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 proprioreceptive cues.

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Abbreviations
DRA   dorsal rim area
PS   polarization sensitivity

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

Figure 1
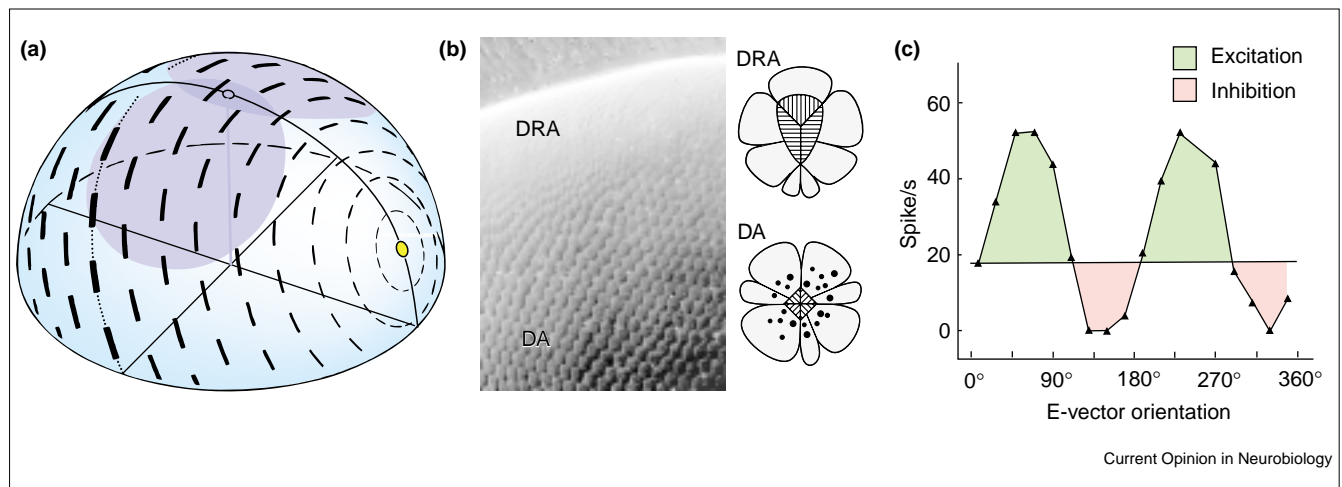
(a) Three-dimensional representation of the celestial polarization pattern for 24° elevation of the sun (yellow circle). The bars indicate e-vector orientations as observed from the center of the celestial hemisphere. Length and width of bars indicate the degree of polarization. The violet shading represents the visual fields of POL1-neurones in the optic lobe of field crickets *Gryllus campestris.* The violet areas outline roughly that part of the visual field defined by at least 25% sensitivity compared with the visual field center.
(b) Comparison between specialized ommatidia of the DRA and regular ommatidia in the adjacent dorsal area (DA) of the compound eye of the field cricket. Left: Scanning electron micrograph of the dorsal-most part of the compound eye, showing strongly reduced faceting in the cornea of the DRA. Right: Schematic representations of cross-sections through ommatidia of the DRA and the DA. DRA retinulae lack screening pigment, and the enlarged rhabdoms have a characteristic triangular or trapezoidal shape with strictly orthogonal microvilli. (c) Response of an optic lobe POL-neuron of the field cricket to the e-vector orientation of polarized light. Although the stimulus has a comparatively low degree of polarization of 19%, the neuron exhibits a strong modulation of spike frequency. Note the polarization-opponency, that is, excitation (green shading) and inhibition (red shading) depending on e-vector orientation. Adapted from [14•,27,29•].

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 photo-receptors 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

Figure 2
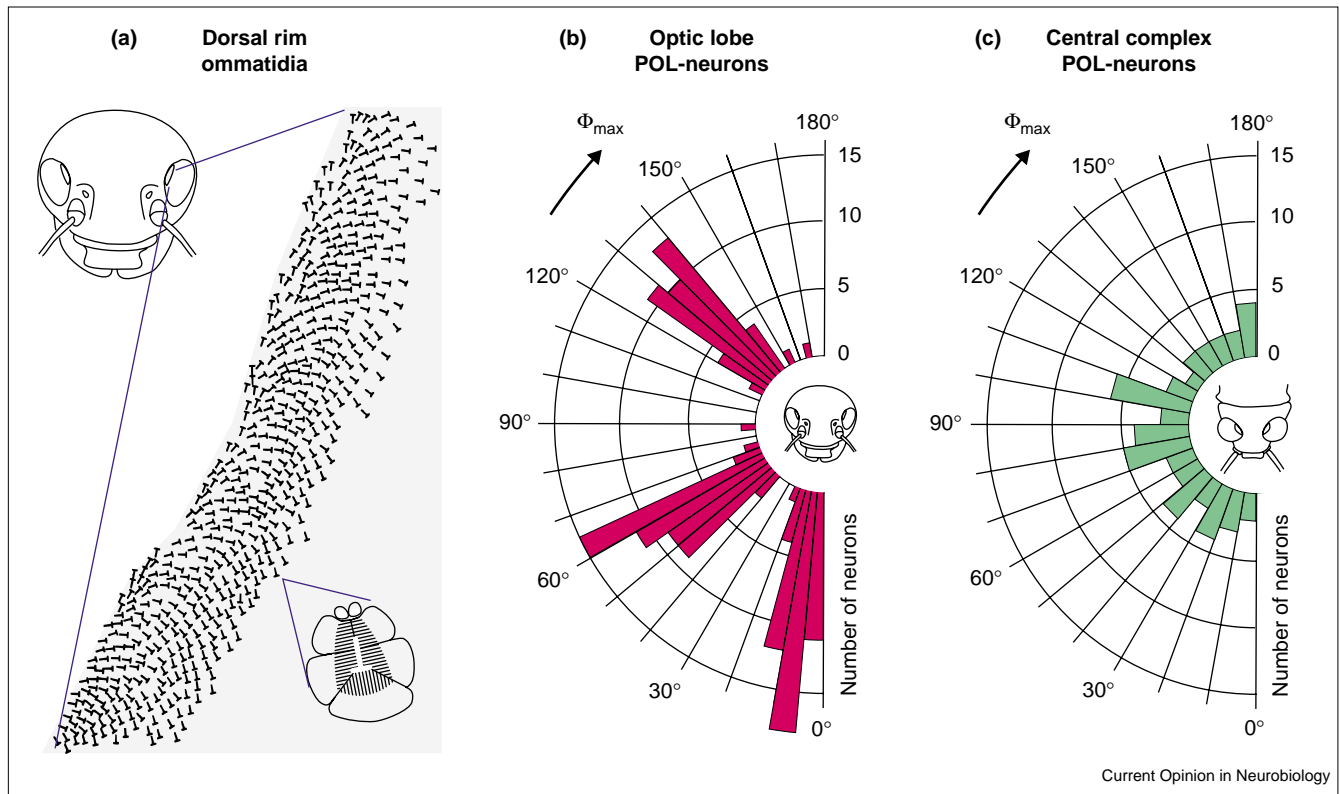
E-vector tuning of neural elements at different stages of the orthopteran e-vector detection system. **(a)** Distribution and orientation of retinulae in the DRA of a field cricket. The T symbols indicate the position and orientation of the retinulae (compare enlarged cross-section through an ommatidium at bottom right). About 65% of the whole length of the DRA is shown. Note that each section of the DRA contains differently oriented retinulae. **(b)** E-vector tuning in optic lobe POL-neurons of field crickets. Histogram of e-vectors eliciting maximal spike frequency Φ_{max}) in 142 POL1-neurons with a zenithal stimulus. Note that there are three types of POL1-neuron tuned to approximately 10°, 60° and 130° relative to the length-axis of the head. Each tuning type collects input from ommatidia of approximately matching orientations (compare (a)). **(c)** E-vector tuning in central complex POL-neurons of the locust *Schistocerca gregaria*. Histogram of e-vectors eliciting maximal spike frequency (Φ_{max}) in 51 tangential and columnar POL-neurons with a zenithal stimulus. Note that the e-vector tuning axes are not grouped in particular classes. Adapted from [29•,34•] including unpublished data from S Gebhardt and U Homberg (personal communication).

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 that are 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 [29•].

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

Figure 3
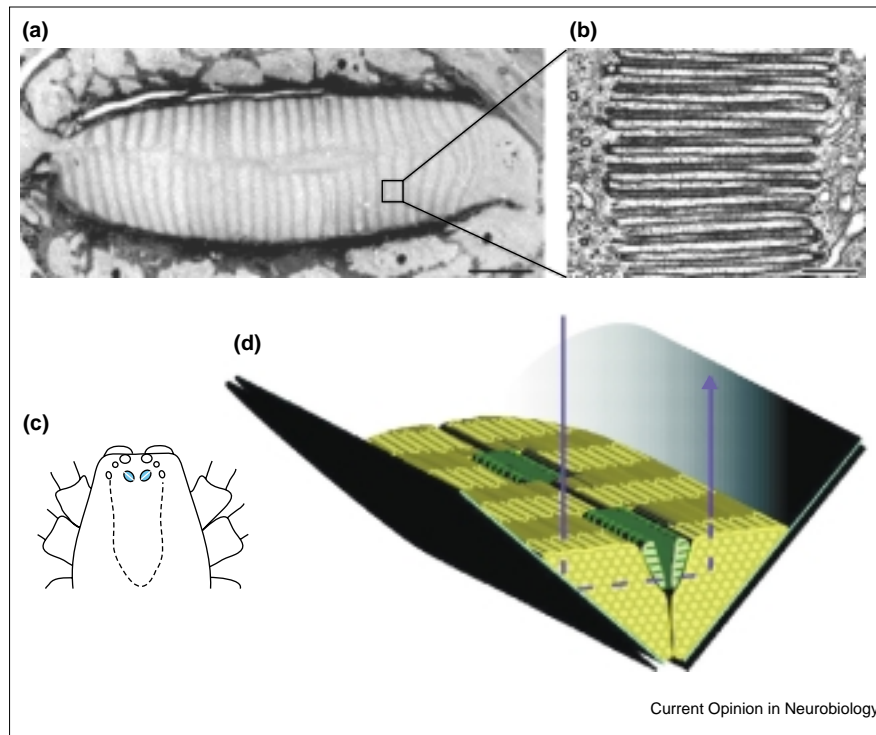
Structure of the posterio-median eyes of the spider *Drassodes cupreus*. (a)) Tangential section through the retina of an eye, revealing a regular rhabdomeric arrangement (light micrograph; scale bar 15 μm). (b) Electron micrograph of the boxed area in (a), showing the parallel microvilli arrangement found over the bigger part of the retina (scale bar 0.5 μm). (c) Position and orientation of the posterio-median eyes on the dorsal cephalothorax (in blue). Note the mutually orthogonal orientation. (d) Schematic representation of the canoe-shaped polarizing tapetum and the retina, with one possible path of light through the eye (arrow). The tapetum polarizes light such that the prevailing e-vector is parallel to the microvilli, which boosts polarization sensitivity of the photoreceptors. (a), (b) and (d) reproduced with permission from [22•].

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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

Figure 4
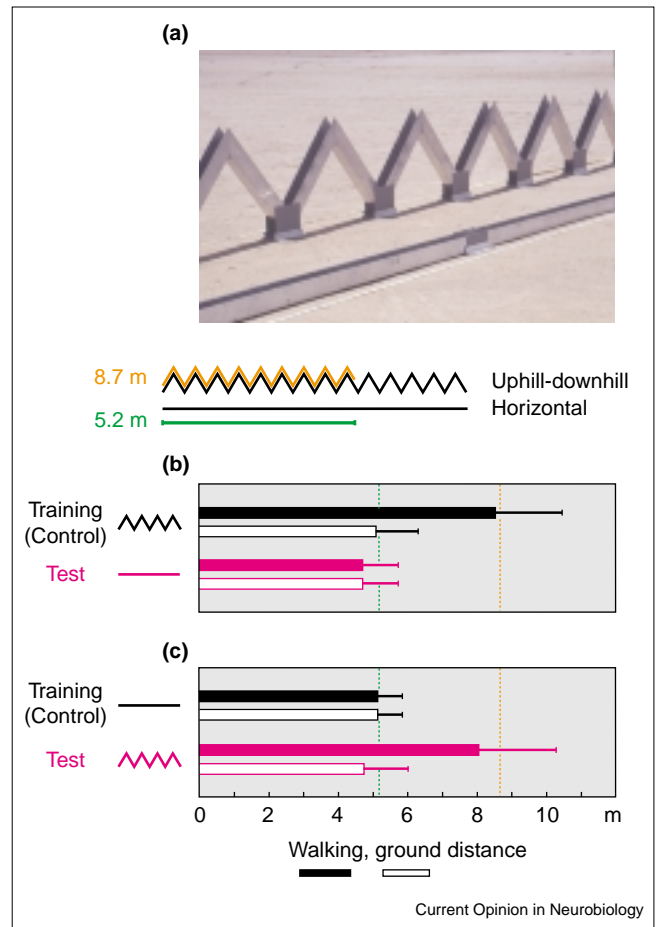
Testing the odometer of the desert ant *Cataglyphis fortis* in the third dimension. **(a)** Photograph of the uphill–downhill channel and the flat channel used to train and test the ants. **(b)** Training along an uphill–downhill path (a schematic side view is shown at the top). Ants were trained to walk over nine hills to a food source 8.7m away and were then tested either in a control channel with the same dimensions as the training channel (black) or in a horizontal (flat) test channel (red). Filled bars indicate actual walking distances in the test channels (means ± SD); open bars indicate the corresponding ground distances (in the flat channel, the two values are identical). The green dotted line indicates the expected ground distance; the orange dotted line indicates the expected walking distance. In the training control, the walking and ground distances do not differ significantly from expectations. In the horizontal test channel, the travelling distance was much shorter than the distances travelled in the hilly array (orange dotted line). Rather, the walking distance corresponded to the ground distance of the training control. Twenty-one animals were tested in both conditions. **(c)** Training in a horizontal channel (to a food source 5.2m away). The green dotted line indicates the expectation for ground and walking distance; the orange dotted line indicates the uphill–downhill walking distance that corresponds to a 5.2m walking distance in the flat channel. In the hilly test channel, the walking distance is significantly greater than in the control but the mean ground distance is not. This experiment involved 17 animals. In conclusion, the ant's odometer does not record the distance actually travelled along an uphill–downhill path, but rather the horizontal projection of that path, that is, the ground distance. Reproduced with permission from [60]; photograph courtesy of R. Wehner.

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 proprioreceptors 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 dependent signals; 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 proprioreceptive 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••].

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

1. Wehner R: **Arthropods.** In *Animal Homing.* Edited by Papi F. London: Chapman & Hall; 1992:45-144.

2. von Frisch K: *The Dance Language and Orientation of Bees.* Cambridge: Harvard University Press; 1993.

3. Wehner R: **Navigation in context: grand theories and basic means.** *J Avian Biol* 1998, **29**:370-386.

4. Collett M, Collett TS: **How do insects use path integration for their navigation?** *Biol Cybern* 2000, **83**:245-259.

5. Collett TS, Collett M: **Path integration in insects.** *Curr Opin Neurobiol* 2000, **10**:757-762.

6. Wehner R, Gallizzi K, Frei C, Vesely M: **Calibration processes in desert ant navigation: vector courses and systematic search.** *J Comp Physiol [A]* 2002, **188**:683-693.

7. Dyer FC, Dickinson JA: **Development of sun compensation by honeybees: how partially experienced bees estimate the sun's course.** *Proc Natl Acad Sci USA* 1994, **91**:4471-4474.

8. Wehner R: **The ant's celestial compass system: spectral and polarization channels.** In *Orientation and Communication in Arthropods.* Edited by Lehrer M. Basel: Birkhäuser Verlag; 1997:145-185.

9. Israelachvili JN, Wilson M: **Absorption characteristics of oriented photopigments in microvilli.** *Biol Cybern* 1976, **21**:9-15.

10. Goldsmith TH, Wehner R: **Restrictions on rotational and translational diffusion of pigment in the membranes of a rhabdomeric photoreceptor.** *J Gen Physiol* 1977, **70**:453-490.

11. Hardie RC: **Properties of photoreceptors R7 and R8 in dorsal marginal ommatidia in the compound eyes of *Musca* and *Calliphora*.** *J Comp Physiol [A]* 1984, **154**:157-165.

12. Wehner R, Bernard GD, Geiger E: **Twisted and non-twisted rhabdoms and their significance for polarization detection in the bee.** *J Comp Physiol* 1975, **104**:225-245.

13. Nilsson D, Labhart T, Meyer EP: **Photoreceptor design and optical properties affecting polarization sensitivity in ants and crickets.** *J Comp Physiol [A]* 1987, **161**:645-658.

14. Labhart T, Meyer EP: **Detectors for polarized skylight in insects: a**
• **survey of ommatidial specializations in the dorsal rim area of the compound eye.** *Microsc Res Tech* 1999, **47**:368-379.
This survey of ommatidial specializations in the DRA demonstrates that the detection of polarized skylight is a common visual function in insects. Although the DRA ommatidia are functionally similar in different insect groups, differences in ommatidial fine structure indicate that the polarization compass arose polyphyletically.

15. Dacke M, Nordström P, Scholtz CH, Warrant EJ: **A specialized dorsal rim area for polarized light detection in the compound eye of the scarab beetle *Pachysoma striatum*.** *J Comp Physiol [A]* 2002, **188**:211-216.

16. Homberg U, Paech A: **Ultrastructure and orientation of ommatidia in the dorsal rim area of the locust compound eye.** *Arthropod Struct Dev* 2002, **30**:271-280.

17. Labhart T, Hodel B, Valenzuela I: **The physiology of the cricket's compound eye with particular reference to the anatomically specialized dorsal rim area.** *J Comp Physiol [A]* 1984, **155**:289-296.

18. Labhart T: **The electrophysiology of photoreceptors in different eye regions of the desert ant, *Cataglyphis bicolor*.** *J Comp Physiol [A]* 1986, **158**:1-7.

19. Labhart T: **Specialized photoreceptors at the dorsal rim of the honeybee's compound eye: polarizational and angular sensitivity.** *J Comp Physiol* 1980, **141**:19-30.

20. Wehner R, Bernard GD: **Photoreceptor twist: a solution to the false-color problem.** *Proc Natl Acad Sci USA* 1993, **90**:4132-4135.

21. Dacke M, Nilsson D-E, Warrant EJ, Blest AD, Land MF, O'Carroll DC:
•• **Built-in polarizers form part of a compass organ in spiders.** *Nature* 1999, **401**:470-473.
This is the first time that a polarizing optical element was found in an eye. The secondary, postero-median eyes of the spider *Drassodes* are highly specialized polarization-detecting organs missing imaging optics and sporting a polarizing tapetum.

22. Dacke M, Doan TA, O'Carroll DC: **Polarized light detection in**
• **spiders.** *J Exp Biol* 2001, **204**:2481-2490.
This paper surveys the polarization detecting organs of spiders. The lycosid type of polarization detector, a specialized ventral area of the principal, antero-median eyes, is functionally analogous to the DRA of insects and is present in several spider families. Secondary eyes with polarizing tapeta were found in many spiders, although their significance for polarization vision is clear for *Drassodes* only.

23. Rossel S: **Navigation by bees using polarized light.** *Comp Biochem Physiol [A]* 1993, **104**:695-708.

24. Petzold J: **Polarisationsempfindliche Neuronen im Sehsystem der**
• **Feldgrille,** *Gryllus campestris*: **Elektrophysiologie, Anatomie und Modellrechnungen.** *PhD thesis, University of Zürich*, 2001. [Translation of the title: Polarization sensitive neurons in optical systems of crickets: electrophysiology, anatomy and model calculations]
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.

25. Labhart T, Petzold J: **Processing of polarized light information in the visual system of crickets.** In *Sensory Systems of Arthropods.* Edited by Wiese K, Gribakin FG, Popov AV, Renninger G. Basel: Birkhäuser Verlag; 1993:158-168.

26. Labhart T: **Polarization-opponent interneurons in the insect visual system.** *Nature* 1988, **331**:435-437.

27. Labhart T: **How polarization-sensitive interneurones of crickets perform at low degrees of polarization.** *J Exp Biol* 1996, **199**:1467-1475.

28. Blum M, Labhart T: **Photoreceptor visual fields, ommatidial array, and receptor axon projections in the polarisation-sensitive dorsal rim area of the cricket compound eye.** *J Comp Physiol [A]* 2000, **186**:119-128.

29. Labhart T, Petzold J, Helbling H: **Spatial integration in polarization**
• **sensitive interneurones of crickets: a survey of evidence, mechanisms and benefits.** *J Exp Biol* 2001, **204**:2423-2430.
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.

30. Labhart T: **How polarization-sensitive interneurones of crickets see the polarization pattern of the sky: a field study with an opto-electronic model neurone.** *J Exp Biol* 1999, **202**:757-770.

31. Herzmann D, Labhart T: **Spectral sensitivity and absolute threshold of polarization vision in crickets: a behavioral study.** *J Comp Physiol [A]* 1989, **165**:315-319.

32. Gál J, Horváth G, Barta A, Wehner R: **Polarization of the moonlit clear night sky measured by full-sky imaging polarimetry at full moon: comparison of the polarization of moonlit and sunlit skies.** *J Geophys Res* 2001, **106**:22647-22653.

33. Gebhardt S, Homberg U: **Columnar neurons of the central complex in the brain of the locust** *Schistocerca gregaria* **are sensitive to polarized light.** In *Proceedings of the 28th Göttingen Neurobiology Conference.* Edited by Elsner N, Kreutzberg GW. Stuttgart:Thieme;2001:520.

34. Vitzthum H, Müller M, Homberg U: **Neurons of the central complex**
• **of the locust** *Schistocerca gregaria* **are sensitive to polarized light.** *J Neurosci* 2002, **22**:1114-1125.
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 skylight information became available.

35. Hofer S, Homberg U: **Anatomical organization of the anterior optic tubercle in the brain of the locust** *Schistocerca gregaria. Proceedings of the 28th Göttingen Neurobiology Conference.* Edited by Elsner N, Kreutzberg GW. Stuttgart, New York:Thieme;2001:521.

36. Pfeiffer K, Homberg U: **Visual signal processing in neurons of the anterior optic tubercle of the locust,** *Schistocerca gregaria. Zoology* 2002, **105(Suppl. V)**:45. [Translation of title: The necessary number of receptors for the determination of the direction of electrical vectors of linear polarized light]

37. Kirschfeld K: **Die notwendige Anzahl von Rezeptoren zur Bestimmung der Richtung des elektrischen Vektors linear polarisierten Lichtes.** *Z Naturforsch* 1972, **27**:578-579. [Translation of the title:]

38. Bernard GD, Wehner R: **Functional similarities between polarization vision and color vision.** *Vision Res* 1977, **17**:1019-1028.

39. Lambrinos D, Maris M, Kobayashi H, Labhart T, Pfeifer R, Wehner R: **An autonomous agent navigating with a polarized light compass.** *Adaptive Behav* 1997, **6**:131-161.

40. Lambrinos D, Möller R, Labhart T, Pfeifer R, Wehner R: **A mobile robot employing insect strategies for navigation.** *Robot Auton Syst* 2000, **30**:39-64.

41. Taube JS, Muller RU, Ranck JB: **Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis.** *J Neurosci* 1990, **10**:420-435.

42. Hartmann G, Wehner R: **The ant's path integration system: a neural architecture.** *Biol Cybern* 1995, **73**:483-497.

43. Wehner R: **Polarization vision – a uniform sensory capacity?** *J Exp Biol* 2001, **204**:2589-2596.

44. Labhart T, Lambrinos D: **How does the insect nervous system code celestial e-vector orientation? A neural model for "compass neurons".** International Conference on Invertebrate Vision, 7–12 August 2001, Bäckaskog Castle, Sweden, p 66.

45. Labhart T: **Neuromimetic models of the polarization compass: using the synthetic approach.** URL: http://www.zool.unizh.ch/neurobiology/labhart/tl_2.html

46. Labhart T: **Polarization-sensitive interneurons in the optic lobe of the desert ant** *Cataglyphis bicolor. Naturwiss* 2000, **87**:133-136.

47. Homberg U, Würden S: **Movement-sensitive, polarization-sensitive and light-sensitive neurons of the medulla and accessory medulla of the locust,** *Schistocerca gregaria. J Comp Neurol* 1997, **386**:329-346.

48. Loesel R, Homberg U: **Anatomy and physiology of neurons with processes in the accessory medulla of the cockroach** *Leucophaea maderae. J Comp Neurol* 2001, **439**:193-207.

49. Helfrich-Förster C, Stengl M, Homberg U: **Organization of the circadian system in insects.** *Chronobiol Int* 1998, **15**:576-594.

50. Esch HE, Burns JE: **Distance estimation by foraging honeybees.** *J Exp Biol* 1996, **199**:155-162.

51. Srinivasan MV, Zhang SW, Bidwell NJ: **Visually mediated odometry in honeybees.** *J Exp Biol* 1997, **200**:2513-2522.

52. Srinivasan MV, Zhang S, Altwein M, Tautz J: **Honeybee navigation:**
•• **nature and calibration of the "odometer".** *Science* 2000, **287**:851-853.
In this cleverly designed behavioral study, forager bees visited a food source by either flying through an environment with relatively distant objects (outdoors) or near visual stimuli (narrow tunnel with textured walls), producing vastly different amounts of image motion on the eye per distance flown. Comparing the foragers' waggle dances for the two situations showed that the odometer is not calibrated in absolute distance units but in optic-flow units.

53. Esch HE, Zhang S, Srinivasan MV, Tautz J: **Honeybee dances**
• **communicate distances measured by optic flow.** *Nature* 2001, **411**:581-583.
This paper demonstrates that the bee's interpretation of waggle dance frequency strongly depends on the visual environment. At a given waggle duration, recruits directed to open terrain fly much further than through a tree-clustered area, that is, the dances provide no information about the visual structure of the foraging area.

54. Hausen K, Egelhaaf M: **Neural mechanisms of visual course control in insects.** In *Facets of Vision.* Edited by Stavenga DG, Hardie RC. Berlin: Springer 1989:391-424.

55. Srinivasan MV, Poteser M, Kral K: **Motion detection in insect orientation and navigation.** *Vision Res* 1999, **39**:2749-2766.

56. Ronacher B, Wehner R: **Desert ants** *Cataglyphis fortis* **use self-induced optic flow to measure distances travelled.** *J Comp Physiol [A]* 1995, **177**:21-27.

57. Ronacher B, Gallizzi K, Wohlgemuth S, Wehner R: **Lateral optic flow does not influence distance estimation in the desert ant** *Cataglyphis fortis. J Exp Biol* 2000, **203**:1113-1121.

58. Schäfer M, Wehner R: **Loading does not affect measurement of walking distance in desert ants** *Cataglyphis fortis. Verh Dtsch Zool Ges* 1993, **86**:270.

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.

60. Wohlgemuth S, Ronacher B, Wehner R: **Ant odometry in the third dimension.** *Nature* 2001, **411**:795-798.

61. Wehner R, Wehner S: **Insect navigation: use of maps or Ariadne's thread?** *Ethol Ecol Evol* 1990, **2**:27-48.

62. Markl H: **Borstenfelder an den Gelenken als Schweresinnesorgane bei Ameisen und anderen Hymenopteren.** *Z Vergl Physiol* 1962, **45**:475-569. [Translation of the title: Areas of bristles on the joints as weight sensing organs in ants and other hymenoptera]

63. Rossel S, Wehner R: **Polarization vision in bees.** *Nature* 1986, **323**:128-131.