its vertical body axis. Evidence for the hypothesis was thought to derive from behavioural findings which showed that orientation in bees can

be evoked by artificial colour patterns presented in the zenith region of the sky. Colour patterns, however, also occur in the natural sky and our experiments show that bees can use such patterns as well as artificial colour patterns for orientation without demanding information from the polarization sensitive receptors in the specialized dorsal eye region (Rossel and Wehner, in preparation). After all, what a 'colour hypothesis' of e-vector discrimination has to explain is the bee's ability to use e-vector information not only from the zenith but also from small patches of blue sky close to the horizon. Certainly, no spatial colour gradients are induced in this case. To account for orientation the hypothesis has in fact to assume the e-vectors being perceived in the form of temporal colour modulations, as suggested in our model.

How should one now proceed to test the role of temporal intensity and/or colour coding in e-vector perception? Presumably, the most promising approach is to confront dancing bees with stimuli in which the intensity or the wavelength is modulated between successive waggle runs. The bee will then perceive a UV peak at some instant during rotation and will use it – if the theory is valid – as a reference to estimate the direction of the solar or the antisolar meridian and subsequently the direction of the food source.

Conclusions

Conventional models dealing with e-vector perception suggest that bees are able to discriminate polarization angles instantaneously in any part of the visual field (e.g. von Frisch 1967). Any such sensory performance would be demanding in terms of complexity and neuronal hardware (Kirschfeld 1972; Wehner et al. 1975; Bernard and Wehner 1977). On the other hand, there is not really a simple alternative if one assumes, as von Frisch and many later workers did, that bees know where a particular e-vector is located relative to the sun.

Thus it was only after we had discovered the bee's simple rules of dealing with polarization patterns that we started to take a fresh look at the problem of e-vector perception. The resulting hypothesis is rather simple indeed. It suggests that celestial polarization is not perceived as an extra quality of light but simply as a modulation of brightness and/or colour while the bee rotates. All the bee then has to know about polarization patterns is how to correlate these modulations with the bearing of the solar or the antisolar meridian. Since for the model bee the positions of all e-vector directions are rigidly fixed by the geometry of the

polarization analysers within the retina, it is immediately clear why the insect cannot cope with the dynamic features of the polarization patterns as caused by the sun's change in elevation. Nevertheless, the model makes the best of it in assuming that the spatial layout of the analysers mimicks the spatial distribution of the most prominent e-vector positions, i.e. the ones given by the line of maximum polarization.

The model shows how an insect might analyse the complex polarization patterns by means of simple neuronal strategies. Clearly simplicity is at the expense of precision and under certain conditions errors must necessarily occur. However, this is not a serious shortcoming as it first might appear, because during free flight the navigating bee can resort to powerful backup systems such as the sun and landmarks (von Frisch 1967).

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