The Role of Dorsal Rim Ommatidia in the Bee's Eye

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A recent model of celestial e-vector analysis by the bee assumes that polarization information is transformed into modulation of perceived brightness while the bee scans the sky by rotating its field of view. It is shown that the suggested simple strategy to read compass information from the polarization pattern of the sky in natural conditions can work only in a part of the sky close to the zenith. The bee would need a different strategy for other regions of the sky.

Karl v. Frisch [1] discovered that honey bees can derive compass information from the sun linked polarization pattern in the sky. The advantage for the bee is that she can orient correctly even if the sun itself is obscured by clouds. A small patch of blue sky (diameter 10° and less) has been considered to be sufficient for the orientation. However, it is not a trivial task for the bee to extract the compass information from such a patch of sky, since a given e-vector direction can be generated by an infinite number of positions of the sun [2].

Recently, Rossel *et al.* [3] and Rossel and Wehner [4–6] published a concept of how the bee solves the problem in an approximative manner. The basis of Rossel's and Wehner's concept is the following:

1. There is a specialized region in the eye (dorsal rim) that is used for the analysis of the polarization pattern of the sky. The UV-receptors in this region are of especially high polarization sensitivity.

2. The analyzer directions of the photo-receptors in the ommatidia of the dorsal rim afford a template of the polarization pattern of the sky.

3. The bee rotates around her vertical axis until the analyzers in the dorsal rim are in register with the polarization pattern of the sky. In this case the body is aligned either with the solar or the antisolar meridian.

4. If there is only a small patch of blue sky visible with a given e-vector direction, by rotating around her vertical axis the bee scans this patch with a ring of ommatidia in the dorsal rims of both eyes, thus exposing a changing set of ommatidia with analyzers of different angular orientation. The bee records that part of the dorsal rim which receives the highest stimulation during the turn and so extracts the compass information. I will call this method *"ring e-vector analysis"*.

The inherent problem in this method is the following: a non-interrupted ring of ommatidia with a complete set of analyzer directions is available in the two dorsal rims only if the patch of the sky to be analyzed is close to the zenith, *i.e.* at an altitude of 70° above the horizon or more (*e.g.* point P_a in Fig. 1). If, however, the patch is at a position such as P_d in the figure, there are scarcely any ommatidia in the dorsal rim area that point at this patch during the "sweep" with their optical axes. Rossel and Wehner offer the following solution to the problem: There are ommatidia in the dorsal rim that have exceptionally large visual fields [7]. They show a relatively narrow sensitivity peak in the center and a wide, flat "brim" extending 30° or more off-axis. This means that ommatidia from the dorsal rim also collect light from portions of the sky which are far off their optical axis, and, in principle, they could be used for *off-axis e-vector analysis*. In agreement with this idea is the finding that the UV photo-receptors in these ommatidia have high sensitivity to polarized light and each exhibits its specific analyzing plane irrespective of the angle of incident light [7].

In principle ring e-vector analysis amounts to comparing the excitation of the analyzers (or the difference between orthogonally aligned analyzers, as also considered by Rossel and Wehner), that scan a patch of blue sky one after the other. *E.g.* in Fig. 1, the e-vector of patch P_a of the sky is assumed to have the same alignment as an analyzer in ommatidium 1: excitation will be maximal in this ommatidium. If the bee rotates by 30°, ommatidium 2 with its optical axis points at the patch P_a. Its analyzer, since rotated by some angle a ≈ 30° relative to the e-vector of P_a will be less excited than ommatidium 1, a.s.o.

Fig. 1 shows ommatidia 1 and 7 as maximally excited during the sweep and ommatidia 4 and 10 as minimally. Maximal excitation in a particular ommatidium of the "ring" indicates to the bee that, at this position her body axis is aligned with the solar meridian or antimeridian, alternately.

What happens, however, if only a patch like P_c is visible (Fig. 1)? Two cases have to be discriminated: In Case I only the patch of sky P_c is exposed and

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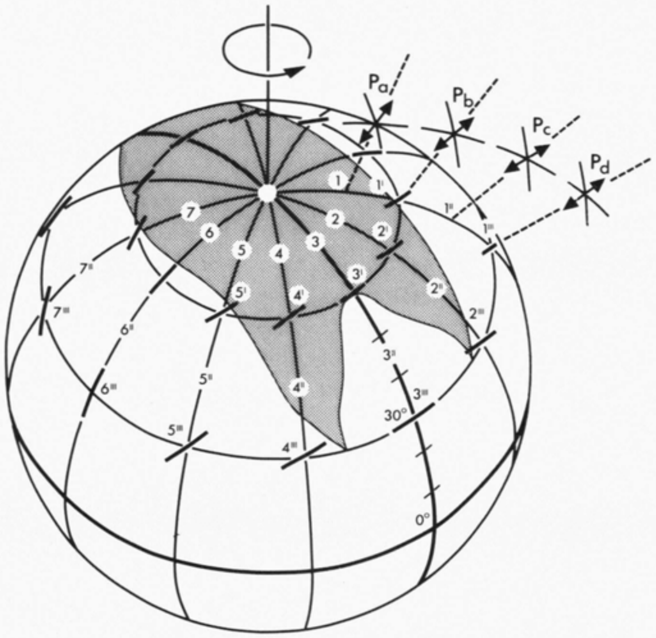

Fig. 1. The visual field of the dorsal rim area of the honey bee's eye (stippled area), as plotted on a spherical coordinate system. The animal is considered to be in the centre of the sphere. Also indicated are effective analyzer directions (short bars), modified from Rossel [13]. The points P_a to P_d are points on the celestial sphere. Double arrows indicate the direction of the vector of polarized light at the points P_{a-d}.

bright, the rest of the sky is covered by a non-transparent plexiglas dome. This has been the test situation in several of Rossel's and Wehner's experiments (*e.g.* [3]).

For the angular position of the bee as depicted in Fig. 1, no ommatidium is facing P_c directly with its optical axis. Ommatidium $1'$ (or 1), however, can be used for off-axis-e-vector analysis as it will be stimulated to a degree which depends upon the off-axis angle and the e-vector direction. If the bee rotates by 30° as discussed above, ommatidium $2''$ will become aligned to P_c.

The excitation in an analyzer in ommatidium $2''$ will be different from that in ommatidium $1'$ for two reasons: firstly, as the angle α between e-vector and analyzer direction is increased to some 30°, so the signal diminishes; and secondly, as the off-axis angle is reduced, so the signal increases. Therefore, the signal in ommatidium $2''$ can either be larger or smaller than that of $1'$, depending upon the particular contribution of these two parameters. Therefore, just comparing the signals in these two ommatidia does not allow any conclusions to be drawn about the e-vector direction of light coming from P_c. The same argument holds if not signals in individual analyzers (= photo-receptors) are compared, but differences between signals of analyzers that are orthogonally aligned.

As a possible mechanism for the extraction of e-vector information it has also been argued that the excitations of many, or even all, analyzers (or differences from orthogonal pairs of analyzers, respectively), will be superimposed upon a higher order neuron. Excitation of this neuron is expected to be maximal if the long axis of the bee's body is aligned with the solar or anti-solar meridian. These assumptions do not hold for the case shown in Fig. 1 where the sum of excitation of all ommatidia may have to be at a certain level. According to the theory if the bee rotates by 30° the sum of excitation should decrease because the animal increases the angle between the long axis of its body and the anti-solar meridian. However, after this rotation the off-axis angle of many ommatidia (*e.g.* $2'$, $2''$, $2'''$) actually *diminishes,* thus the sum of the signals of individual photoreceptors would, in fact, increase (since usually the contribution of the off-axis angle is larger than that of α) and hence lead to erroneous information on α. The situation could be improved if not the signals from individual analyzers are compared, but if differences between signals of orthogonal analyzers are evaluated and if, in addition, a gain control mechanism normalizes the mean activity *e.g.* at the second order neuron level of every pair of orthogonal analyzers.

A gain control mechanism would not help in Case II that is more realistic, and that makes the following assumption: the patch P_c of blue sky is to be surrounded by clouds that are of similar UV brightness as the patch. This light, however, is considered to be not or only slightly polarized. In this case the situation becomes still more complicated: the signal from off-axis ommatidia does not only depend upon the angle α and the off-axis angle, but also upon the contribution of unpolarized light that is collected by the wide-field dorsal rim ommatidia.

Evaluations based on measurements of light from the sky under different conditions [8] and on the angular sensitivity distributions for the dorsal rim ommatidia as measured by Labhardt [7], show that if a patch of sky of diameter of 10° is more than 10° off-axis, from a dorsal rim ommatidium it can no longer be used as an analyzer for polarized light: the contribution of the unpolarized or weakly polarized light overrides that of the polarized light to such a degree, that the signals in the analyzers fall below the detection threshold for polarized light. This threshold for a small patch of sky corresponds to a degree of polarization of some 10% [1, 9].

These consideration show that ring e-vector analysis in its elementary form is insufficient to solve the problem of e-vector analysis for small patches of sky. However, many experiments clearly showed that bees are capable of determining the direction of the e-vector of a small patch of sky, not only if the patch is close to the zenith, but also if it is as low as 30° above the horizon [3, 14]. This not only if the patch of sky alone is bright, but also if the natural sky could be seen through a translucent Plexiglas hemisphere [4]. What could be the mechanism bees use for this analysis? We can only speculate: It could be that not only dorsal rim ommatidia are used, but also analyzers in other ommatidia or even the ocelli, but this seems to be unlikely [10]. It could also be that bees are capable of analyzing the e-vector direction with the dorsal rim ommatidia by a "simultaneous" [11] method. The fact that in the dorsal rim the ommatidia have microvillus directions not only in two orthogonal but also in oblique directions [12], would be in agreement with such an assumption.

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