

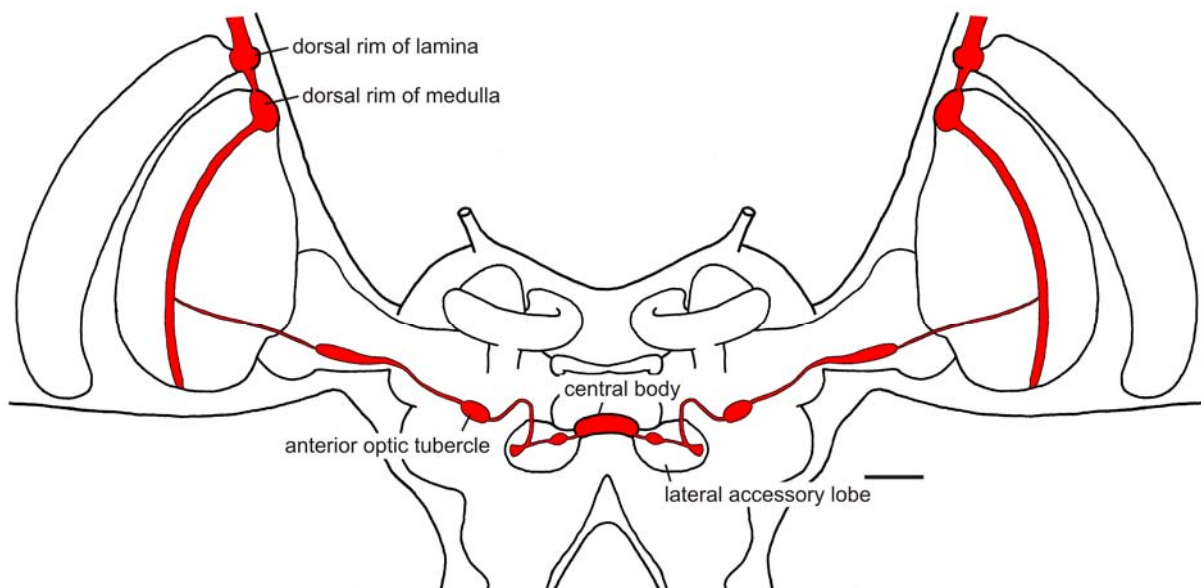
Central mechanisms of polarization vision and sky compass orientation in the desert locust *Schistocerca gregaria*

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Many insects use a celestial compass for spatial orientation and navigation. Several studies showed that insects strongly rely on the polarization pattern of the blue sky as a guiding cue (e.g., Wehner and Müller 2006, Proc Natl Acad Sci 103, 12575) but the position of the sun and the chromatic gradient in the sky offer useful information, too. To elucidate the neuronal mechanisms underlying sky compass orientation, we have analyzed the polarization vision system in a favourable insect, the desert locust *Schistocerca gregaria*.

As in other insect species, polarization vision in the desert locust relies on specialized photoreceptor cells in a small dorsal rim area of the compound eye. These photoreceptors project to dorsal rim areas in the lamina and medulla. Central processing stages for polarized light include the anterior optic tubercles, the central complex and surrounding areas in the median protocerebrum. Most neurons in the optic tubercle and central complex show polarization opponency, i.e. they receive excitatory and inhibitory input from photoreceptors with orthogonal microvilli orientations. In the anterior optic tubercle, polarized-light sensitivity is combined with UV-green color coding mechanisms suggesting that these neurons code for solar azimuth by concurrent combination of signals from the spectral gradient, the intensity gradient and the polarization pattern of the sky (Pfeiffer and Homberg, 2007, Current Biol 17:960). In the central complex, neurons combine polarization-vision inputs from both eyes and have zenith-centered receptive fields. Single-cell recordings revealed a compass-like linear map of *E*-vector tunings in the columns of the protocerebral bridge, a subcompartment of the central complex (Heinze and Homberg 2007, Science 315:995). The receptive field organizations and compass-like arrangement of *E*-vector tunings suggests that the central complex computes and codes for azimuthal directions. This may be used for azimuth-dependent recognition of objects in space as well as for azimuth coding during long-range navigation. Supported by DFG grants HO 950/16-1 and 16-2.



Polarization vision pathway in the brain of the locust

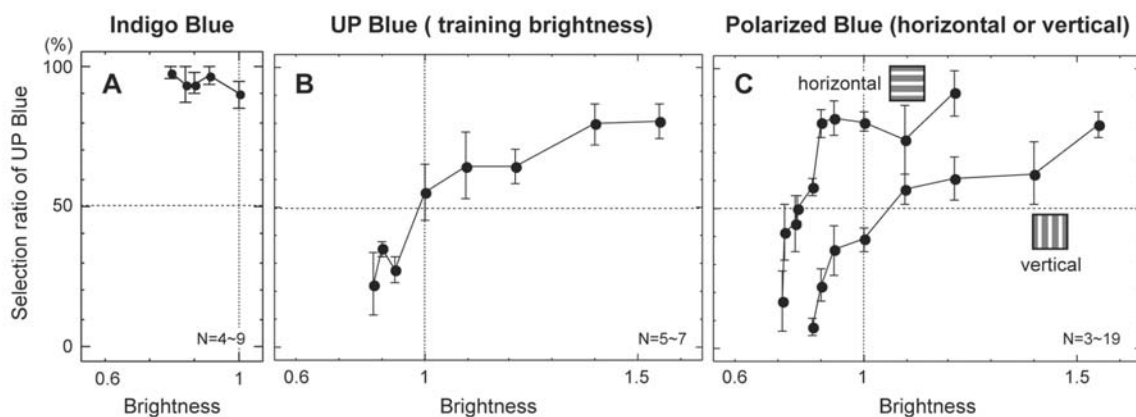
Do *Papilio* butterflies see polarized light as color or brightness?

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Japanese yellow swallowtail butterfly, *Papilio xuthus*, use color vision when searching nectar source. Recent study has demonstrated that *Papilio* color vision is based on four out of six classes of spectral receptors in the retina (Koshitaka et al, 2008). In addition to the specific spectral sensitivity, each receptor has a particular polarization sensitivity. An animal having such retinal organization might see different *e*-vector angle of polarized light as different colors. In fact, Kelber (1999) demonstrated evidence supporting this hypothesis in egg-laying *Papilio*. Is it also the case in foraging *Papilio* butterflies?

We first let newly emerged *Papilio* select one of two stimuli; horizontal and vertical *e*-vector angles of polarized light. The butterflies preferred vertical polarized light. Since *Papilio* could not be trained to polarized light, we trained them to visit unpolarized (UP) blue. In the test, we presented two lights: one was always training UP blue and the other is either UP indigo blue, another UP blue or polarized blue. Then we measured how *Papilio*'s selection changed depending on the different brightness of the UP blue. *Papilio* selected UP blue from indigo blue even though the brightness of UP blue decreased (A). The result indicates that the color dependent selection is not affected by the brightness. When both stimuli were UP blue, *Papilio* selected brighter one (B). The selection of UPB also changed depending on its brightness when it was presented with polarized blue (C). Taken together, we conclude that foraging *Papilio* see different polarization as brightness difference rather than color difference.



The sensitive and robust polarized-skylight navigation system of crickets

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Skylight polarization offers insects a useful reference for compass orientation or cruising-course control. Crickets have served as model organisms for studying the neural mechanisms of polarization vision for many years. Using behavioral, electrophysiological, histological, optical and synthetic approaches, we have found that the polarized-skylight detection system of crickets (*Gryllus spp.*) is extremely sensitive and robust.

Sensitivity: A) As in other insects, polarized skylight detection is mediated by specialized ommatidia in the dorsal rim area (DRA) of the compound eye (1). High polarization sensitivity is achieved by strict microvilli alignment in the photoreceptors ($PS \approx 10$)(2,3) and by the polarization antagonism of polarization-sensitive neurons (POL neurons) in the optic lobe (4), allowing e-vector detection at just 7% polarization (5). **B)** The absolute threshold of polarization vision ($2.5 \cdot 10^7$ photons $\text{cm}^{-2} \text{s}^{-1}$) is lower than the effective photon flux under the clear, moonless night sky (6). This results from the large rhabdoms and the wide visual fields of the DRA receptors (median half-width $\approx 20^\circ$)(2,3,7,8). In addition, optic lobe POL neurons receive input from a large number of DRA ommatidia (9).

Robustness: C) Due to this spatial integration the polarization detection system is a non-imaging visual system. It disregards the geometry of a polarized stimulus and is largely insensitive to disturbances of the celestial polarization pattern caused by clouds or tree canopies (5,10). **D)** The physiology of POL neurons in the central complex (CC) suggests that the system is also insensitive to the variable degrees of polarization observed in the sky (at least down to $d = 0.18$), probably by enhancing weak signals by a neural feedback circuit (11). **E)** Above the absolute threshold, the system is indifferent to the absolute light level because the polarization antagonism produces a differential signal removing intensity information (4,12). **F)** Containing only blue-receptors, the DRA is monochromatic and thus the system is insensitive to the spectral variations of skylight (4,6,8). **G)** The short-wavelength sensitivity reduces the influence of stimuli of longer wavelengths (e.g. leaves, clouds) interfering with the polarization pattern of the blue sky (13).

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Summary of mechanisms assisting high sensitivity and robustness in polarized skylight detection

		Mechanisms	Neural elements
High sensitivity	A) Polarization sensitivity	Microvilli alignment Polarization antagonism	Photoreceptors Optic lobe POL neurons
	B) Absolute sensitivity	Large rhabdoms, wide visual fields Neural integration	Photoreceptors Optic lobe POL neurons
Robustness	Indifference to:		
	C) Stimulus geometry	Optical integration Neural integration	Photoreceptors Optic lobe POL neurons
	D) Degree of polarization	Feedback circuit	CC POL neurons
	E) Light intensity	Polarization antagonism	Optic lobe POL neurons
	F) Spectral composition	Monochromacy	Photoreceptors
	G) Longwave stimuli	Short-wavelength sensitivity	Photoreceptors

A small fly under the open sky: How *Drosophila* views the celestial polarization pattern

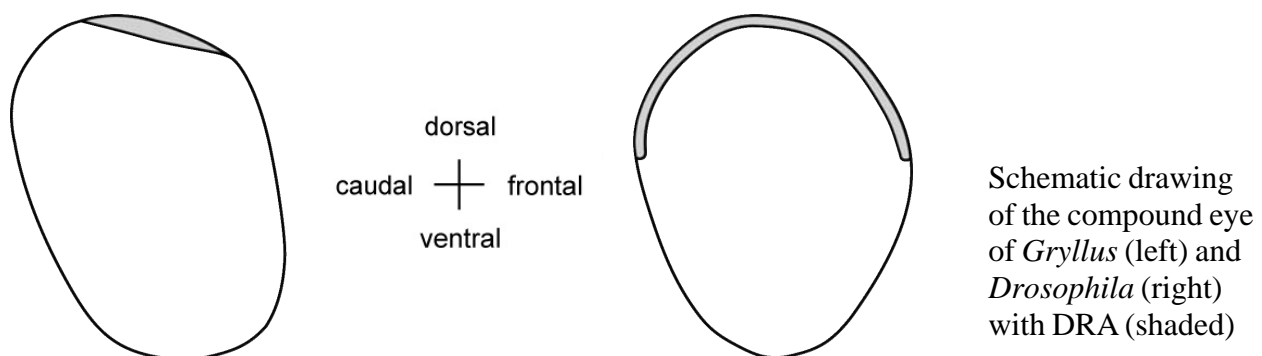
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Among insects, the ability to exploit skylight polarization for orientation is widespread. Photoreceptors in the so-called dorsal rim area (DRA) of the compound eye are specialized to be strongly sensitive to the electric vector (e-vector) of linearly polarized light. In all insects studied so far celestial e-vector detection is mediated by the DRA, and the ommatidia are functionally comparable (1). However, the geometry of the DRA and thus sensory input to the polarization vision pathway differs considerably. In crickets (*Gryllus spp.*) the DRA is relatively wide and short, being restricted to the dorsalmost part of the eye. Spatial resolution is extremely low due to the large angular sensitivities of the DRA ommatidia (half-width $\sim 20^\circ$) (2). By contrast, polarization-sensitive photoreceptors in fruit flies (*Drosophila melanogaster*) are located in just one or two rows of ommatidia along the entire dorsal eye margin (3). The ommatidia lack optical specializations suggesting narrow visual fields of only few degrees. This results in an arc-shaped DRA in which the frontal, dorsal and caudal sections receive input from vastly different parts of the sky including the zenith and areas near the horizon. It is therefore unlikely that celestial e-vector information in fruit flies is analyzed in the same way as in crickets, in which the ommatidia of different DRA sections receive light from roughly the same area of the sky.

In order to understand the consequences of different DRA geometries in insects, we have modeled the input to the polarization vision system in *Drosophila*. Based on optical and histological measurements, we are able to calculate the activities of photoreceptors for different orientations of the fly relative to the celestial polarization pattern. This allows us to compare *Drosophila* with *Gryllus* for which these data already exist (4) and provides an insight into possible reasons for different DRA designs.

1 Labhart T, Meyer EP (1999) *Microsc Res Tech* 47: 368-379. **2** Blum M, Labhart T (2000) *J Comp Physiol A* 186(2): 119-128. **3** Wernet MF et al. (2003) *Cell* 115: 267-279. **4** Petzold J (2001) PhD thesis, University of Zurich, Switzerland.



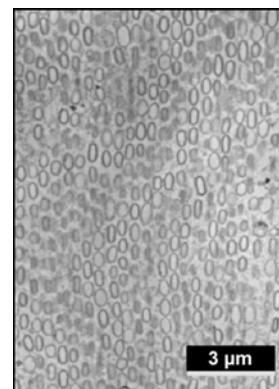
Optics of Biological Polarizers of Marine Invertebrates

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The photic environment in water is rarely spectrally predictable, due to variations in depth, tidal state, water quality, or time of day. This variability, as well as the spectral narrowing of incident illumination with increasing depth, reduces the reliability of color signals. Consequently, some marine invertebrates use signals based on polarized light, which have the potential to be relatively constant with changing lighting conditions. Such biological polarizers have been described in several species of cephalopod mollusks as well as in numerous species of stomatopod crustaceans. All these animals are known to have well-developed polarization vision sensitive to the reflected polarization spectrum of the signals. Biological polarizers are based on at least three fundamentally different optical systems. In the cephalopods, the polarization is produced by multilayered reflectors within iridophores. These reflectors are formed from individual iridosomes, which are arranged to produce a relatively constant polarization reflection independent of the direction of illumination, and the degree of polarization in the reflected light can be controlled by the animal producing the signal. In contrast, the stomatopods have polarizers based on two different optical mechanisms, but there is no evidence that their signals can be modulated other than by postural or orientational changes of the surface containing the polarizer. One polarizer type, which appears blue to the human eye, is based on resonant scattering of light from parallel rows of ovoid vesicles. These polarizers reflect horizontally polarized light in the blue to blue-green region of the spectrum and vertically polarized light in the infrared (which is not used in the signal). The other type is based on dichroic molecules arranged parallel within biological membranes. In this arrangement, the polarizer preferentially transmits horizontally polarized light at medium wavelengths when viewed appropriately. Various species of stomatopods have one or the other type of polarizer, and a few species have both types. The diversity of optical mechanisms used in biological polarizers has only recently been determined and provides a surprising example of convergent evolution.

Figure 1. An electron micrograph of the polarizers in the 1st maxilliped of the stomatopod *Haptosquilla trispinosa*. Note the rows of vesicles arranged with their short axes parallel in the horizontal plane and their long axes parallel in the vertical plane. These vesicles scatter horizontally polarized light peaking near 500 nm and vertically polarized light peaking near 850 nm.



Tracks in the Moonlight

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By investigating the eyes of diurnal and nocturnal navigators, we want to quantitatively compare the morphologies and limitations of the diurnal and the nocturnal built-in polarization compasses. On a full moon night, the celestial polarisation pattern is a million times dimmer than during the day and within the first and last quarter it becomes ten times dimmer again. Do nocturnal navigators trade precision for increased sensitivity? At which phase of the moon is the celestial polarisation pattern bright enough to support reliable orientation? In this ongoing study, we wish to answer these questions by measuring the precision with which animals orient to polarised skylight during the day, as well as at night, at different times of the lunar month. The foraging behaviour of ball-rolling dung beetles - which takes them along straight tracks – gives us an excellent and completely non-invasive tool to establish when the moon is too small – and the polarisation pattern too dim – to provide a reliable polarisation pattern for orientation. On a full moon night, we observe that the beetles move along straight tracks (Fig. A), but what will happen as the moon wanes? Will the course become progressively less straight, or does straightness stay the same and then suddenly break down once the polarisation pattern is too weak to be perceived? Our data so far indicate that the performance of the nocturnal polarisation compass is sustained at least on nights lit by a quarter moon (Fig. B).

By quantitatively comparing the morphologies of compasses in diurnal and nocturnal navigators, we also wish to describe the adaptations for high sensitivity in the nocturnal compass system. Increased sensitivity is potentially achieved already at the level of the retina, where the rhabdoms in the crepuscular and nocturnal species of dung beetles are up to four times as wide as those in diurnal relatives. Field observations of an eye shine in the nocturnal beetles further indicate that a tracheal tapetum reflects light back through the rhabdom a second time, effectively making the rhabdom twice as long. This would again make the nocturnal compass more sensitive.

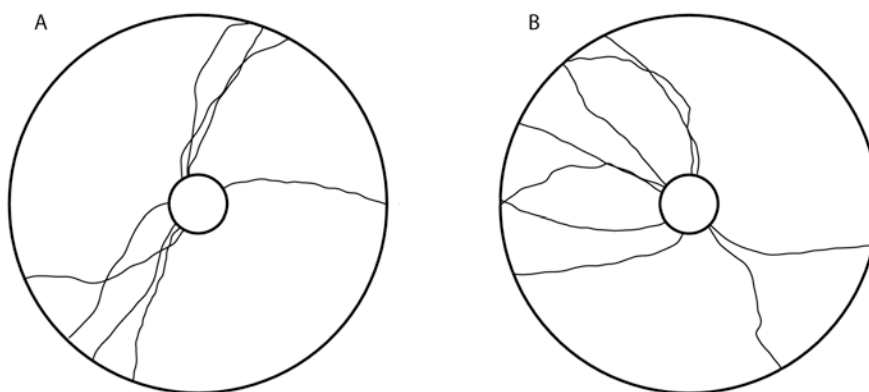


Fig: Paths of the ball rolling dung beetle *S. zambesianus* rolling out from the centre of an arena at full moon (A) and quarter moon (B). The diameter of the arena is 3 m.