THE HYMENOPTERAN SKYLIGHT COMPASS: MATCHED FILTERING AND PARALLEL CODING*

By RÜDIGER WEHNER

Zöologisches Institut der Universität, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland

Summary

In deriving compass information from the pattern of polarized light in the sky (celestial e-vector pattern), hymenopteran insects like bees and ants accomplish a truly formidable task. Theoretically, one could solve the task by going back to first principles and using spherical geometry to compute the exact position of the sun from single patches of polarized skylight. The insect, however, does not resort to such computationally demanding solutions. Instead, during its evolutionary history, it has incorporated the fundamental spatial properties of the celestial pattern of polarization in the very periphery of its nervous system, the photoreceptor layer. There, in a specialized part of the retina (POL area), the analyser (microvillar) directions of the photoreceptors are arranged in a way that mimics the e-vector pattern in the sky (*matched filtering*). When scanning the sky, i.e. sweeping its matched array of analysers across the celestial e-vector pattern, the insect experiences peak responses of summed receptor outputs whenever it is aligned with the symmetry plane of the sky, which includes the solar meridian, the perpendicular from the sun to the horizon. Hence, the insect uses polarized skylight merely as a means of determining the symmetry plane of the polarization pattern, and must resort to other visual subsystems to deal with the remaining aspects of the compass problem (*parallel coding*).

The more general message to be derived from these results is that in small brains sensory coding consists of adapting the peripheral rather than the central networks of the brain to the functional properties of the particular task to be solved. The matched peripheral networks translate the sensory information needed for performing a particular mode of behaviour into a neuronal code that can easily be understood by well-established, unspecialized central circuits. This principle of sensory coding implies that the peripheral parts of the nervous system exhibit higher evolutionary plasticity than the more central ones. Furthermore, it is reminiscent of what one observes at the cellular level of information processing, where the membrane-bound receptor molecules are specialized for particular molecular signals, but the subsequent molecular events are not.

Outline of the problem

Ever since the exciting discoveries were made that ants and bees could derive

* Dedicated to Professor Dr Martin Lindauer in honour of his 70th birthday.

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compass information not only from the sun (Santschi, 1911) but also from small patches of blue sky (Santschi, 1923), and that in the latter case they relied on the perception of polarized skylight (von Frisch, 1949), neurophysiologists have tried to understand how the insect's eye and brain accomplished this formidable task of sensory coding. The task is formidable indeed. Just take a look at the sky: light emanating from different points on the celestial hemisphere differs not only in intensity and colour, but also – though invisible to the unaided human eye – in its state of polarization. This is because the scattering of skylight within the earth's atmosphere creates not only intensity and spectral gradients, but polarization gradients as well. In detail, the state of polarization contains two parameters: the orientation of the plane in which the electric vector, or e-vector, of light vibrates (the so-called *direction of polarization* or *e-vector direction*) and the strength of this phenomenon (the so-called *degree of polarization*). Whereas the celestial gradients of intensity, spectral composition and degree of polarization are highly susceptible even to weak atmospheric disturbances like haze, pollution or thin clouds, the gradient of e-vector directions (the so-called *e-vector pattern*) is not, and thus provides the most reliable cue for navigation. In fact, it is this e-vector pattern that the insect uses as a compass cue (for experimental evidence see reviews by Wehner, 1982; Wehner & Rossel, 1985), and it is this pattern which the insect, during its evolutionary history, has incorporated as an internal image into its neural hardware. But by mentioning this internal image of the sky – this matched sensory filter – I am already getting ahead of my story.

For the sake of perspective, let us first examine the more traditional ways of trying to understand how the insect's polarization compass (*e-vector compass*) works. Since the early 1970s there has been a remarkable resurgence of interest in that subject. Simultaneously several research groups started, in one way or another, to tackle the problem of the insect's skylight compass in two species of insect, the honeybee (*Apis mellifera*) and the desert ant (*Cataglyphis bicolor*) (Wehner & Duelli, 1971; Kirschfeld, 1972; Zolotov & Frantsevich, 1973; von Helversen & Edrich, 1974; van der Glas, 1975; Brines & Gould, 1979).

The reason for this sudden rise in interest was twofold. First, there existed some animal species endowed with a complex sensory capacity that extended beyond our human ken. In this context 'polarization vision' was regarded as something analogous to colour vision in so far as the insect was assumed to perceive 'polarization' as a unique sensory quality, much as we perceive 'colour' as something that is qualitatively unique and different from any other sensory experience. Models were designed in which the insect could disentangle the information provided by the intensity, spectral content, degree of polarization and direction of polarization within a single beam of light, and process the latter information independently and unambiguously. This approach was entertained most strongly by Kirschfeld (1972) and his co-workers (Ribi, 1980). Second, the use of polarized skylight for navigational means was considered to be one of the most remarkable computational tasks the insect's brain was able to solve. The hope of understanding how a small brain could accomplish such feats of

computation was certainly a major challenge to the newly formed guild of insect neuroethologists.

Seen in this light, one can easily understand why the principal question posed above – how does the insect's polarization compass work? – was broken down by most researchers into two apparently smaller questions. How does the insect unambiguously detect particular e-vectors in the sky? What 'knowledge' about the spatial distribution of celestial e-vectors does the insect use for steering its compass courses?

As mentioned above, solving the first problem was considered to be analogous to solving a set of four equations with four unknowns (with the four unknowns being intensity, spectral composition, degree of polarization and direction of polarization). To acquire the necessary input data the insect could perform four measurements: either simultaneously by using four different receptors, or successively by employing only one receptor. The successive method requires that polarization-sensitive photoreceptors (the insect's analysers) can rotate about their direction of view, and that the e-vector direction of the stimulus is inferred from the angular position of the analyser at which the maximum response occurs. However, as insects cannot rotate their photoreceptors within their eyes, it is difficult to see how such a mechanism could work in practice. The simultaneous method avoids this difficulty by assuming that several photoreceptors, each with its own analyser direction, perceive the same stimulus simultaneously – the same pixel of sky – and that the outputs of these photoreceptors are compared and further processed by some appropriate neural network.

Having solved the e-vector detection problem, the insect was considered to face the second problem, which was an even more formidable one than the first: to infer, say, the position of the sun from the individual e-vectors available in the sky. To accomplish this task the insect should somehow 'know' how the various e-vectors were distributed across the sky. In theory, it could resort to first principles – in this case the laws of atmospheric light scattering – and perform something analogous to a three-dimensional geometrical construction, i.e. spherical geometry. With this picturesque flight of imagination, however, the human researcher has perhaps been more ingenious than his experimental animal.

According to these hypotheses, based on the idea of perfect design, the insect was supposed to make full use of all the skylight information available to the physicist's instruments. It was supposed to be able to determine individual e-vector directions, and to know accurately in which azimuthal position each individual e-vector direction occurred in the sky. By referring to the famous, though limited, experiments of von Frisch (1965) this accuracy was taken for granted.

As we now know, this assumption was mistaken. Bees and ants do *not* come programmed with a complete knowledge of the e-vector distribution in the sky. By presenting the animals with the full e-vector pattern during training, and with a spatially restricted part of the pattern during testing, or *vice versa*, we were able to show that bees and ants were endowed with only a partial knowledge of the actual

skylight pattern (but that this partial knowledge met the insect's navigational requirements amazingly well). The concept of the insect's simplified map of the sky was derived from behavioural experiments (Rossel & Wehner, 1982) long before we had data that defined the map in neurobiological terms. These results are now available (Wehner & Rossel, 1985; Wehner, 1987; Labhart, 1988) and they are conclusive (Rossel & Wehner, 1986, 1987). The answer is surprising: the map resides in the outermost periphery of the insect's visual system, the retina. There a specialized array of photoreceptors forms a 'matched filter' (Wehner, 1987), matched to the spatial properties of the navigational problem to be solved. In this 'compound polarization filter' the spatial layout of the analysers matches, by and large, the spatial distribution of e-vector directions in the sky. It is to this matched filter, and how it is read and used by the insect's brain, that we shall turn now.

Matched filtering

External world: celestial e-vector patterns

The whole range of e-vector directions is distributed across the celestial hemisphere in an orderly way. Because skylight polarization arises from the scattering of sunlight by the air molecules within the earth's atmosphere, the whole e-vector pattern is fixed relative to the sun. The way in which the gradient of e-vector directions is related to its pole, the sun, is portrayed in the three-dimensional representation given in Fig. 1A. As demonstrated by this figure, and even more strikingly by the two-dimensional representations shown in Fig. 1B,C, a global plane of symmetry passes across the entire celestial hemisphere. It contains the solar meridian and the antisolar meridian. The former is the arc passing from the zenith through the sun down to the horizon, the latter is the continuation of that arc on the other side of the celestial hemisphere. The e-vector directions form concentric circles around the sun. This follows simply from the laws of Rayleigh (primary) scattering, according to which light is always polarized perpendicular to the plane of the scattering angle, i.e. the plane containing the sun, the observer and the point observed.

By comparing Fig. 1B and 1C the reader will note that all e-vector directions change their position with respect to the axis of symmetry as the sun changes its elevation in the sky. Of course, as mentioned previously, the pattern remains fixed within a sun-related system of coordinates, but it changes within a horizon system of coordinates – and it is within the horizon system that the insect navigates. Mirror-image symmetry is an invariable feature of all possible e-vector patterns, but the e-vector distributions to the left and the right of the symmetry plane change their intrinsic spatial properties as the sun moves up and down the solar meridian.

Of course, it is not only the elevation, but also the azimuth of the sun that changes during the course of the day. Consequently, due to the westward movement of the sun, the symmetry plane, and with it the whole e-vector pattern,
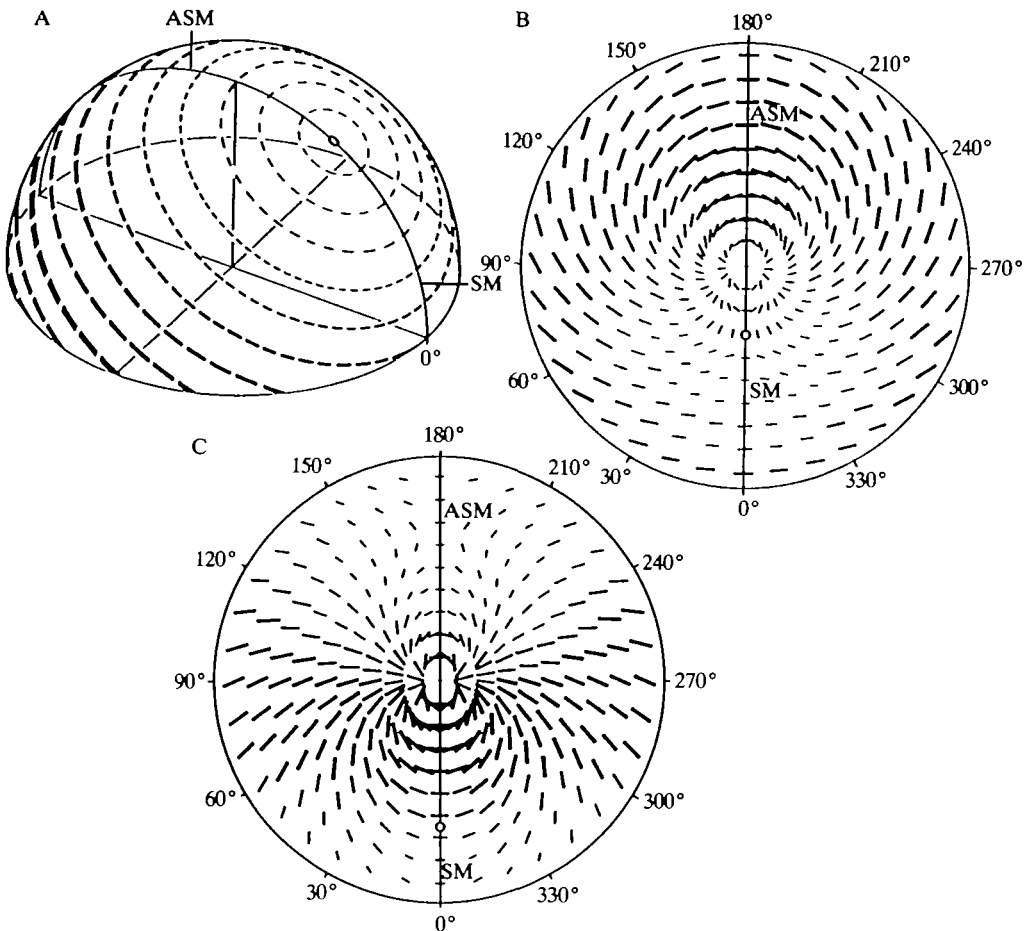
Fig. 1. Celestial e-vector pattern. (A) Three-dimensional representation. Elevation of sun 60°. (B,C) Two-dimensional representations for two elevations of the sun, 60° (B) and 24° (C). The orientation and width of each black bar mark the e-vector direction and the degree of polarization, respectively. The direct light from the sun (white disc) is unpolarized. SM and ASM, solar and antisolar meridian, respectively.

rotates about the zenith. In the present account we can disregard the problem of time compensation resulting from this movement of the sun's azimuth because all experimental animals were tested immediately after training and, thus, the celestial pattern could be regarded as stationary. Note, however, that animals trained and tested at different times of day, and thus under different elevations of the sun, experienced different e-vector patterns (compare again Fig. 1B and 1C).

Internal map: compound polarization filter

Spatial structure of the celestial map

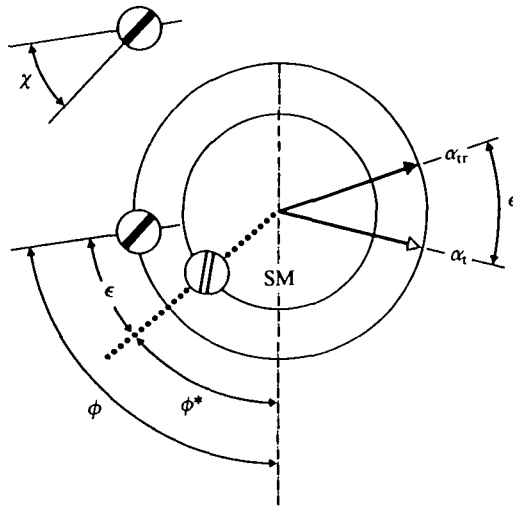Behavioural studies are the only means by which one can ultimately deduce

Fig. 2. How to derive the insect's internal e-vector map from the navigational errors observed under the experimental conditions outlined in the text. With the whole e-vector pattern at their disposal, bees and ants are trained to a particular foraging direction, α_{tr}. When tested they are presented only with a single e-vector direction, χ. In the real sky, this e-vector direction occurs at an angular distance ϕ from the solar meridian, SM. In the test, the insect chooses the direction α_t rather than α_{tr}, i.e. it deviates by the error angle ϵ from α_{tr}. Thus it assumes χ to occur at the azimuthal position $\phi^* = \phi - \epsilon$. For all elevations of the sun and the e-vector observed, a strong correlation between χ and ϕ^* holds (see Fig. 3).

what the insect's internal representation of the celestial e-vector pattern looks like. Hence, we engaged in a long series of behavioural experiments yielding more than 10 000 data points from which the detailed spatial structure of the bee's and ant's e-vector map emerged. As the technical procedures and detailed results have been described elsewhere (Rossel & Wehner, 1982, 1984a; Wehner, 1982, 1984; Wehner & Rossel, 1985; Fent, 1985), in the present context it may suffice to outline the rationale behind the experiments.

It is convenient to regard the solar meridian as the reference direction, or zero-point, of the celestial compass, much in the same way as magnetic north defines the zero-mark of the magnetic compass scale. Taking a compass reading then means recording the angle between the solar meridian and any direction of interest; say, the direction of a food source. In Fig. 2 this angle is denoted by α. The solar meridian can be determined either directly, by recording the position of the sun and taking the perpendicular from the sun to the horizon (sun compass), or indirectly, by inferring it from whatever e-vectors are available in the sky (polarization compass).

In the case of the polarization compass a major question arises. How well can the insect infer the position of the solar meridian from any particular e-vector direction in a patch of natural sky (or in an artificial beam of polarized light)? The
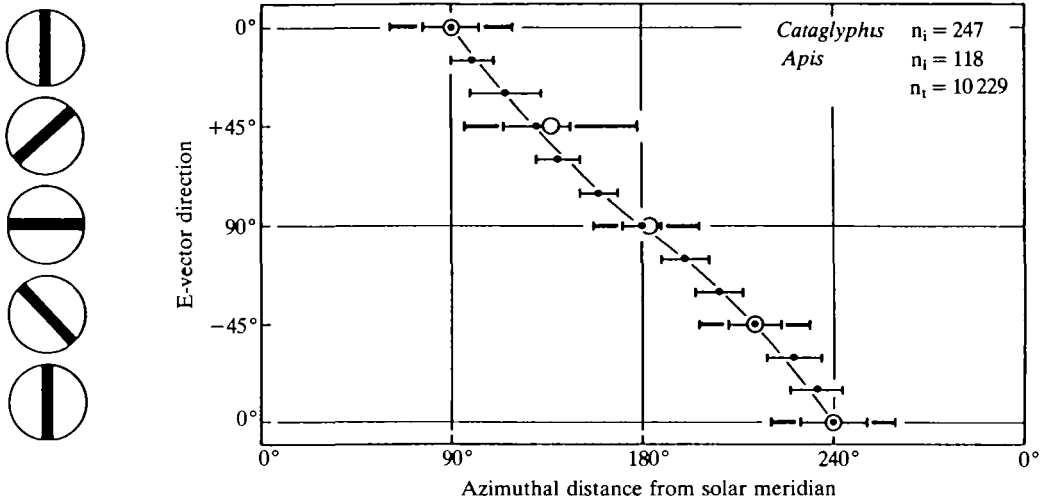
Fig. 3. The bee's and ant's e-vector compass. The figure describes at which azimuthal distance from the sun (abscissa, ϕ^* in Fig. 2) the insect expects any particular e-vector direction (ordinate, χ) to occur. Mean values and standard deviations are given (for the antisolar half of the sky). Closed circles and thin bars: bee; open circles and heavy bars: ant. n_i, number of individuals tested; n_t, number of tests performed. For a more pictorial representation of this e-vector 'map' see inner circles of Fig. 8.

answer was perplexing at first, but finally extremely rewarding. When bees and ants were trained to a given direction (α_{tr}) under the full blue sky, and then asked to recall α_{tr} when presented with an individual e-vector direction (χ), they made consistent navigational errors by selecting the compass course $\alpha_t = \alpha_{tr} - \epsilon$ rather than α_{tr} itself. The error angles (ϵ) exhibited by both bees and ants mean that the insects assume the e-vector χ to occur in the sky at a position ϕ^* that deviates by the azimuthal distance ϵ from the actual position of χ (i.e. ϕ).

Having established this basic result, we now displayed all possible e-vector directions, recorded the error angles exhibited by the trained animals, and derived from these error angles where in the sky the animals assumed any particular e-vector direction to occur relative to the sun. What emerged from this rather tedious enterprise was the insect's internal representation of the e-vector pattern in the sky, the insect's celestial map.

This map is very simple indeed. It is essentially the same in bees and ants. Either species assumes that any particular e-vector direction occurs at a *fixed* azimuthal position ϕ^* with respect to the solar meridian. In the real sky, the positions ϕ of all e-vector directions vary with the elevation of the sun and the point observed (Fig. 1B,C), but in the insect's internal model of the sky they do not (Fig. 3). Hence, navigational errors might occur whenever e-vector positions in the sky do not coincide with e-vector positions predicted by the insect's e-vector map, and it was on the basis of these navigational errors that we were able to unravel the fine spatial structure of this map.

Neurophysiological basis of the map: the POL area of the insect's eye

With the latest craze in experimental psychology – finding and establishing cognitive maps everywhere (Gallistel, 1989), even in insects (Gould & Towne, 1987) – one could now lean back and claim that the bee's and ant's e-vector map certainly qualifies for the most detailed cognitive map ever found in any animal species. However, by referring to cognition, one of the most suspect pieces of conceptual baggage in recent behavioural neurobiology, one obscures rather than stimulates the search for the neural basis of the map. Those who invoke the concept of cognitive maps in animal brains most ardently are forced to resort to guesswork when it comes to the crucial question of where and how the invoked maps are laid down in the hardware of the animal's nervous system.

Fortunately, in the case of the insect's celestial map we are in a better position. This is mainly because the map resides at the very periphery of the nervous system, the photoreceptor layer. A specialized part of the retina, positioned at the uppermost dorsal margin of the eye and comprising only 2·5 % (*Apis*) or 6·6 % (*Cataglyphis*) of all ommatidia of the eye, is necessary and sufficient for e-vector navigation (*Apis*: Wehner & Strasser, 1985; *Cataglyphis*: Wehner, 1982; Fent, 1985; M. Müller & R. Wehner, in preparation). Hence we have called this part of the eye the insect's POL area (Wehner & Strasser, 1985). It is the spatial distribution of the polarization analysers within this POL area that represents the insect's celestial map.

Let us build up to this hypothesis as follows: the primary analysers of the POL area are spatially arranged and neurologically wired up in such a way that a hierarchy of analysers results (Fig. 4).

First-order analysers. The primary analysers are the ultraviolet receptors (Duelli & Wehner, 1973; von Helversen & Edrich, 1974) of the POL area (Wehner, 1982, 1983*a*). They exhibit high polarization sensitivities, being 6–8 times more sensitive to light polarized parallel to the microvillar (analyser) direction of the cell than to light polarized perpendicular to this preferred direction (Table 1). Anatomically all photoreceptors of the POL area run straight through the entire length of the retina, whereas in the remainder of the eye they are twisted (*Apis*) or otherwise misaligned (*Cataglyphis*) (Wehner *et al.* 1975; Räber, 1979; Wehner & Meyer, 1981). It can be shown by both optical calculation (Wehner *et al.* 1975; Nilsson *et al.* 1987) and electrophysiological measurement (Labhart, 1980, 1986) that it is the microvillar misalignment that reduces the polarization sensitivity of the photoreceptors outside the POL area. Anatomical and physiological pecularities similar to the ones found in the POL area of bees and ants have meanwhile been described for other groups of insects (other hymenopterans: Aepli *et al.* 1985; crickets: Burghause, 1979; Labhart, 1988; flies: Wada, 1974; Wunderer & Smola, 1982; Hardie, 1984; lepidopterans: Meinecke, 1981; Kolb, 1986).

Second-order analysers. In each spatial sampling station (ommatidium) of the POL area there are two groups of ultraviolet receptors the analysers of which are arranged at right angles to each other. For example, in *Cataglyphis* the microvillar directions of cells 1 and 5 coincide, but run at right angles to the microvilli of cells
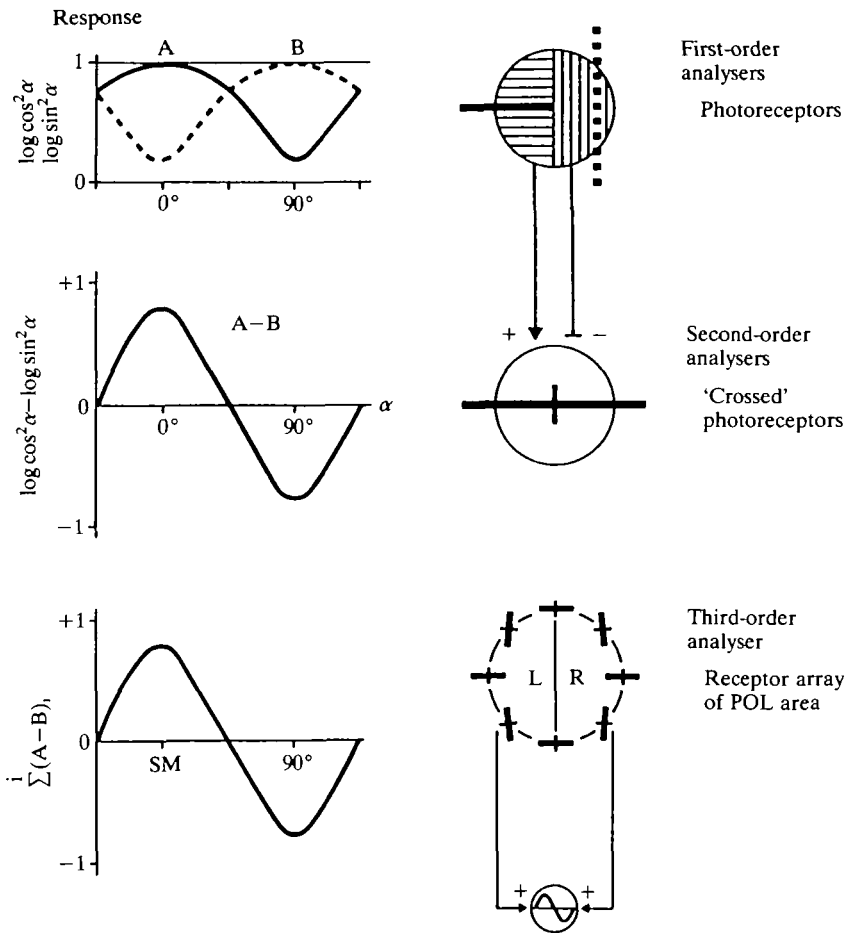
Fig. 4. Hypothetical scheme of the hierarchy of polarization analysers in the hymenopteran visual system. SM, symmetry plane.

Table 1. *Polarization sensitivity of hymenopteran photoreceptors*

	Ultraviolet receptors		Green receptors
	POL area	Remainder of eye	POL area
Spectral sensitivity	**350**	**350**	**510**
λ_{max} (nm)	350	350	540
Polarization sensitivity	**6·3 ± 2·4**	**2·9 ± 1·6**	**2·2 ± 0·7**
$S_{\parallel}/S_{\perp}$ (s.d.)	7·9 ± 4·5	1·6 ± 0·4	1·8 ± 0·3
N	**18**	**13**	**26**
	26	7	10

Bold-faced numbers refer to *Cataglyphis bicolor*, normal-type numbers to *Apis mellifera*. Data from Labhart (1980, 1986).
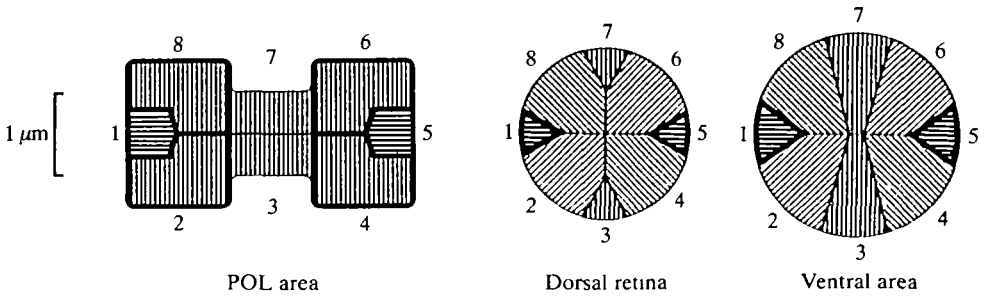
Fig. 5. Types of rhabdom in the retina of *Cataglyphis bicolor*. The microvillar directions of photoreceptors 1–8 are given for the POL area, the remainder of the dorsal retina and the ventral retina. Ultraviolet receptors are indicated by heavy outlines. Note the crossed-analyser arrangement of the ultraviolet receptors within the POL area. (From Wehner, 1982.)
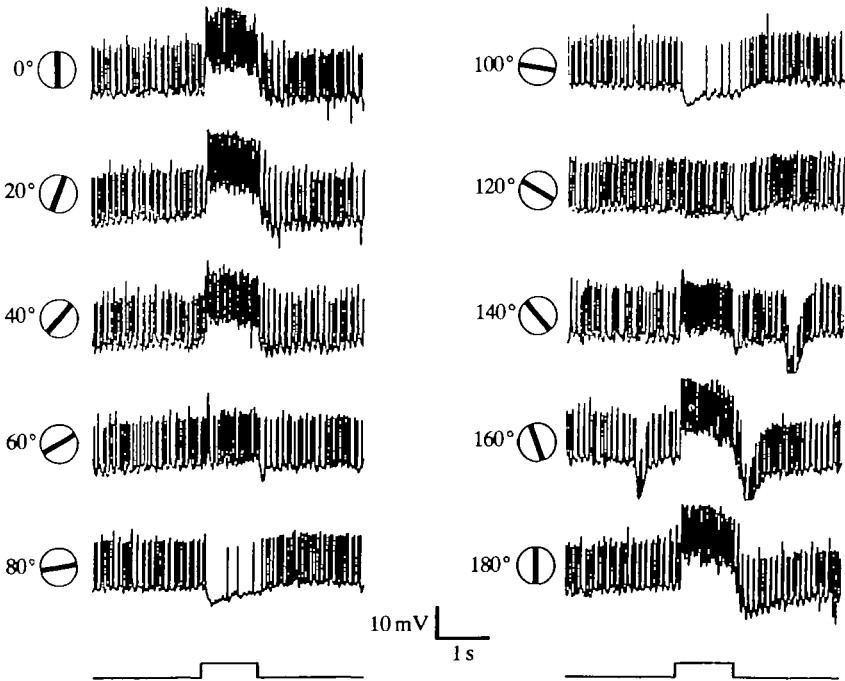

Fig. 6. Responses of a polarization-opponent interneurone in the medulla of the cricket. When the retina is stimulated with a vertically polarized beam of light, the neurone exhibits depolarization and an increase in its spontaneous firing rate. Horizontal e-vectors elicit hyperpolarization and a decrease in spike frequency. (From Labhart, 1985.)

2, 4, 6 and 8 (Fig. 5). The outputs of the two sets of ultraviolet receptors interact antagonistically, i.e. one set of photoreceptors inhibits the other (Fig. 6; Labhart, 1985). Consequently, the second-order analysers exhibit largely enhanced polariz

ation sensitivities when compared with the photoreceptors, and – more import-
antly – respond only to variations in e-vector direction rather than in light
intensity. Intensity invariance is an important property of any detector of celestial
e-vector directions because, without it, the marked and unpredictable intensity
fluctuations found in the sky would severely affect the responses of the analyser. It
can be shown directly, by behavioural experiments, that the bee's e-vector
compass is susceptible to fluctuations in radiant intensity whenever only one type
of first-order analyser (e.g. only receptors 1 and 5) is stimulated. This kind of
stimulation can be achieved by placing miniature, and precisely aligned, polariz-
ation filters in front of the bee's eyes (Rossel & Wehner, 1986, 1987).

Third-order analyser (compound polarization filter). Now comes the most
thought-provoking finding of our neurophysiological studies. The spatial distri-
bution of the second-order analysers forms a striking fan-shaped pattern that
spreads across the entire POL area (Räber, 1979; Sommer, 1979; Wehner, 1982;
Meyer, 1984; Fig. 7). It matches the e-vector map as previously derived from
behavioural experiments. In fact, the array of second-order analysers *is* the
insect's e-vector map. Rather than being a cognitive construction, the celestial
map turns out to be a specialized array of polarization-sensitive ultraviolet
photoreceptors (analysers) the analyser directions of which are arranged similarly
to the distribution of e-vector directions in the sky. Of course, the match between
receptor array and e-vector array cannot be complete, because the latter changes
with the height of the sun (Fig. 1B,C), whereas the former is hard-wired and stays
in place.

The reader may wonder why I have called this matched filter, the spatial array of
second-order analysers, a third-order analyser. This will become apparent when
we now turn to the question of how the insect navigator uses its matched
polarization filter, or – in more poetic terms – how it reads its celestial map.

Reading the map: scanning the sky

Imagine a very simple method by which the insect could use its matched
polarization filter to determine the symmetry plane of the celestial pattern. In
Fig. 8A the matched polarization filter is portrayed at the inner circle (see also
Fig. 3), and the celestial e-vector pattern at the outer circle of the figure. Now
assume that the insect scans the sky, i.e. rotates about its vertical body axis. The
maximum overall response, summed over all second-order analysers of the POL
area, occurs whenever the animal is aligned with the symmetry plane of the sky.
This is because the array of second-order analysers in the eye matches, on average,
the array of e-vectors in the sky. Further, assume that the entire array of second-
order analysers projects onto a common underlying interneurone. Maximum
responses of this integrative interneurone would tell the animal that it is aligned
not with an individual e-vector direction (as is the case with the first- and second-
order analysers), but with the symmetry plane of the whole pattern.

As the symmetry plane of the skylight pattern includes two compass cues, the
solar meridian and the antisolar meridian, there is still a 180° ambiguity to be

Anterior

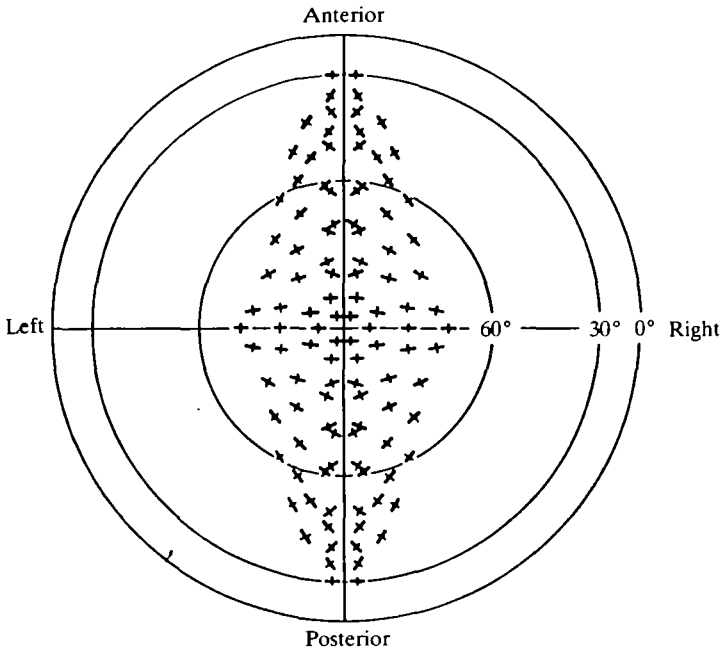Left ———————————————————— 60° ——— 30° 0° Right

Posterior

Fig. 7. Generalized schematic representation of the insect's compound polarization filter. Directions of view of the individual sampling stations (ommatidia) of the POL area. The directions of view, as shown here in a zenith projection of the dorsal visual hemisphere, were determined ophthalmologically by exploiting the phenomenon of the antidromic pseudopupil. In addition, for each sampling station the microvillar directions of the 'crossed analysers' (see Fig. 4, upper figure) were determined neuroanatomically. Data refer to *Cataglyphis bicolor*. The POL areas of the left and right eye see contralaterally. Note that the figure depicts the distribution of the visual axes of the ommatidia, not the entire fields of view of the POL areas. The latter are much larger than the area indicated by the analyser symbols in the figure because the ommatidia of the POL area exhibit rather wide acceptance angles (Labhart, 1980, 1986). Further note that a complete correspondence of the array of analysers, as shown here, and the e-vector map, as determined behaviourally, is not necessary, because neural convergence and divergence will certainly modify the outputs of the retinal array.

solved. This can be accomplished by referring, in addition, to spectral information in the sky (for behavioural evidence see below) and by sampling the anterior and posterior parts of the POL area separately (for physiological evidence see below).

By scanning the sky, i.e. sweeping its matched polarization filter across the celestial e-vector pattern, the animal translates the *spatial* information provided by the e-vector pattern into *temporal* modulations of neuronal responses. The array of second-order analysers and the integrating neurone can be regarded as a third-order analyser, transferring information from the spatial domain to the temporal.

How can we prove that the insect scans the sky and reads the output of its third-order analyser to determine the position of the sun?
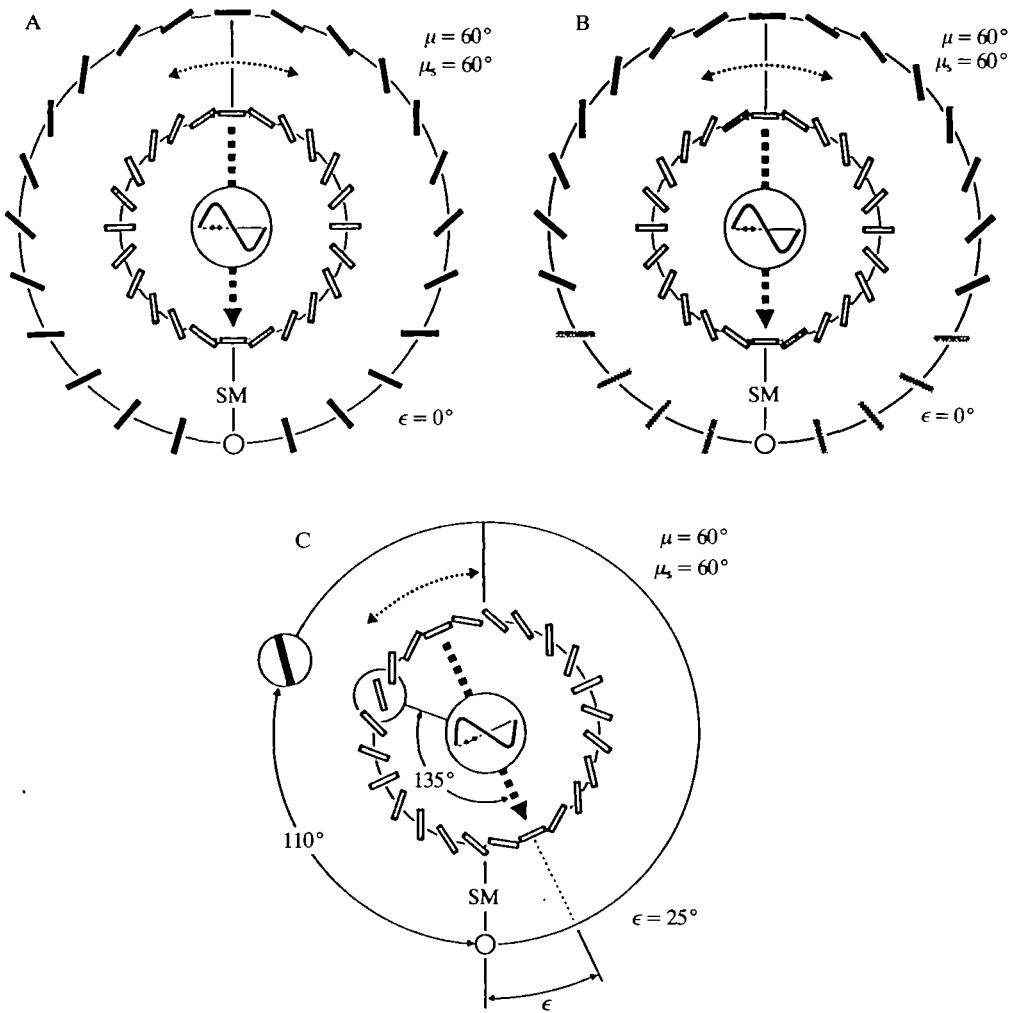
Fig. 8. Scanning model. Inner circle, schematic representation of the compound polarization filter (matched filter). Outer circle, (A,B) full e-vector gradients, (C) individual e-vector direction ($\chi = 50°$), all shown for an elevation of $\mu = 60°$ above the horizon. The elevation of the sun (μ_s) is either 24° or 60°. Note in B that the skylight regions around the sun exhibit low degrees of polarization. The grey bars mark those positions in the sky in which the degree of polarization is less than 0·1 and thus below the bee's perceptual threshold (von Frisch, 1965). The hatched heavy line and the dotted double arrow indicate the insect's longitudinal body axis and the insect's scanning movements, respectively. In the centre of all figures the time course of the output response of the compound polarization filter is shown. ϵ, error angle as observed in behavioural experiments. SM, solar meridian. For an explanation of the scanning process see text. Note that for the full argument to hold, the entire POL area rather than only an individual parallel of altitude must be considered.

First, all the behavioural experiments described so far are consistent with this hypothesis. Consider, for example, the extreme case in which the insect, during the testing phase of the experiment, is provided with nothing but an individual e-vector. In Fig. 8C the direction of this e-vector is $+50°$. At the elevation of the point observed and at the elevation of the sun during the time of the experiment, this e-vector direction is located $110°$ to the right of the solar meridian. The corresponding $50°$ analyser, however, is located $135°$ rather than $110°$ to the right of the insect's forward direction. Thus, a match is achieved only when the animal deviates by $25°$ to the left of the solar meridian. When the animal is oriented that way, the hypothetical sampling neurone exhibits maximum responses, and the animal 'thinks' that it is aligned with the solar meridian. (The $180°$ ambiguity is not considered here.) This false localization of the solar meridian must lead to navigational errors – in this case to an error of $25°$ – when the animal finally sets its compass course. These error angles are exactly the ones we had initially observed and from which the spatial structure of the insect's e-vector compass had been derived in the first place.

Now consider the more natural case in which the insect is presented with large parts of the natural blue sky containing many different e-vector directions. As predicted, even in this case navigational errors occur. More importantly, the errors induced by the experimental procedure are exactly as large as the arithmetic mean of the errors due to each individual e-vector alone (Rossel & Wehner, 1984a; Wehner & Rossel, 1985). This finding is consistent with the hypothesis that the insect sweeps its matched polarization filter across the sky and samples the peak responses induced by the array of e-vector directions within the skylight window. In this respect, one type of experiment is especially convincing. Substantial experimental errors occur when a large skylight window is displayed to the left (or the right) of the celestial symmetry plane, but none are observed when a window of exactly the same size and shape is centred on the symmetry plane (Wehner, 1983b). The answer is now clear. As the e-vector patterns in the left and right celestial hemispheres are mirror-images of each other (Fig. 1B,C), the error angles induced by e-vectors in the left and right half of the sky are equal in amount, but opposite in sign, and thus cancel each other out. This is also the reason why no navigational errors occur when a full ($360°$) e-vector gradient is displayed (Fig. 8A).

Second, there is a more telling way of confirming the hypothesis. Indirect evidence based on consistency of hypothesis and experiment is good as far as it goes, but it does not provide direct proof. Such proof could be obtained if the most fundamental prediction of the model, namely that the insect translates spatial e-vector information into temporal modulations of a proper neural signal, were tested rigorously by trying to fool the insect into taking an *unpolarized* stimulus whose intensity oscillates with time for a polarized stimulus of a certain e-vector direction. In practice, an experiment should be designed in which the compound polarization filter is stimulated by a patch of unpolarized light whose intensity is time-modulated as the insect engages in its scanning movements. The hypothesis'

then predicts that the insect interprets the time-modulated, but unpolarized, light stimulus as a particular e-vector direction, and that the direction of this erroneously perceived e-vector, and the azimuthal position associated with it, is determined by the particular part of the retina that produces the largest responses to the unpolarized beam of light.

Of course, this is more easily said than done, but it *has* been done. For experimental design, details and precautions (e.g. the way in which only one type of first-order analyser was stimulated in the bee's eyes) the reader is referred to the full description of this crucial experiment performed in honeybees (Rossel & Wehner, 1986, 1987). Here it might suffice to say that the source of unpolarized light was time-modulated in such a way that it reached peak intensities whenever a predetermined part of the bee's compound polarization filter was stimulated. Under these experimental conditions one expects the bee to orient exactly as it would when presented with the appropriate e-vector rather than the unpolarized stimulus. In all cases, this expectation was fully met.

Third, does the proposed *final common interneurone* of the matched polarization filter indeed exist? It most probably does. Labhart (1988) in our laboratory has recently recorded, in the cricket, from three types of interneurones (A,B,C) that sample the outputs of the frontal, lateral and caudal part of the POL area, respectively. Although the details of the neural machinery have still to be worked out, this should not distract from the charming simplicity by which evolution has designed a hierarchical system of first-, second- and third-order analysers to solve the polarization compass problem: by translating the spatial information inherent in the skylight patterns into temporal modulations of the output signal of a matched filter. Consequently, 'polarization' does not provide an exotic new dimension of the insect's perceptual space as hitherto assumed.

Parallel coding

Coding of spectral and e-vector information

As mentioned above, the celestial hemisphere displays not only e-vector gradients, but also coarse spectral gradients. Bees (Edrich *et al.* 1979; Brines & Gould, 1979; Rossel & Wehner, 1984*b*; Wehner & Rossel, 1985) and ants (Wehner, 1982) can derive at least some compass information from these spectral gradients as well. For example, when bees are prevented from using their e-vector compass, they orient rather well when they are presented with a full celestial colour gradient that includes the solar and the antisolar meridian (Rossel & Wehner, 1984*b*). However, when only a small part of the sky is available, spectral cues are used only to discriminate between sun and sky: a long-wavelength stimulus is taken for the sun, whereas a short-wavelength stimulus is expected to lie anywhere within the antisolar half of the sky (Fig. 9; Rossel & Wehner, 1984*b*). The sun stimulates predominantly the bee's green receptors, the sky the ultraviolet receptors. Under natural conditions, spectral gradients can also be useful in discriminating between the solar and the antisolar meridian.
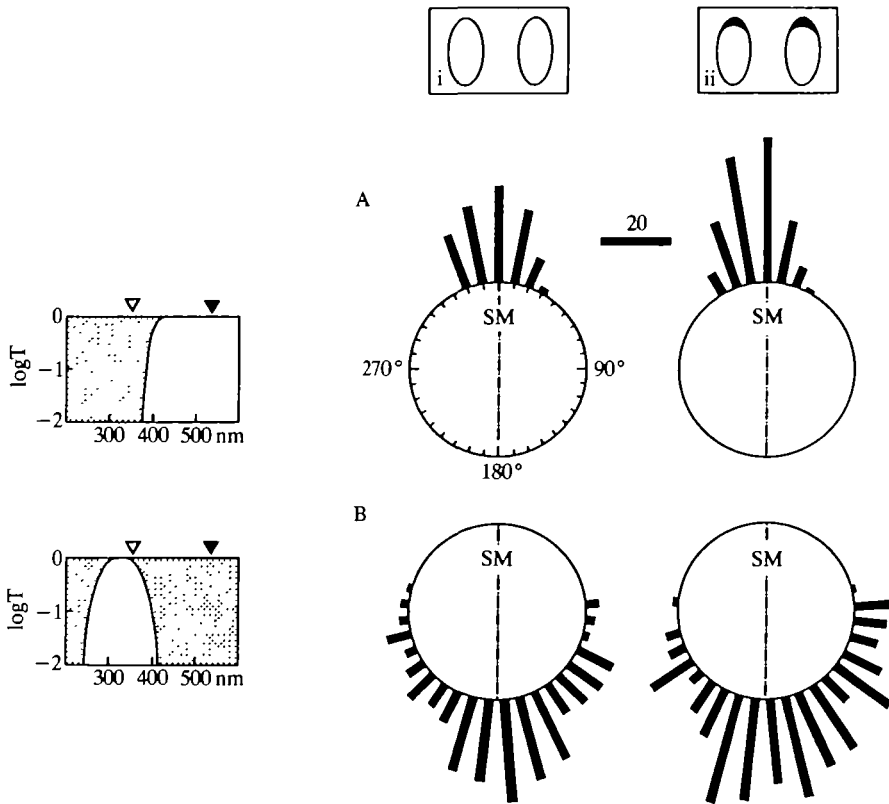
Fig. 9. Use of spectral information. Bees are presented with an unpolarized beam of green (A) or ultraviolet light (B). Diameter of stimulus 10°. For spectral composition of stimuli see left inset figures (T, transmission; the open and filled arrowheads indicate λ_{max} values of the bee's ultraviolet and green receptor, respectively). The data are plotted so as to indicate in what azimuthal position the bees expect the stimulus to occur in the sky. i, Eyes of experimental animals unobscured; ii, POL areas covered by opaque paint. (Combined from Rossel & Wehner, 1984b, and Wehner & Rossel, 1985.) SM, solar meridian.

For our purposes, it is important to note that e-vector information and spectral information are picked up by different parts of the bee's and ant's retina: e-vectors by the small POL area at the dorsal margin of the eye, and spectral information by the dorsal retina. When the POL areas of both eyes are covered with opaque paint, the ability to use spectral information is not at all impaired. However, when the entire dorsal halves of the two eyes are occluded, celestial navigation breaks down completely (Wehner, 1982; Fent, 1985). In conclusion, in the hymenopteran eye different parts of the retina are specialized for detecting and using different kinds of skylight information.

Sun compass and e-vector compass

The insect's use of sun and polarization (e-vector) compasses can be disen

tangled experimentally in a number of ways. On the one hand, the insect is prevented from using its polarization compass whenever ultraviolet radiation is excluded from the celestial stimuli (see inset of Fig. 9), or when the POL area of the eye is occluded, but the remainder of the dorsal retina left open. On the other, the sun compass cannot be used by the insect when the sun and the surrounding parts of the sky are screened off (Wehner, 1982; Wehner & Rossel, 1985). The latter precaution is necessary because the insect is able to determine the sun's position from surrounding intensity gradients (Lanfranconi, 1982).

As one can already conclude from these experimental procedures, the sun and the polarization compass use different input channels: the dorsal retina and the POL (dorsal rim) area, respectively. That the dorsal retina is the input station of the sun compass is in accord with the finding, mentioned in the previous section, that spectral information provided by the sky is picked up by the dorsal retina as well. This is because the sun is part of the spectral skylight gradient: it is that point in the sky that exhibits the highest relative amount of long-wavelength radiation. Furthermore, the information provided by both input channels does not seem to converge at a peripheral level. When ants are trained under conditions in which they can use both the sun and the polarization compass, i.e. when they are presented with the unobscured celestial hemisphere, they obtain compass information nearly exclusively through their polarization channel. (For simple geometrical reasons the polarization compass allows for much higher accuracy in reading the compass scale than the sun compass does.) This can be demonstrated by later confronting the ants with either sun or e-vector information. They orient well only in the latter case; in the former they exhibit widely scattered navigational courses. Apparently, they encounter extreme difficulties in transferring information obtained by one compass system to the other. However, when they are forced to use the sun rather then the polarization compass during both training and testing, they again orient well (M. Müller & R. Wehner, in preparation).

There is yet another experiment demonstrating that the sun and the polarization compass represent separate information channels. Full interocular transfer occurs when the ants use their polarization compass (they are oriented as well when tested with the naive eye as when tested with the trained eye; Wehner & Müller, 1985), but there is no interocular transfer at all when the ants use sun compass information.

What I have described in this chapter is the minimum performance of the insect's e-vector-detecting system, as it has been unravelled by our previous work. We have no data yet about how the insect, after having determined the spatial position of the solar meridian, finally sets its compass course. Thus, it would be premature to exclude any other information the insect could gain from celestial e-vector patterns.

Conclusions and implications

It is almost a truism that sensory systems have been shaped, during the course of

evolution, by the specific sensory needs a particular species has to fulfil. What is not a truism, however, and not understood well at all, is how *directly* the animal fulfils its sensory needs. In principle, it could indiscriminately pick up all information available in its surroundings, feed it into a central processing unit, and then compute whatever aspect of its sensory world is important at any one moment. In reality, however, the brain, especially that of a small animal such as an insect, does not seem to work in that way. Selective and adaptive specializations begin at the very periphery of the nervous system. In fact, I would now like to argue that in the insect nervous system it is the periphery rather than the central circuitry that is adapted most intricately to the specific behavioural tasks to be solved.

Conclusions

The adaptation of peripheral circuitry is exemplified most strikingly by the hymenopteran e-vector compass. First, only one spectral type of receptor, the ultraviolet, is plugged into the more central parts of the compass system. In the ant's POL area there are three times as many ultraviolet receptors per ommatidium as in the remainder of the eye, and the ultraviolet receptors of the POL area exhibit the highest polarization sensitivities of all photoreceptors of bees and ants (Table 1). In terms of their adaptive significance, these functional properties of the system make a lot of sense. With increasing angular distance from the sun, skylight is increasingly dominated by short-wavelength radiation, and the parts of the sky that exhibit the highest degree of polarization also exhibit the most saturated ultraviolet tinge. Thus, a fundamental physical aspect of light scattering within the earth's atmosphere has been incorporated into the insect's compass system. It is also very likely indeed that ultraviolet receptors evolved originally as a means of detecting skylight rather than for extending the spectral range of the insect's colour vision system (Wehner, 1982).

Second, the design of the POL area of the retina reflects not only the spectral, but also the spatial properties of the celestial e-vector patterns. The polarization analysers are spatially arranged in a way that mimics, on average, the distribution of e-vectors in the sky. In other words, the navigating insect employs a compound polarization filter that is matched, in its spatial properties, to the external pattern of polarization. The match is by necessity incomplete, because the static array of analysers cannot match all possible versions of the dynamic pattern of polarization. However, in its natural world, when the insect is not at the mercy of an inquisitive experimenter, it is not severely handicapped by this incompleteness of the match.

At this stage of the argument – and with the matched filter well established – the developmental biologist will certainly address an important question. How is it possible that the spatial array of analyser directions is laid down during the ontogenetic development of the insect's retina in the way predicted by the skylight pattern? The immediate answer is that this is not as horrendous an undertaking as it may sound. Within the POL area the individual (second-order) analyser
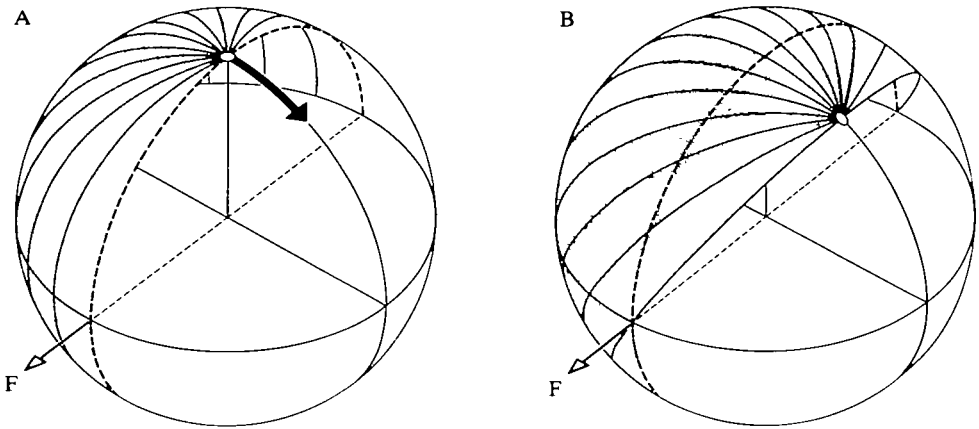
Fig. 10. Geometrical design of the distribution of analyser directions within the bee's and ant's compound eye. The analyser directions (i.e. the microvillar directions of photoreceptors nos 1 and 5) run parallel to the meridians of the compound eye. These meridians are projected out into visual space (sphere). The open arrow marks the animal's forward direction (F), the disc marks the pole of the retinal array of receptors. (A) The visual field of the right eye is restricted to the ipsilateral side (light grey shading); (B) it extends to the contralateral side, as is the case in the real eye. The shaded area looking contralaterally symbolizes the insect's POL area. (From Wehner, 1987.)

directions run parallel to the meridians of the compound eye, and all these meridians converge at the pole of the retinal system of coordinates, at the uppermost dorsal margin of the eye. As this pole, and with it the entire POL area, sees contralaterally (Fig. 10), a situation is created in which the polarization analysers are spatially related to their pole, namely the uppermost dorsal ommatidium, in the very same way that the celestial e-vectors are geometrically related to their pole, the position of the sun. Had it not been for this more-or-less automatic correspondence between the internal (analyser) pattern and the external (e-vector) pattern, the insect's e-vector compass might never have evolved. Generally speaking, this is a striking example of the inherently opportunistic way in which natural selection works.

Implications

What are the more general implications of our findings and inferences? Let me make five points. First, the insect has dissected the problem of celestial navigation into several digestible bits, which can be shaped by natural selection more-or-less separately. It has evolved, probably step by step, a hierarchy of polarization analysers for the sole purpose of determining the symmetry plane of the sky, and then it uses other visual subsystems to set its final compass course (*stepwise coding*).

Second, the insect does not go back to first principles and solve the problem by performing a number of abstract computations in some kind of central processing
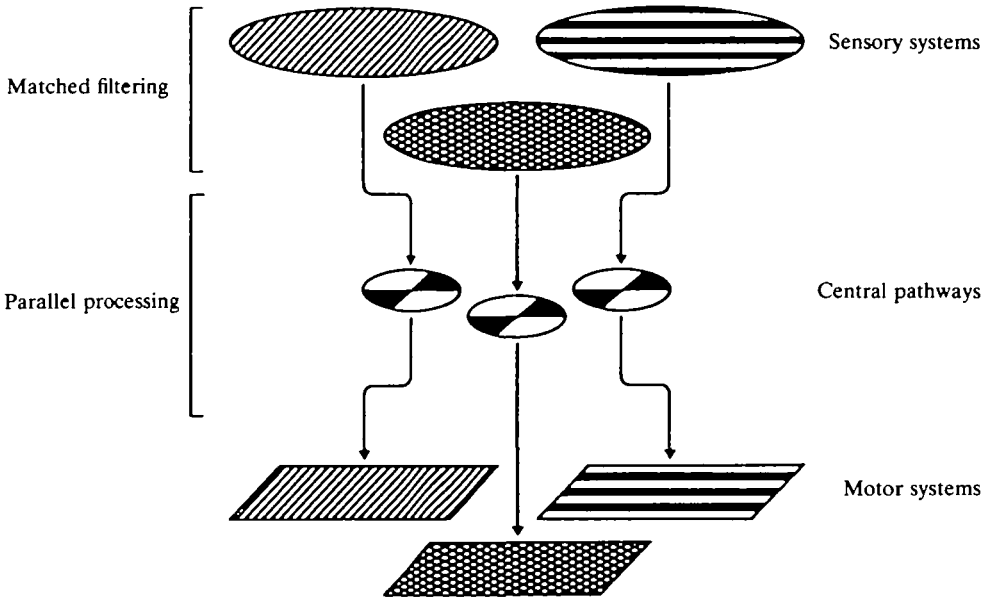
Fig. 11. Schematic representation of the general view entertained in this chapter: sensory coding in small brains relies heavily on matched filtering and parallel processing. For the sake of perspective, this point is overstated in the figure. Furthermore, in this chapter, experimental evidence is provided only for the sensory (input) side of the scheme.

unit. Its trick is to incorporate the fundamental spatial properties of the navigational problem into the very periphery of its nervous system, into the spatial design of its sensory surface, and then to rely on rather simple circuitry to further process the output of the specialized sensory surface. It is the periphery which solves the tricky part of the problem, and there algebra gives way to geometry (*peripheral coding: decentralized processing*).

Third, using a specialized sensory surface, a 'matched filter', implies that coding is restrictive. Viewing the world through a matched filter severely limits the amount of information the brain can pick up from the external world, and restricts it to particular aspects of that world, but it frees the brain from the need to perform more intricate computations (*matched filtering: restrictive coding*).

Fourth, the subsequent stages of central processing can rely on rather simple decision rules. To determine the symmetry plane of the sky, all a central processor has to do is to determine when, during a scanning cycle, a particular interneurone fires maximally. Hence, the central pathways need not be particularly specialized. Circuits which have already evolved for other purposes can be used. If, at least in small brains, the hallmark of peripheral systems is specificity, then the hallmark of the central circuitry is redundancy (Fig. 11). This principle of sensory coding implies that the peripheral networks exhibit higher evolutionary plasticity than the more central ones, and this is indeed what one observes. For example, in the

regressive evolution of the visual systems of subterranean driver ants the peripheral layers of the visual system are the ones that are degraded first (Werringloer, 1932). Peripheral coding, as described here for the level of multicellular networks, is analogous to what happens at the cellular and molecular level. Membrane-bound receptor molecules are specific for particular molecular signals, but the subsequent stages of information processing – signal-coupling G-proteins and cytoplasmatic second messengers – are common final pathways (*central processing: using common circuitry*).

Fifth, matched filtering solves only a limited part of the problem. The POL area determines the symmetry plane of the sky and nothing else. Other visual subsystems must be used to discriminate between the solar and the antisolar meridian, and finally to set the proper compass course (*parallel processing*).

Seen in this light, parallel processing is more-or-less necessarily associated with matched peripheral filtering. Hence, small brains are modular brains in the extreme. The longer I work with my favourite experimental animals, the long-legged, high-speed desert ants, the more I come to believe that *Cataglyphis* is just a massively parallel small computer running about in the desert.

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