Research

Central neural coding of sky polarization in insects

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Many animals rely on a sun compass for spatial orientation and long-range navigation. In addition to the Sun, insects also exploit the polarization pattern and chromatic gradient of the sky for estimating navigational directions. Analysis of polarization–vision pathways in locusts and crickets has shed first light on brain areas involved in sky compass orientation. Detection of sky polarization relies on specialized photoreceptor cells in a small dorsal rim area of the compound eye. Brain areas involved in polarization processing include parts of the lamina, medulla and lobula of the optic lobe and, in the central brain, the anterior optic tubercle, the lateral accessory lobe and the central complex. In the optic lobe, polarization sensitivity and contrast are enhanced through convergence and opponency. In the anterior optic tubercle, polarized-light signals are integrated with information on the chromatic contrast of the sky. Tubercle neurons combine responses to the UV/green contrast and e-vector orientation of the sky and compensate for diurnal changes of the celestial polarization pattern associated with changes in solar elevation. In the central complex, a topographic representation of e-vector tunings underlies the columnar organization and suggests that this brain area serves as an internal compass coding for spatial directions.

Keywords: polarization vision; insect brain; e-vector map; central complex; compass navigation; locust

1. INTRODUCTION

Insect photoreceptor cells are inherently sensitive to polarized light owing to high alignment of rhodopsin in microvillar membranes. Photon absorption is maximal for light with an e-vector parallel to the microvillar axis [1]. Because polarization sensitivity interferes with the perception of colour and brightness, it is reduced or actively suppressed in most parts of the eye by rhabdomeric twist or misalignment of microvillar orientation along the rhabdomere [1–3]. In many insect species, however, including locusts, crickets, ants, bees, butterflies and beetles, ommatidia in a small dorsal margin of the compound eye, termed dorsal rim area (DRA), are particularly adapted for high polarization sensitivity (reviewed in [1]). Behavioural experiments in desert ants and honeybees showed that this eye region plays a key role in the perception of celestial polarization, and a similar role is strongly suggested for the DRA in field crickets, desert locusts, scarab beetles, flies and monarch butterflies (reviewed in [1,3]; figure 1). Sky polarization

is generated by scattering of sunlight in the atmosphere, and the polarization pattern of the blue sky is, therefore, directly linked to the position of the Sun [4–6]. The degree of polarization ranges from 0 per cent (direct sunlight) to a maximum of about 75 per cent at an angular distance of 90° from the Sun under optimal conditions (clear, dry sky) (figure 1a; [4]). The electric field vectors (e-vectors) in the sky are arranged along concentric circles around the Sun (figure 1a). This allows the animal to extract directional information from the sky, independently of the visibility of the Sun, provided that a small patch of blue sky is visible. Experiments in bees and ants showed that, in addition to the sky polarization pattern, insects can also derive sky compass information from the position of the Sun and from the chromatic gradient of the sky [7–11].

Whereas a polarization-sensitive dorsal eye region has been demonstrated in many insect species [1], central nervous mechanisms of polarization vision and sky compass orientation have been studied in a few species only, especially the cricket *Gryllus campestris* and the locust *Schistocerca gregaria* [12,13]. This review outlines central neural pathways and mechanisms of polarization vision in the insect brain with specific emphasis on the desert locust, *S. gregaria*, and provides data on how sky polarization signals are integrated with spectral cues for sky compass navigation.

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Figure 1. Sensory basis of polarization vision in the locust *S. gregaria*. (a) Pattern of polarized light of the blue sky. Electrical field vectors (e-vectors, double arrows) are arranged along concentric circles around the Sun (yellow). Direct sunlight is unpolarized. The degree of polarization in the sky increases gradually to a maximum of about 0.75 along a circle at 90° from the Sun. (b) Polarization-sensitive dorsal rim area (DRA) in the left compound eye of a locust, arrangement of ommatidia and organization of a DRA ommatidium. In each DRA ommatidium, the microvilli of photoreceptor cell 7 are oriented perpendicularly to the microvilli of photoreceptors 1, 2, 5, 6 and 8. Microvilli of photoreceptors 3 and 4 are irregular. a, anterior. (c,d) Yaw-torque responses of tethered flying locusts under a slowly rotating dorsal polarizer. Each histogram shows average yaw torques from six 180° rotations of the polarizer divided in 5° bins. The animal in (c) shows strong polarotaxis. After painting the DRAs of the eyes black (d), polarotaxis is abolished. (b) From Homberg & Paech [18] and (c,d) from Mappes & Homberg [37].

2. THE INPUT STAGE: POLARIZATION-SENSITIVE PHOTORECEPTORS IN THE DORSAL RIM AREA

A DRA specialized for high polarization sensitivity has been demonstrated in the compound eye of a variety of insect species [1]. The DRA faces the sky, and its ommatidia have optical axes directed upwards and slightly contralaterally. Microvilli of DRA photoreceptor cells are highly aligned in parallel, and self-screening is reduced, particularly in open rhabdoms, by the short length of the rhabdomers [2,14]. Visual fields of DRA photoreceptors may be increased (to about 20° in crickets) by degraded optics, reduction or lack of screening pigment between adjacent ommatidia, and by enlarged cross-sectional area of the rhabdoms [1]. Taken together, these measures result in high polarization-sensitivity (PS) values ranging from 5 to 15 [3]. Two blocks of photoreceptor cells with orthogonal microvillar orientations occur in each ommatidium, representing a set of crossed e-vector analysers (figure 1b). To avoid interference with colour vision, the two sets of photoreceptor cells within each ommatidium are homochromatic with maximum sensitivity in the UV (honeybee, desert ant, monarch butterfly), blue (locust, cricket) or green (cockchafer) range [1,15]. Across the DRA, microvillar orientations of ommatidia vary

systematically, in many species in a fan-like pattern, following the geometrical layout of the ommatidial lattice ([3,16]; figure 1b).

3. POLARIZATION-VISION PATHWAYS IN THE BRAIN OF ORTHOPTEROID INSECTS

DRA photoreceptors project to DRAs in the lamina and medulla of the optic lobe [17,18]. Studies in crickets showed that photoreceptor axons from R1, R2, R5 and R6 with parallel microvilli terminate in the lamina, while the axons from R7 receptor cells, with microvilli orientation orthogonal to those of R1, R2, R5 and R6, project to the medulla [17]. Lamina-to-medulla interneurons have not been characterized in any insect, but medulla tangential neurons with dendritic branches in the dorsal rim of the medulla have been studied in detail in the field cricket (figure 2a). These neurons, termed POL1, interconnect the right and left medulla and have side branches in the accessory medulla [3,19]. Tracer injections in locusts revealed a polarization-vision pathway from the DRA of the medulla to the central brain (figure 3). Medulla line tangential neurons with ramifications in the DRA of the medulla send axonal projections through the anterior lobe of

Figure 2. Polarization-sensitive POL1 neuron in the brain of the cricket *Gryllus campestris*. (a) Morphology of POL1. The neuron has dendritic arborizations in the dorsal medulla (Me) and an axonal projection to the contralateral medulla. Side branches are in the accessory medulla (AMe) of both brain hemispheres. S, soma. Scale bar, 250 μm . Reprinted from Labhart & Petzold [19], with permission from Birkhäuser Verlag. (b) Intracellular recording from POL1 in the ipsilateral optic lobe. The neuron shows polarization opponency when the animal is stimulated dorsally through a polarizer rotating from 360° to 0° and back. (c) The receptive field of POL1 (shaded area) extends through an area of about 60° in the contralateral (c) dorsal field of view. a, anterior; i, ipsilateral; p, posterior. (b,c) Reprinted from Wehner & Labhart [3], with permission from Cambridge University Press. (d) Histogram of e-vector tunings from 142 recordings from POL1 neurons. Three physiological types can be distinguished with Φ_{max} orientations around 10°, 60° and 130° with respect to the longitudinal axis of the animal. Reprinted from Labhart & Meyer [13], with permission from Elsevier.

the lobula and via the anterior optic tract into the lower unit of the anterior optic tubercle ([20]; figure 3). Dextran injections into the anterior optic tubercle demonstrated that neurons from the lower unit of the tubercle project to small areas in the lateral accessory lobe (LAL), termed the lateral triangle and the median olive. These areas are selectively innervated by dendritic processes of tangential neurons of the lower division of the central body, a subcompartment of the central complex [21]. Following these studies, a network of polarization-sensitive neurons has been identified in the locust central complex [22–25], suggesting a role as an internal sky compass. Outputs from the central-complex network to the LAL and posterior protocerebrum probably provide connections to descending pathways [23].

4. POLARIZATION SENSITIVE NEURONS IN THE OPTIC LOBE: SENSITIVITY ENHANCEMENT THROUGH CONVERGENCE AND POLARIZATION OPPONENTY

Polarization-sensitive (POL) interneurons in the optic lobe have been characterized in ants, cockroaches and locusts (reviewed in [5]), but most detailed studies exist on an identified type of interneuron in crickets, termed POL1 [13,19]. POL1 neurons are commissural neurons with ipsilateral ramifications in the dorsal medulla and an axon projecting to the contralateral medulla (figure 2a). When a linear polarizer is rotated above the animal, POL1 shows polarization opponency, i.e. the neuron is maximally excited by

a particular e-vector orientation, termed Φ_{max} , and is maximally inhibited by an e-vector orientation orthogonal to Φ_{max} (figure 2b). POL1 neurons, therefore, receive antagonistic input from crossed e-vector analysers in the compound eye, which may be represented by the two sets of photoreceptor cells with orthogonal microvilli orientation in each DRA ommatidium. Polarization opponency is a common property of POL neurons in the insect brain and has been found in other optic-lobe neurons, in the anterior optic tubercle and the central complex (see below). Polarization opponency greatly enhances e-vector contrast and makes POL1 neurons virtually unresponsive to changes in ambient light levels [19,26]. Spatial integration of input from about one-third of all ipsilateral DRA ommatidia [17] results in large receptive fields of about 60° in diameter (figure 2c) and an extremely high absolute sensitivity [19]. As a further consequence, the neurons respond to the mean e-vector orientation in their receptive field rather than to details of celestial e-vector distribution. Therefore, POL1 neurons still signal e-vector orientation down to a degree of polarization of about 5 per cent, which matches the behavioural performance of the animals [27]. POL1 neurons occur as triplets, since three physiological subtypes have been encountered with Φ_{max} orientations around 10°, 60° and 130° ([13]; figure 2d). The different activity levels in the three POL1 subtypes would allow the cricket to instantaneously extract unambiguous information on mean e-vector orientation of the stimulus.

Figure 3. Polarization–vision pathway to the central complex in the brain of the locust, as revealed through tracer injections into the dorsal rim area of the eye, into the dorsal rim of the medulla (DMe), into the anterior optic tubercle (AOTu) and through dye injection into single neurons of the central body. Central processing stages for polarized light include the dorsal rim of the lamina and medulla (DLa and DMe), layer 1 of the anterior lobe of the lobula (ALol), the lower unit of the AOTu (AOTu-LU), the median olive (MO) and lateral triangle (LT) of the lateral accessory lobe (LAL), and the lower division of the central body (CBL). Ca and P, calyx and pedunculus of the mushroom body; La, lamina; Me, medulla; PB, protocerebral bridge. Scale bar, 200 μm . Adapted from Träger *et al.* [38].

5. INTEGRATION OF CELESTIAL CUES IN THE ANTERIOR OPTIC TUBERCLE

Perception of e-vector orientation in a patch of blue sky does not provide unambiguous information on solar azimuth and, therefore, on navigational directions because it does not allow the animal to distinguish the solar from the anti-solar hemisphere of the sky (figure 1a). Moreover, outside the solar meridian, orientation of polarization changes with changing Solar elevation during the day. Neurons of the anterior optic tubercle in the brain of the locust show response characteristics that may be suited to overcome both problems. As in other insect species, the anterior optic tubercle of the locust consists of a large upper unit and a smaller lower subunit (figure 4a,b). Intracellular recordings showed that all neurons encountered in the lower subunit are polarization sensitive [28]. These include two types of heterolateral interneurons, termed LoTu1 and TuTu1, that connect the lower subunits of both brain hemispheres (figure 4) and two types of projection neurons that connect the lower unit to the next stages of processing, the median olive and lateral triangle of the LAL of the midbrain [28]. LoTu1 and TuTu1 have been studied most extensively. As in cricket POL1 neurons, their spiking activity is sinusoidally modulated with changing e-vector orientation, and their responses are dominated by input from the ipsilateral eye (figure 4g). Like DRA photoreceptors, LoTu1 and TuTu1 are most sensitive to polarized blue (approx. 450 nm) light [29]. In contrast to the cricket POL1 neurons, however, both neurons also show wavelength-dependent responses to unpolarized light [29]. Responses to a long wavelength (green) and a short wavelength (UV) light spot depend on stimulus azimuth (figure 4d,e) and show spectral opponency combined with spatial opponency (e.g. excitation versus inhibition to a UV light from opposite directions; figure 4e). These chromatic properties are suited to distinguish the solar half of

the sky from the anti-solar half, by its higher content of long-wavelength light. The difference angles between spatial tuning to polarized light and to the green light spot are large in experiments performed in the late afternoon but small at noon, when the Sun is high in the sky (figure 4f). These changes reflect changes in celestial e-vector orientation that occur with changing solar elevation during the day and are matched particularly well by a model curve taken from the geographical coordinates of northern Africa, the natural habitat of the animals (figure 4f). Therefore, TuTu1 and LoTu1 (i) combine responses to the UV/green contrast and polarization contrast of the sky for a robust compass signal and (ii) compensate for diurnal changes in celestial e-vector orientation owing to changes in solar elevation [30]. They are, thus, suited to code solar azimuth independently of time of day.

6. COMPASS-LIKE REPRESENTATION OF CELESTIAL e-VECTORS IN THE CENTRAL COMPLEX

Projection neurons from the anterior optic tubercle provide input to the central-complex network via specialized regions in the LALs (figure 3). The central complex consists of the protocerebral bridge (PB) and the upper and lower divisions of the central body (CBU and CBL, figures 5a and 6). All subunits are arranged in linear rows of 16 columns and both subdivisions of the central body consist of several layers. Single-cell recordings in locusts and matching data in crickets showed that 13 types of central-complex neurons are sensitive to polarized light. Based on anatomical and physiological evidence, the resulting polarization–vision network can be divided into several processing stages ([23,24]; figures 5 and 6). At the input stage, tangential neurons carry polarized-light information from specialized regions of the LAL to specific layers of the CBL ([25,31];

Figure 4. Polarization-sensitive neurons of the anterior optic tubercle in the locust brain. (a,b) Morphology of two types of polarization-sensitive commissural neurons, termed LoTu1 and TuTu1, that connect the lower units of the anterior optic tubercles (AOTu-LU) of both hemispheres. LoTu1 has additional ramifications in the ventralmost layer 1 of the anterior lobe of the lobula (ALo) of both hemispheres. AOT, anterior optic tract; CB, central body; MB, mushroom body; AOTu-UU, upper unit of the anterior optic tubercle. Scale bars, 200 μm . (c–e) Responses of a TuTu1 neuron to different orientations of polarized blue (470 nm) light in the zenith (c) and different azimuthal positions of a green (530 nm; d) and a UV (350 nm; e) light spot. Background spiking activity is indicated by the red circles. Black bars show preference angles ($\Phi_{\max}^{\text{POL}}$, $\Phi_{\max}^{\text{green}}$, $\Phi_{\max}^{\text{UV}}$) of the neuron to the different stimuli. (f) Absolute angular differences $\Delta\Phi_{\max}$ between $\Phi_{\max}^{\text{POL}}$ and $\Phi_{\max}^{\text{green}}$ from all recordings plotted against time of day of the experiments reveal diurnal changes in the difference angles. Celestial $\Delta\Phi_{\max}$ functions strongly depend on geographical coordinates and are fitted to the data for coordinates of Marburg, Germany (blue line) and northern Africa (red line). (g) e-vector response plots for stimulation of both eyes (blue triangles), the ipsilateral eye (red squares) and the contralateral eye (green circles) show that polarization input to TuTu1 is strongly dominated by the ipsilateral eye. (a,b,g) From Pfeiffer *et al.* [28] and (c–f) from Pfeiffer & Homberg [30].

figure 6). At an intermediate stage, CL1 neurons with arborizations restricted to single columns (columnar neurons) are likely to provide a link between the CBL and the PB ([23]; figure 6). Finally, at the output stage, TB1 tangential neurons of the PB appear to integrate polarized-light information from several CL1 columnar cells across both hemispheres (figure 6). Via unknown mechanisms, this results in the generation of a compass-like representation of zenithal e-vectors in the columnar output arborizations of these tangential cells, covering roughly $2 \times 180^\circ$ along the 16 columns of the PB. Hence, activity in the columns of the PB is correlated to the orientation of the locust with respect to solar azimuth ([22]; figures 5b and 6). Finally, different sets of columnar neurons (types CP1, CP2 and CPU1) provide the output from the central complex. These cells

participate in the azimuthal e-vector representation in the PB columns and probably receive input from PB-tangential cells (figure 5c), while ultimately projecting to several regions of the LAL [22]. These neurons are anatomically suited to combine azimuthal e-vector information from the PB with information present in the CBU to provide an integrated output signal from the central complex (figure 6).

All polarization-sensitive neurons of the central complex share polarization opponency with neurons at the more peripheral processing stages. In contrast to neurons of the anterior optic tubercle, most central-complex neurons integrate information from both eyes (except TL3 input stage neurons). Within the central complex, physiological properties are successively altered from one processing stage to the next [24]. Hereby, initially eccentric and comparably

Figure 5. Polarization-sensitive neurons of the locust central complex. (a) Camera lucida drawings of different neuron types projected onto a three-dimensional reconstruction of the central complex. Tangential neurons of the CBL (TL2, TL3) provide input to the central complex; columnar CL1 neurons connect the input to the protocerebral bridge (PB), where tangential TB1 cells integrate and process information from both sky hemispheres. Columnar CP1, CP2 and CPU1 neurons constitute the output from the central complex. All neurons show polarization opponency with maximum excitation at a particular e-vector ($\Phi_{\max}$) and maximum inhibition at an e-vector orthogonal to $\Phi_{\max}$. (b,c) Linear regression analysis of columnar arborization domains and (b) $\Phi_{\max}$ values of TB1 neurons and (c) columnar CP1, CP2 and CPU1 neurons. Regression for TB1 neurons only covers one hemisphere, owing to bilateral columnar arborization domains, but values are plotted twice for visualization purposes. (d) Intracellular recordings (lower traces) and mean spiking frequencies (upper traces; gliding average, 0.5 s bin size) of TL2, CL1, TB1 and CPU1 neurons during 360° rotations of the polarizer, illustrating the changing response characteristics at different processing stages. (e) Mean receptive field widths of TL2 and TB1 neurons. Mean response strength (normalized to the maximal value of the receptive field) is plotted at different elevations along the meridian orthogonal to the longitudinal body axis of the locust. Values are plotted with respect to the location of the soma of each neuron (i, ipsilateral; c, contralateral). Dashed lines represent mean relative background variability. CBU, CBL, upper resp. lower division of the central body; LAL, lateral accessory lobe; LT, lateral triangle; MO, medial olive; POTu, posterior optic tubercle. Data from Heinze & Homberg [22,23,39], Vitzthum *et al.* [25] and Heinze *et al.* [24].

small receptive fields are transformed into very large (up to 180° wide), zenith-centred receptive fields (figure 5e). In addition, the signal-to-noise ratio decreases from the input to the output stage of the central complex, suggesting that neuronal activity is increasingly influenced from sources of neuronal activity other than polarized light ([24]; figure 5d). Taken together, a highly specialized system for e-vector coding present at the central-complex input stage appears to be transformed into a position-invariant, potentially multimodal system coding for azimuth direction and head orientation within central-complex output neurons.

7. CONCLUSIONS AND OPEN QUESTIONS

Information on celestial e-vector orientation in the sky is processed in a stage-specific manner in the insect brain. Contrast enhancement through convergence of inputs and polarization opponency occurs at early levels in the lamina and outer medulla; a combination with sky chromatic input including compensation for changing solar elevation probably occurs in medulla outputs converging on the anterior optic tubercle. Integration of binocular inputs together with compass-like arrangement of e-vector tunings, finally, takes place in the central complex. The central complex may not only be essential for navigational

Figure 6. Proposed scheme of the polarization coding network in the locust central complex. Neurons at the input stage are shown in shades of blue, neurons at an intermediate stage in green and neurons at the output stage in shades of red. Polarization–vision information from the optic lobe (blue arrows) enters the lower division of the central body (CBL) via TuLAL1a/b neurons from the lower unit of the anterior optic tubercle (AOTu-LU). These neurons synapse in the lateral triangle (LT) and medial olive (MO) of the lateral accessory lobe (LAL) upon tangential TL2/3 neurons of the CBL. At the following intermediate stage, CL1 neurons (green) are candidates to transmit polarization–vision signals from the CBL to the contralateral hemisphere of the protocerebral bridge (PB). For clarity, only four of 16 neurons are shown. Via small axons, these neurons also provide a first, direct output pathway to a small region near the LT in the LAL (green asterisks). Neurons at the final output stage (TB1, CPU1; red) contribute to the topographic representation of e-vectors in the PB columns, illustrated for CPU1 neurons as double arrows above the PB. Whereas TB1 neurons project to the posterior optic tubercle (POTu), CPU1 cells and other columnar neurons target post-synaptic neurons in the LAL (red asterisks). CPU1 neurons (only two of 16 shown) receive additional input in the upper division of the central body (CBU). Based on data from Heinze & Homberg [22,23,39], Pfeiffer *et al.* [28], Vitzthum *et al.* [25], Heinze *et al.* [24] and Träger *et al.* [38].

purposes, but probably provides a more general code of spatial directions, which might include recognizing and memorizing objects in space [32]. How outputs of the central complex are connected to descending pathways is slowly beginning to emerge [23], and recent recordings have identified the first polarization-sensitive descending neurons [33]. A still unresolved issue is the question how daytime changes in solar azimuth are compensated in long-range migratory species. It would require input from an internal circadian clock. A candidate brain area for convergence of polarization and timing information is the posterior optic tubercle (figure 5a). In locusts, it receives direct input from the accessory medulla [34], the internal circadian clock in cockroaches and flies [35]. Recent recordings showed that neurons with arborizations in the accessory medulla are sensitive to polarized light [36]. These data open the possibility that time-compensated polarized-light signals may reach the central complex via a second, posterior polarization-vision pathway for time-compensated sky compass navigation.

Questions in the broader context of spatial orientation that may be accessible in future studies concern the neural mechanisms underlying path integration using a sky compass, the integration of landmark information with vector-guided signalling and the unique transformation of sun azimuth-related directional coding into a gravity-related signal during dance communication in honeybees. All of these

behaviours require some form of spatial learning, which might well be associated with an internal compass structure like the central complex.

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