SHORT COMMUNICATION

Polarization-Sensitive Interneurons in the Optic Lobe of the Desert Ant *Cataglyphis bicolor*

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Received: 29 September 1999 / Accepted in revised form: 13 December 1999

Abstract Desert ants, *Cataglyphis bicolor* (Hymenoptera), navigate by using compass information provided by skylight polarization. In this study, electrophysiological recordings were made from polarization-sensitive interneurons (POL-neurons) in the optic lobe of *Cataglyphis*. The POL-neurons exhibit a characteristic polarization opponency. They receive monochromatic input from the UV receptors of the specialized dorsal rim area of the compound eye. Both polarization opponency and monochromacy are features also found in the POL-neurons of crickets (Orthoptera).

Introduction

Desert ants, *Cataglyphis* sp. (Formicidae, Hymenoptera), are impressive navigators. To find their way during their extended foraging excursions in often featureless terrain they rely mostly on the directional information offered by the e-vector pattern of skylight polarization. There are a host of behavioral experiments dealing with the polarization compass of *Cataglyphis* (reviews: Wehner 1997, 1998), but physiological data on the underlying neuronal mechanisms are restricted to the level of the retina. Electrophysiological recordings from the ant's photoreceptors (Labhart 1986) confirmed the behavioral finding (Fent 1985) that polarization vision is mediated by the strongly polarization-sensitive photoreceptors in the dorsal rim area (DRA) of the compound eye, the eye region dedicated to the analysis of skylight polarization. The present study is a first attempt to unravel the properties of interneurons processing e-vector information in *Cataglyphis*. The findings are compared with those from the physiologically well studied field cricket, *Gryllus campestris* (Orthoptera; e.g., Labhart 1988, 1996, 1999; Labhart and Petzold 1993).

Methods

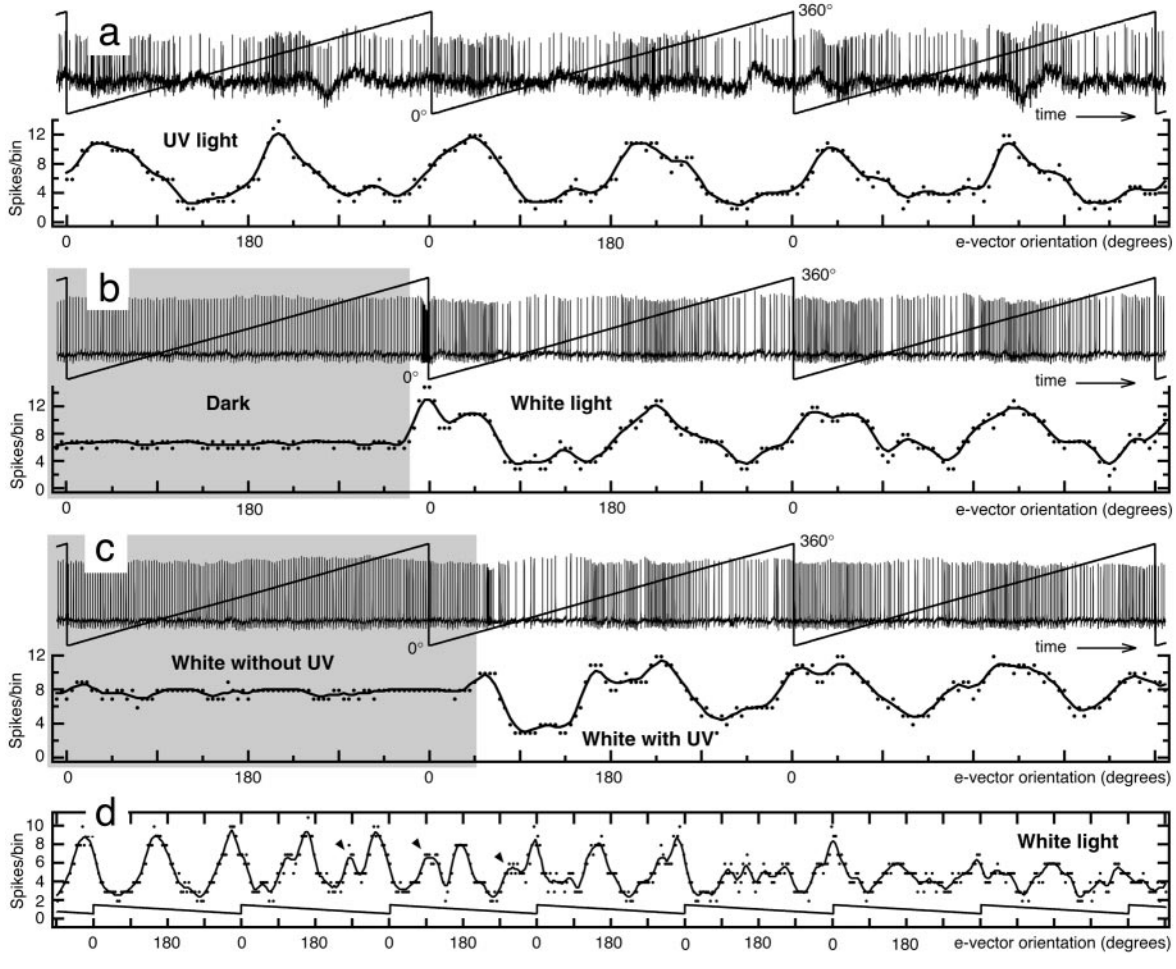
A colony of desert ants, *Cataglyphis bicolor*, collected in Tunisia was kept in an artificial nest that was connected to a small foraging arena (55×55 cm). To roughly simulate natural lighting the arena was lit by partially polarized light using daylight lamps (Osram L20W/10S) and a large polarizer (Polaroid HN38) combined with a diffusing screen covering most of the arena. Using a conventional electrophysiological setup, I made recordings from interneurons in the right optic lobe (medulla). Micropipettes pulled from quartz capillaries had to be used to penetrate the tough glial sheath around the optic lobe (Laser Puller P-2000, Sutter Instrument). The compound eyes were stimulated with a wide-field polarized light stimulus that had its center at zenith (with respect to natural head position) covering about 80% of the total visual field of the DRA (polarizer HNP'B backed with a diffuser providing 100% polarization over a circular area of 75° diameter; xenon arc white light or broad-band UV). To ensure that observed e-vector responses of neurons were mediated by the DRA (and were not a result of stray light stimulating other eye parts), most of the non-DRA part of the compound eye and the ocelli were blinded by black paint. To assess the visual field of polarization-sensitive neurons the stimulus size was restricted to 20° by using a circular blind. In most experiments the eyes were continuously stimulated with the e-vector orientation rotating at 75°/s; in a few experiments 0.5°s flashes with different e-vector orientations were applied. Neuron activity (in AC mode) and a signal coding e-vector orientation were recorded on a DAT recorder (Sony PC-108M), transferred to a computer and evaluated using data analysis software (IGOR Pro, WaveMetrics).

Results

I recorded from six polarization-sensitive neurons (POL-neurons) in a total of some 40 *Cataglyphis* preparations. The neurons exhibited spontaneous spiking activity in the dark (Figs. 1b left, 2a) ranging from a few spikes/s to about 30 spikes/s. With polarized light, spike frequency was a sinusoidal function of e-vector orientation with alternating portions of excitation and inhibition (Figs. 1a–c, 2b). The e-vector orientation eliciting maximal spike frequency (Φ_{max}; about 35–60 spikes/s) was oriented approximately 90° to the e-vector orientation of minimal spike frequency (0 to about 20 spikes/s) (Fig. 1a–c). Thus, the POL-neurons of *Cataglyphis* are polarization-opponent units receiving antagonistic input from two e-vector-sensitive analyzer channels with orthogonal orientation of maximal sensitivity. This property was evident with both continuously rotating e-vector orientation (Fig. 1; all six neurons tested) and flashes of polarized light (Fig. 2; two neurons tested).

Removing the UV from the stimulus by a UV-blocking filter (cutoff at 420 nm) abolished the e-vector response (Fig. 1c; tested in three cells). Thus, the POL-neurons are driven by UV light. By inserting a small black screen between the polarizer and the ant's head, either the left, the right, or both eyes

Fig. 1a–d. Response of POL-neurons to rotating e-vector orientation. Data of two neurons shown in a,d and b,c, respectively. a) Response with UV light. b) Spontaneous spiking activity in the dark vs. response with xenon arc white light. c) Missing response (spontaneous activity) with a white stimulus in which the UV was blocked by a 420 nm cutoff filter vs. response with full xenon arc white. a–c) *Above* Original recording traces. Spike amplitudes are about 3 mV (a) and 20 mV (b,c). Ascending *sawtooth trace* indicates rotation of e-vector orientation in clockwise direction and gives a time calibration (4.75 s from 0° to 360°). *Below* Corresponding spike frequencies. *Dots* spike counts per 20° bin of e-vector rotation (corresponding to 0.26 s) taken at 5° intervals; *line* five-bin smoothed data; *abscissa* represents e-vector orientation relative to the ant's long axis. d) Noise and habituation interfering with the e-vector response. *Left* Normal sinusoidal response; *middle* interfering spike bursts and gaps (e.g., see *arrowheads*); *right* strongly habituated response. *Dots*, *line* as in a–c. Descending *sawtooth trace* indicates anticlockwise rotation of e-vector orientation



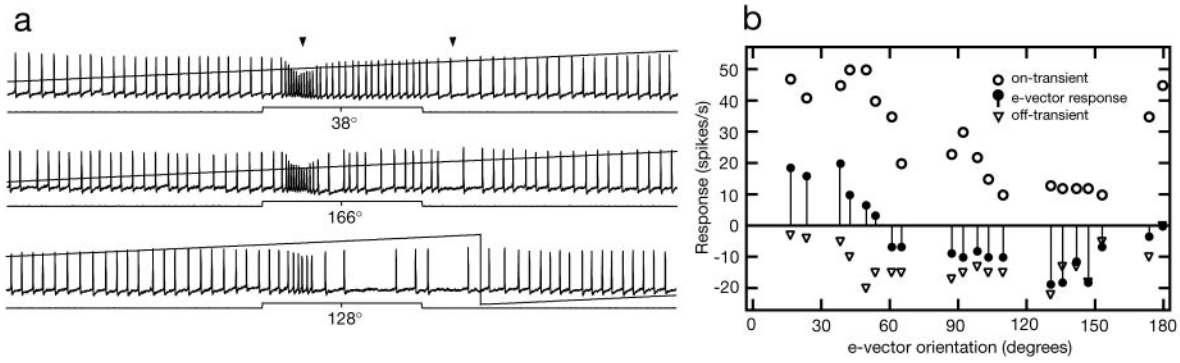


Fig. 2a,b. Response of a POL-neuron to flashes of polarized light. While the polarizer rotated, the shutter opened every 5.4 s, producing 500 ms flashes of polarized light with different e-vector orientations. a) Original recording traces for flashes at three different e-vector orientations. *Ascending line* in each panel indicates rotation of e-vector orientation in clockwise direction; *bottom trace* occurrence of flash; *numbers* e-vector orientation with respect to the ant's long axis at midflash time; total range of e-vector orientation during a flash was 38°. The e-vector response was inhibitory or excitatory depending on e-vector orientation; it was preceded by a short, excitatory light-on transient and followed by an inhibitory light-off transient (*arrowheads*). b) Responses at different e-vector orientations, expressed as response spike frequency minus spontaneous spike frequency, in spikes/s. Positive values indicate excitation, and negative values indicate inhibition. Responses were calculated from the spike counts during the light-on transient (first 200 ms of flash; *empty circles*), the e-vector response (last 300 ms of flash; *filled circles with line to zero*), and the light-off transient (from end of flash to 200 ms postflash; *empty triangles*)

could selectively be shielded from the stimulus during a recording. This experiment could be carried out with one POL-neuron only; the neuron responded only when the right eye was stimulated, i.e., it received input from the DRA of the ipsilateral eye.

The POL-neurons could be driven by both the large-field stimulus (75°) and – depending on the position – by small-field stimuli (20°). Selective stimulation of the section of the DRA just anterior or just posterior to the middle of the elongated DRA (medioanterior and medioposterior stimulus) elicited clear responses (tested in five and four neurons, respectively). Stimuli placed more anterior or contralateral that just touched the visual field of the DRA gave inconsistent results, i.e., they drove only some of the cells. In all, these data indicate that each POL-neuron received input from photoreceptors of different parts of the DRA.

The e-vector orientation of maximal spike frequency, Φ_{max}, was determined for both large-field and small-field stimuli. Although different Φ_{max} values were observed (covering the full 180° range with small medioanterior and medioposterior stimuli), clearly defined Φ_{max} classes as found in crickets (Labhart 1988; Labhart and Petzold 1993) could not be recognized. The following finding suggests that the definition of Φ_{max} in the POL-neurons of *Cataglyphis* is more complicated than in those of crickets. As tested in one cell, selective stimulation with small stimuli of the medioposterior section and the anterior section of the DRA produced substantially different Φ_{max} values, and the Φ_{max} measured with the large stimulus was the resultant of these two angles. Apparently, a large field stimulus containing only one e-vector orientation is not optimal for such a neuron. In cricket POL-neurons Φ_{max} is constant within the whole visual field (Labhart and Petzold 1993).

The observed e-vector responses of the POL-neurons were disturbed in two ways. (a) After some turns of the polarizer the response typically habituated, i.e., spike frequency modulation decreased or was sometimes completely lost (Fig. 1d, compare left and right quarter of graph). The response recovered when stimulation was discontinued for a while either by darkening the stimulus or – when using a small stimulus – by temporarily moving it to another position. (b) The e-vector-controlled sinusoidal spike modulation was often disturbed by "untimely", short spike bursts or activity gaps of unknown origin (Fig. 1d, middle part; for obvious examples see arrowheads). These effects make a quantitative analysis of the physiological properties of *Cataglyphis* POL-neurons difficult. The strong habituation and interfering spike noise are features not observed in cricket POL-neurons (Labhart 1988; Labhart unpublished).

Discussion

The POL-neurons of *Cataglyphis* share some important properties with the POL-neurons studied in field crickets, *Gryllus campestris*. Both exhibit a characteristic polarization opponency (for crickets see Labhart 1988), which is the result of the antag-

onistic action of two e-vector-sensitive analyzer channels with mutually orthogonal orientation of maximal sensitivity. These "opponent analyzers" are represented by the two sets of polarization-sensitive photoreceptors with orthogonally arranged microvilli present in each ommatidium of the dorsal rim area of both insects (Burghause 1979; Herrling 1976; Räber 1979). The antagonism has two advantages: it enhances sensitivity for e-vector contrasts, and it makes the response independent of absolute light intensity (Labhart 1988, 1999).

Both ant and cricket POL-neurons are monochromatic systems. However, whereas cricket POL neurons are driven by blue receptors (Labhart 1988; Labhart and Petzold 1993), those of the ant are UV sensitive (Fig. 1c). This is in accordance with the findings that *Cataglyphis* depends on the polarized UV radiation of the sky for e-vector navigation (Duelli and Wehner 1973), and that the dorsal rim area contains strongly polarization-sensitive UV receptors (Labhart 1986). Thus, of the two spectral types of photoreceptor present in the *Cataglyphis* eye (UV type: $\lambda_{max} = 350$ nm; green type: $\lambda_{max} = 510$ nm; Labhart 1986; Mote and Wehner 1980) it is the UV receptor that gives input to the POL-neurons. Crickets also have UV and green receptors in the unspecialized part of the eye, but for polarization vision they use blue receptors that are present exclusively in the DRA (Labhart et al. 1984). Monochromacy, which implies color blindness, prevents interference between spectral and e-vector information from the sky.

Our knowledge about the POL-neurons of *Cataglyphis* still remains fragmentary. However, the experiments described in this report demonstrate that the POL-neurons of the desert ant *Cataglyphis* (Hymenoptera) are accessible to electrophysiological analysis, and that they share some fundamental properties with the POL-neurons of crickets (Orthoptera).

Acknowledgements. This research was supported by the Swiss National Science Foundation (grant 31-43317.95 to R. Wehner). I thank Dr. Rüdiger Wehner and Martin Speck for critical comments on the manuscript.

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