Neural mechanisms in insect navigation: polarization compass and odometer
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Insect navigation relies on path integration, a procedure by which information about compass bearings pursued and distances travelled are combined to calculate position. Three neural levels of the polarization compass, which uses the polarization of skylight as a reference, have been analyzed in orthopteran insects. A group of dorsally directed, highly specialized ommatidia serve as polarization sensors. Polarization-opponent neurons in the optic lobe condition the polarization signal by removing unreliable and irrelevant components of the celestial stimulus. Neurons found in the central complex of the brain possibly represent elements of the compass output. The odometer for measuring travelling distances in honeybees relies on optic flow experienced during flight, whereas desert ants most probably use proprioceptive cues.

Introduction
Social insects, such as honeybees and desert ants, are known for their exquisite homing abilities [1–3]. To find their way during foraging excursions that lead them through an unknown or unstructured environment, they cannot rely on landmarks but use a navigation procedure called path integration: by constantly keeping track of compass bearings pursued and distances travelled, the insects are informed about their position relative to the nest at all times. The mechanisms by which compass and distance information are accumulated to accomplish path integration have been reviewed recently [4–6]. This review focuses on recent findings on the mechanisms underlying the two measuring instruments on which path integration relies: the compass for measuring directions, and the odometer for measuring distances.

Apart from the sun [7] and the spectral gradients in the sky [8], skylight polarization offers insects a useful reference for a visual compass, which can be used for navigation involving path integration or just for keeping a course during the journey. As a result of sunlight scattering in the atmosphere, skylight is partially plane-polarized, and the prevailing oscillation plane (e-vector orientation) is oriented orthogonal to an imaginary straight line connecting the observed point in the sky to the sun (Figure 1a).

Specialized detectors for polarized skylight in the insect retina
The microvillar photoreceptors of arthropods are inherently polarization-sensitive. This is because the visual pigment molecules are aligned within the microvilli membrane in such a way that plane-polarized light is maximally absorbed when the e-vector is parallel to the microvilli axis [9–11]. However, the high microvillar polarization sensitivity (PS) is available to the photoreceptor as a whole only when the microvilli are well aligned along the rhabdomere (the light-sensitive part of the receptor formed by a stack of microvilli) and so avoid randomizing effects, and when the rhabdomere is reasonably short and so avoids self-screening [12,13].

The detection of polarized skylight in insects is mediated through the ommatidia of just a small part of the compound eye, the dorsal rim area (DRA), which is dedicated exclusively to this task. The ommatidia of the DRA are specialized in ways that make them especially suitable for polarization vision. First, as suggested by its position, the DRA is directed upwards and mainly to the contralateral side. Second, in each ommatidium, the photoreceptors come in two sets that have their microvilli oriented at about 90° to each other, that is, the receptors are tuned to mutually orthogonal e-vectors subserving polarization-antagonism (see below). Third, the microvilli are well aligned along the rhabdomere and consequently the photoreceptors exhibit a high PS. Fourth and finally, in many insects, the optical properties of the ommatidia are degraded in a way that significantly increases the visual field of the DRA ommatidia. Thus, the cornea can contain light-scattering structures; the screening pigment or the tracheal sheath, that normally shield the ommatidia from each other, are missing or reduced; and/or there is a mismatch in focal length. These four features were found in the DRAs of many species from different insect orders, including odonates, orthopterans, coleopterans, hymenopterans, lepidopterans and dipterans (for a typical example of a DRA see Figures 1b and 2a) [14,15,16]. In the regular ommatidia of most insect eyes (ommatidia that do not belong to the DRA), PS is comparatively weak, because of misalignment of the microvilli [13,17,18]. In the honeybee eye, PS is almost completely lost, because the ommatidia are twisted by 180° [12,19]. This is probably because it avoids the perception of false colors when the bee views shiny, and thus partially polarizing, objects [20].

An interesting parallel to the insect DRA has developed in the simple lens eyes of spiders. In lycosid spiders, the

**Abbreviations**
- DRA: dorsal rim area
- PS: polarization sensitivity

**References**

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ventral-most, skywards-directed part of the principal eyes contains two types of photoreceptor with mutually orthogonal microvilli, and the receptors lack screening pigment. The gnaphosid spider *Drassodes* devotes at least one full pair of secondary eyes to polarization vision. Of these, the dorsally directed, posterio-median eyes lack a refracting lens. Each eye is dominated by photoreceptors with the same microvilli orientation, but because the two eyes are oriented orthogonal to each other, in combination they exhibit the familiar pattern of mutually orthogonal microvilli orientation. A speciality of this polarization detector is a tapetum underlying the receptor layer that boosts PS by acting as a reflecting polarizer (Figure 3; \[21••,22•\]).

In summary, arthropod polarization detector organs consist of specialized dorsally directed, strongly polarization-sensitive photoreceptors, often with large visual fields. A special characteristic is the presence of two populations of receptors that are tuned to 90° different e-vectors.

**Polarization-sensitive neurons: the orthopteran case**

How are signals from the polarization-sensitive photoreceptors evaluated to inform the insect about its compass bearing? Although most behavioral studies on the polarization compass have been performed in bees and ants [2,8,23], for technical reasons most electrophysiological data are from orthopteran insects.

**POL-neurons in the cricket optic lobe: signal conditioning**

In the cricket optic lobe, several morphological types of polarization-sensitive neurons (POL-neurons) have been recorded. Although they seem to have similar physiological properties, only one of them could be studied in detail \[24•\]. The POL1-neurons are commissural neurons with dendritic arborizations in the ipsilateral dorsal medulla and axonal projections to the contralateral medulla \[24•,25\]. Spiking activity is a sinusoidal function of e-vector orientation with alternating parts of excitation and inhibition and with the maxima and minima separated by 90° (Figure 1c). Thus, these neurons have a polarization-opponent characteristic, receiving antagonistic input from two analyzer channels with orthogonal orientations of maximal sensitivity [26]. The two analyzer channels are represented by the two sets of photoreceptors with mutually orthogonal microvilli present in each DRA ommatidium (Figure 1b). The polarization-antagonism has two important effects: it enhances e-vector contrast, which allows the neurons to respond to very low degrees of polarization (Figure 1c; \[27\]); and it makes the system insensitive to the variations of absolute light level [25], that is, the neurons act as differential polarization detectors.

The visual fields of POL1-neurons are directed about 25° contralaterally to the upper part of the sky and are very wide (>60°). This is the result of both optical integration by the large-field DRA photoreceptors (acceptance angle...
about 20°) and neural integration by the POL1-neurons, which collect input from some 200 DRA ommatidia [28,29•]. The e-vector to which a neuron is tuned is independent of the position of a polarized stimulus [24•,29•]. This spatial integration has two important functions: first, by integrating over a large area of sky, the neurons act as spatial low-pass filters and become insensitive to disturbances of the polarization pattern by clouds or terrestrial objects [30]. Second, both optical and neural integration enhance absolute sensitivity to a degree that crickets could in principle exploit the polarization of the moon-lit night sky [31,32].

Thus, POL-neurons in the optic lobe have important filtering properties that remove unreliable and irrelevant features from the celestial stimulus; that is, they condition the polarization signal for further processing. This enables the system to work under vastly different light intensities, degrees of polarization and sky visibility. There are three types of POL1-neuron tuned to different e-vectors, orientated approximately 10°, 60° and 130° relative to the length-axis of the head (Figure 2b; [24*,29*]). Each of them collects input from DRA ommatidia of approximately matching orientations (compare (a)).

**POL-neurons in the locust central brain: e-vector coding?**

Recordings from the central complex of the locust brain revealed PS in certain types of tangential neurons (TL1, TL2, TL3) and columnar neurons (CP1, CP2, CPU1) [33,34•]. The tangential neurons project from the lateral triangle to different layers of the lower division of the central body, whereas the columnar neurons connect individual columns of the central complex and project to the lateral triangle. Like the optic lobe POL-neurons of crickets, these neurons are spontaneously active and show polarization-opponent properties. However, the central complex neurons differ in two important aspects: the e-vector tuning axes are not grouped in particular classes (Figure 2c; [34*]); and some of the central complex neurons receive bilateral input, that is, they can be stimulated...
through either eye and the tuning e-vector was (with one exception) the same for both eyes. The visual fields as measured in some columnar neurons were >90° in diameter [33,34*]. We shall consider the significance of central complex POL-neurons below.

In transmitting e-vector information from the optic lobe to the central brain, the anterior optic tubercle (AOT) seems to serve as a relay station [35,36]. In addition, both the contralateral projection of the POL1-neurons and the bilateral projection of polarization-sensitive AOT-neurons suggest extensive bilateral exchange of information [25,36].

A neural model for a polarization compass
The signals of three differently tuned polarization-sensitive light sensors unambiguously define the e-vector of a stimulus [37]. Thus, by evaluating the signals of the three tuning types of POL1-neurons, a cricket could in principle determine the e-vector within the common visual fields of the neurons. Using this e-vector as a compass reference is difficult, however, because the visual fields of the POL1-neurons are eccentric with respect to the zenith and, thus, their activity depends on both solar azimuth and elevation (Figure 1a). By pooling the responses of corresponding tuning types of POL1-neuron of the left and the right optic lobe, as in fact observed in the locust central complex neurons [33,34*], the system becomes zenith-centered, and the mean zenithal e-vector (integrated within the visual field) is always orthogonal to the solar azimuth (Figure 1a).

There are mathematical procedures for extracting e-vector orientation from the pooled POL-neuron signals, some of which were successfully used in the polarization compass of robots [38–40]. However, these procedures did not take into account the constraints of actual neural circuits, and neural implementations were not proposed. In the rat brain, a set of neurons called head direction cells was found. Each neuron is active only when the rat’s head points in a certain direction with respect to its cage environment [41]. Could body orientation relative to the celestial e-vector be mapped in a similar way in the insect brain? We are presently testing a simple neural network consisting of just 21 neurons that uses only well-known neuronal operations. The input of the network consists of the pooled POL1-neurons, the output layer contains an array of narrowly tuned ‘compass neurons’ [42–45] each representing a certain body orientation. Preliminary simulations show that the network evaluates the POL-neuron signals just as well as a mathematical algorithm. With their large range of e-vector preferences (Figure 2c), the central complex POL-neurons are candidates for compass neurons, indicating different body orientations with their activity maxima. However, their activity is not restricted to a small e-vector range but they show the same polarization-antagonism as the optic lobe POL-neurons.

Polarization-sensitive neurons in other insects
Although the presence of polarization-opponent neurons was also demonstrated in the desert ant Cataglyphis, physiological details are not yet available [46]. In contrast to
orthopterans, the visual fields of DRA ommatidia are narrow and, owing to the strict fan-arrangement, each part of the sky is viewed by differently oriented ommatidia, so that a gradient of e-vector tuning directions within the visual field of a POL-neuron is expected [46]. This might indicate that crickets and ants use different strategies to gain directional information from the polarization pattern. Several types of optic lobe POL-neurons in crickets, locusts and cockroaches exhibit arborizations in the accessory medulla [24•,25,47,48], a small neuropil in the optic lobe regarded as the circadian pacemaker in insects [49].

Two possible functions of these projections have been proposed: skylight polarization could assist in setting the clock, or the clock might provide information for time compensation necessary for a celestial compass [48].

**Measuring travelling distance: the odometer**

A few years ago it became clear that for bees the primary cue of distance estimation is self-induced optic flow. Interestingly, flight distance is not perceived in absolute units but as the total amount of image motion experienced during flight time [50,51]. Forager bees communicate the location of a nectar source to their hive mates by the waggle dance: the longer the duration of one waggle, the further the indicated goal [2]. Because the extent of image motion in the eye depends on the distance of objects passed during flight, the calibration of waggle duration versus distance is variable even for one hive, that is, it is a function of the actual visual environment [52••,53•]. In contrast, the calibration of waggle duration versus amount of image motion in the eye seems to be a natural constant and independent of object density, flight speed or wind conditions: 1 ms of waggle duration corresponds to 17.7° of image motion in the eye [52••]. Although optic flow is a robust distance measure for bees commuting along a certain route, it is of limited use for bees exploring new terrain with unpredictable visual conditions. In this situation, bees might rely on conspicuous landmarks for resetting the odometer from time to time more than they usually would [51]. The neural basis of the optic flow meter is unknown. It is tempting to invoke the well-known optomotor system [54]. However, unlike the bee’s odometer, the output of the insects’ optomotor system is critically dependent on image speed [55].

In contrast to the situation in bees, in the ant *Cataglyphis* optic flow plays a minor role in gauging distance. Although ventral optic flow can have some influence on distance estimation, lateral image motion plays no role in the ant’s odometer [56,57]. Even if deprived of optic-flow information, *Cataglyphis* can measure travelling distances relatively well [56,57]. As the use of energy consumption was also ruled out as a cue [58,59••], idiothetic cues remain as the main source of information. The ants could either use a step counter or monitor the output of the central pattern generator for walking [59••]. The ants’ odometer must not only operate on flat terrain, as usually chosen for experiments, but also on uneven, bumpy terrain that constantly leads the ants uphill and downhill. Under these conditions, *Cataglyphis* does not measure the actual distance travelled but the
ground distance covered, that is, it takes the sum of the horizontal projections of all segments of its journey (Figure 4; [59**, 60]). Because foraging *Cataglyphis* ants often take different outbound and inbound paths [61], this strategy avoids errors in distance estimation caused by different terrain structures. To determine ground distance, the ants must measure the surface inclination constantly, and the cosine values of the readings could serve as correction factors of the odometer output. Gravity perception, and thus probably the measurement of slopes, is mediated by proprioceptors located in the joints between the ants’ body parts [60, 62].

Conclusions and outlook

The task of the peripheral elements of the polarization compass system is to provide the brain with robust e-vector input. Hence, the strong PS of DRA photoreceptors, and the differential-polarization and spatial integration properties of optic lobe POL-neurons, as shown directly by electrophysiology [26, 34*, 46] or inferred from behavioral [63] or histological studies [14*, 15, 16], these mechanisms are powerful enough to exist not only in all insect groups studied but also in spiders [21**, 22*]. The functional significance of central POL-neurons found so far [34*] is less clear, because they combine properties of peripheral POL-neurons (polarization-opponency) and the hypothetical compass neurons (many tuning classes, bilateral input). Clearly, this calls for further electrophysiological analyses of central POL-neurons. Studies based on the synthetic approach using neural networks in combination with navigating robots [30, 39, 40] might assist the analysis of the polarization compass.

Insects apparently use different sensory cues to feed their odometer, but it remains unclear why bees and ants differ in this respect. As the eyes of walking animals automatically keep a constant distance to the ground, ants would be destined to exploit ventral optic flow; nevertheless, they use proprioceptive information. The ability of desert ants to compute ground distance in hilly terrain is astonishing. It remains to be tested whether this finding is an indication for true three-dimensional path integration [59**].

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References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

* of special interest
** of outstanding interest

Describes the morphology and physiology of POL-neurons in the cricket optic lobe, including e-vector tuning, visual field properties and absolute sensitivity. On the basis of these experiments performed with small-field polarized stimuli, the response profiles of neurons with the celestial polarization pattern as stimulus were simulated using model calculations.


On the basis of histological and electrophysiological data, the paper explains the optical and neural mechanisms leading to spatial integration in POL-neurons and discusses reasons why the cricket polarization vision system has abandoned spatial resolution.


The physiology and morphology of POL-neurons in the central brain of locusts were examined by intracellular recording and dye marking. This is the first time that data on neurons representing central processing of polarized locusts were examined by intracellular recording and dye marking. This is the first time that data on neurons representing central processing of polarized light became available.


59. Wohlgemuth S, Ronacher B, Wehner R: Distance estimation in the third dimension in desert ants. J Comp Physiol (A) 2002, 188:273-281. This paper extends the navigation studies with Cataglyphis to the third dimension. The ants were trained to walk in an array of uphill and downhill channels. When tested on flat terrain, the ants indicated homing distances corresponding to the ground distances travelled (compare Figure 4). These and several carefully designed control experiments feed a thorough discussion on the nature of the ant’s odometer.


