The Journal of Experimental Biology 210, 3266-3276
Published by The Company of Biologists 2007
doi:10.1242/jeb.007831

Haze, clouds and limited sky visibility: polarotactic orientation of crickets under difficult stimulus conditions

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Accepted 23 July 2007

Summary

Field crickets (*Gryllus campestris* L.) are able to detect the orientation of the electric vector (e-vector) of linearly polarized light. They presumably use this sense to exploit the celestial polarization pattern for course control or navigation. Polarization vision in crickets can be tested by eliciting a spontaneous polarotactic response. Previously, wide and 100% polarized stimuli were employed to induce this behavior. However, field crickets live on meadows where the observation of the sky is strongly limited by surrounding vegetation. Moreover, degrees of polarization (*d*) in the natural sky are much lower than 100%. We have therefore investigated thresholds for the behavioral response to polarized light under conditions mimicking those experienced by the insects in the field. We show that crickets are able to rely on polarized stimuli of just 1° diameter. We also provide evidence that they exploit polarization down to an (average) polarization level of less than 7%, irrespective of whether the stimulus is homogeneous, such as under haze, or patched, such as a sky spotted by clouds. Our data demonstrate that crickets can rely on skylight polarization even under unfavorable celestial conditions, emphasizing the significance of polarized skylight orientation for insects.

Key words: skylight navigation, polarization vision, behavior, *Gryllus campestris*.

Introduction

The sky offers a variety of useful references for visual compass orientation. Celestial cues are effectively at infinity and thus their retinal position in a terrestrial observer does not shift with translational motions but only with rotations. Apart from the sun, the moon, the stars and intensity and spectral gradients, there is a prominent directional signal in the sky that is invisible to the human eye: the celestial polarization pattern. On its way through the atmosphere, sunlight is scattered by air molecules (Rayleigh scattering) and is thereby linearly polarized; i.e. the electric vector (e-vector) of light waves preferentially vibrates in one orientation. The proportion oscillating in the prevailing orientation is called the degree of (linear) polarization (*d*). Both the orientation of the e-vector (angle of polarization) and the degree of polarization depend on the scattering angle (the angle between incoming and outgoing rays). As a result, a pattern of polarized skylight is generated that is linked to the dominant light source illuminating the celestial hemisphere; i.e. the sun during the day and the moon at night (Coulson, 1988; Cronin et al., 2006; Gál et al., 2001; Horváth and Wehner, 1999; Strutt, 1871). In contrast to the sun and the moon, the polarization pattern has the advantage that it extends over the whole sky and therefore it is not shielded completely by scattered clouds or terrestrial objects. Other stray light parameters in the sky, such as the gradients of spectral composition and intensity, are highly susceptible to atmospheric disturbances. This is also true for the degree of polarization whereas the distribution of e-vector orientations is rather stable. Depending on illumination conditions, it can even continue underneath clouds, haze or under a canopy (Barta and Horváth, 2004; Brines and Gould, 1982; Können, 1985; Pomozi et al., 2001). The e-vector pattern thus provides a reliable reference for visual compass orientation or course control.

In crickets, as in many other insect species, a specialized, upward-directed region at the dorsal margin of the compound eye, the so-called dorsal rim area (DRA), is dedicated to polarization vision (Brunner and Labhart, 1987; Burghause, 1979; Labhart and Meyer, 1999). The photoreceptors of the cricket DRA are homochromatic, containing exclusively blue-absorbing visual pigment (λ_{max} ~440 nm), and are strongly sensitive to the e-vector of linearly polarized light. In each ommatidium, two sets of photoreceptors are tuned to mutually orthogonal e-vector orientations. Due to the absence of corneal faceting, missing screening pigment and wide rhabdoms, the visual fields of these ommatidia are substantially increased (half-width of average angular sensitivity ~20°) (Blum and Labhart, 2000; Burghause, 1979; Labhart et al., 1984; Nilsson et al., 1987; Ukhanov et al., 1996; Zufall et al., 1989).

Polarization-sensitive neurons (POL neurons) in the optic lobe are thought to represent the first processing layer in the polarization vision system of crickets. Their spiking activity is a sinusoidal function of e-vector orientation with a 180° period. POL neurons receive antagonistic input through two channels with orthogonal orientations of maximal e-vector sensitivity, which are most likely represented by the two sets of photoreceptors in each ommatidium. The receptive fields of POL neurons are directed to the upper part of the sky and are extremely wide (>60°). This is the result of both optical integration by the photoreceptors and neural integration by the POL neurons, which collect input from about 200 DRA ommatidia (one-third of all dorsal rim ommatidia). POL neurons condition the e-vector information for further processing: as a consequence of the antagonistic input, the contrast of the polarization signal is enhanced and fluctuations in ambient light intensity are ineffective. Spatial integration increases the absolute sensitivity and causes the neurons to respond to the mean e-vector within their visual field rather than to structural details of the polarization pattern (Labhart, 1988; Labhart and Meyer, 2002; Labhart et al., 2001; Petzold, 2001).

Behaviorally, a spontaneous polarotactic response could be elicited by exposing crickets to a large, 100%-polarized stimulus from above (Brunner and Labhart, 1987; Burghause, 1979; Herzmann and Labhart, 1989). However, field crickets live on meadows where sky visibility is often restricted by surrounding vegetation to little more than the zenith. Furthermore, in the blue range of the spectrum, *d* does not exceed 75% in the upper part of the sky even under optimal conditions when the sun is low and the air is dry and clear (Coulson, 1988). In fact, field crickets are normally confronted with considerably lower zenithal *d*-values, since they are active around the clock (Rost and Honegger, 1987) and live in temperate regions (Zahradník, 2002), where haze and clouds are frequent. Yet, there is some evidence that they do indeed rely on skylight polarization when homing to their burrows in the ground (Beugnon and Campan, 1989).

In the present study, we have investigated cricket polarization vision in the laboratory under stimulus conditions mimicking those experienced by the animals in the field. We measured the strength of a spontaneous polarotactic response (Brunner and Labhart, 1987) and assessed the behavioral thresholds of polarization vision by varying stimulus size and degree of polarization. The data are discussed in the light of structural and physiological properties of insect polarization vision systems.

Materials and methods

Animals

Wild field crickets (*Gryllus campestris* L.) were collected near Zurich, Switzerland, as late-instar larvae or adults and kept indoors under long-day conditions (14 h:10 h light:dark cycle; L20W/10S daylight lamps; Osram, Munich, Germany) at 23°C and 60% relative humidity. For our experiments, we used both sexes after the imaginal molt.

Experimental setup

Our testing procedure was based upon the approach used by Brunner and Labhart (Brunner and Labhart, 1987). A small metal pin was attached to the pronotum of the crickets with wax. Therewith, they could be mounted to a balanced arm that kept them in a fixed position and orientation on a white, air-suspended Styrofoam^{TM} ball (diameter 8 cm) with a regular pattern of 32 black dots (diameter 6.5 mm) on its surface (Fig. 1A). Translational and rotational walking movements of the cricket were conveyed to the ball and detected by two pairs of photodiodes that registered the dots on the ball passing by.

The ball protruded from a platform surrounded by a cylinder (inner diameter 19 cm), both painted in matt white. A slowly rotating turntable ($1.8\,^{\circ}\,s^{-1}$) holding the visual stimuli was located 46 mm above the head of the cricket. The position of the turntable was registered by a counter that was reset every 360° by a reed switch to avoid error accumulation. A cone of light produced by a blue LED (Luxeon^{TM} Star Royal Blue; Roithner Lasertechnik, Vienna, Austria; λ_{max}=455 nm, spectral half-width 20 nm) equipped with a collimator lens (Roithner Lasertechnik; beam width 30°) evenly illuminated a circular window (diameter 9.5 cm) in the center of the turntable.

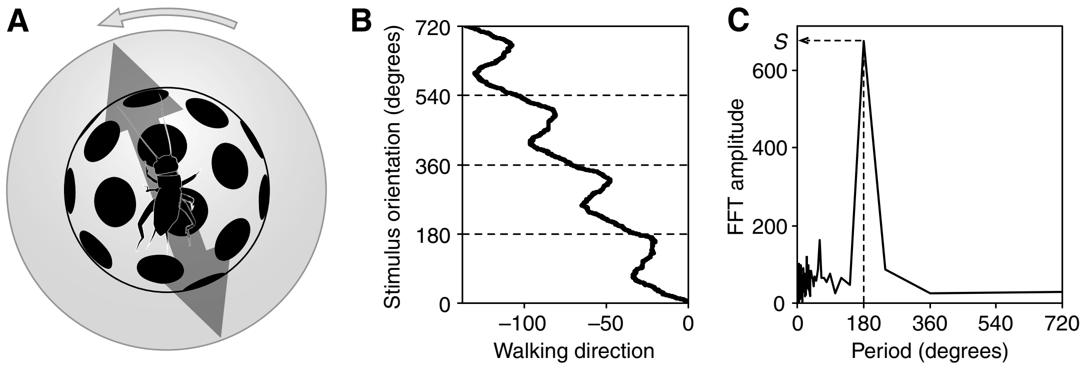

Fig. 1. Data recording and evaluation. (A) Top view of a cricket walking on a Styrofoam^{TM} ball under a slowly rotating, polarized stimulus. The animal is kept on the spot by a balanced arm (not shown). Its walking movements are transferred to the ball and registered by detecting the moving dots on the surface of the ball. (B) Rotational movements of the cricket recorded during two full revolutions of the stimulus (4×180°). Abscissa: walking direction (rotational component of the run) given by the number of dots that passed the detector; positive and negative values indicate right and left turns, respectively. Ordinate: stimulus orientation. Provided that the translation (forward movement) of the cricket was constant, the resulting curve also reflects the virtual walking path. Note the bias in walking direction caused by the inherent turning tendency of the animal. (C) Fourier spectrum of turning speed per degree. Data shown in B were differentiated to remove the bias and then analyzed by a fast Fourier transform (FFT). Abscissa: period of modulation of walking direction. Ordinate: amplitude of FFT signal. Because of the 180° periodicity of the polarized signal, the amplitude at 180° (*S*) was taken as a measure of the strength of the polarotactic response.

Depending on the experiment, different insets were fitted into the window.

The signals encoding the position of the turntable and the walking movements of the cricket were sent to a computer and recorded by a custom-made program based on LabView software (National Instruments, Austin, TX, USA). To eliminate stray light of short wavelengths, the computer monitor was fitted with a yellow Plexiglas window.

Visual stimuli

In all experiments, the basic optical element (‘polarization screen’) consisted of a linear polarizer (HNP’B; Polaroid Corporation, Waltham, MA, USA) overlaid with a diffuser (two sheets of translucent drawing paper) (Fig. 2). It provided a strongly polarized stimulus (d=100%) of a diameter of 92°. For zero controls, this polarization screen was inverted, such that the animal faced the diffuser instead of the polarizer and was thus presented with an unpolarized stimulus (d=0%) of the same intensity.

Depending on the experiment, we combined the polarization screen with additional optical elements (see below).

Stimulus size: To examine the influence of stimulus size on the polarotactic performance of the crickets, the radius (r) of the stimulus was narrowed down stepwise from $2r$=92° to 1° by placing black cardboard annuli below the polarization screen (irradiance 4.0×10^{14} to 1.6×10^{11} quanta cm^{-2} s^{-1}).

Haze: To simulate a hazy sky we combined the polarization screen with an optical retarder (a quarter-wave plate made of overhead projector transparency film). This produced a uniform stimulus of an effective degree of linear polarization between 100% and 0% depending on the ellipticity of light. The ellipticity could be changed by adjusting the principal axis of the retarder relative to the transmission axis of the polarizer. For theoretical reasons, and as demonstrated experimentally, partially plane-polarized light and elliptically polarized light with the same d-value are equivalent for an insect photoreceptor (Labhart, 1996). To make sure that light rays reaching the cricket passed approximately perpendicular through the retarder, the size of the stimulus was limited to 25° (irradiance 6.5×10^{13} quanta cm^{-2} s^{-1}).

Clouds: We also tested the response of the animals to a large (92°) compound stimulus composed of a polarized centre (d=100%) and an unpolarized periphery (d=0%). This simulated an overcast sky with a window in the zenith. We reduced the mean degree of polarization ($\bar{d}$) progressively from 100% to 0% by placing diffuser annuli of different sizes (two sheets of translucent drawing paper with a central aperture) below the polarization screen. In order to avoid strong differences in light intensity, a circular diffuser equal in size to the central aperture was positioned on top of the polarization screen for apertures larger than 8.2°. For the same reason, an additional diffuser was placed below the inverted polarization screen in zero controls and above the polarization screen in motivation controls (irradiance range 2.2×10^{14} to 1.9×10^{14} quanta cm^{-2} s^{-1}).

Light intensities and degrees of polarization were determined by a radiometer (photodiode 222AUV with model 161 optometer; United Detector Technology, Santa Monica, CA,

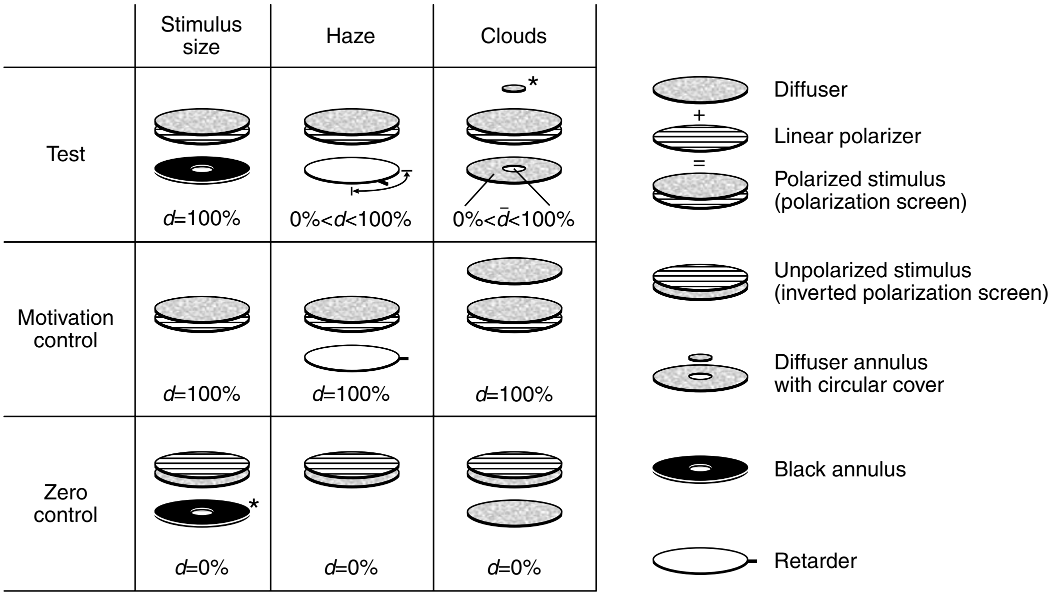

Fig. 2. Optical elements and their combinations for generating the visual stimuli. To produce polarized stimuli for tests and motivation controls, we used a linear polarizer overlaid with a diffuser, a combination termed ‘polarization screen’. For the zero controls, the polarization screen was inverted, thus resulting in an unpolarized stimulus. Depending on the experiment, the polarization screen was combined with an additional diffuser, with an optical retarder or annuli consisting of opaque or diffusing material (for details see text). Note that the maximal diameter of the stimulus (not shown) was 92° for Stimulus size and Clouds experiments but 25° for the Haze experiment due to technical reasons. Elements marked with an asterisk were used under specific experimental conditions only. The resulting degree of polarization (d or $\bar{d}$) is indicated at the bottom of each table cell.

USA) at the position of the cricket head. For polarization measurements, the detector was fitted with a wideband blue filter (BG 28; Schott AG, Mainz, Germany) and a high-quality linear polarizer (HNP'B; Polaroid Corporation). The degree of polarization d for homogeneous stimuli (Haze) and $\bar{d}$ for composed stimuli (Clouds) was calculated from the photometer signals (intensity I) as follows: d or $\bar{d}=(I_{\max}-I_{\min})/(I_{\max}+I_{\min})$, with $I_{\max}$ and $I_{\min}$ being the mean values of the two maximal and the two minimal intensities recorded during a full rotation (360°) of the turntable.

Testing procedure

All three experiments (Stimulus size, Haze, Clouds) were carried out in a darkroom at 24–28°C and 45–60% relative humidity. A single run (recording of walking movements) lasted for 400 s. During this time, the turntable completed two full revolutions, i.e. each e-vector orientation (if present) occurred four times because of the 180° periodicity of the linear polarizer. A series of runs (recordings from one individual for all different conditions of an experiment) included tests, zero controls (runs under an unpolarized stimulus) and motivation controls (runs under a large or medium-sized, 100%-polarized stimulus). Depending on the experiment, either every single test run (Clouds) or each complete series recorded in one session (Stimulus size, Haze) was preceded and followed by a motivation control. Stimulus transitions were smooth, in order not to startle the walking cricket, and took just a few seconds.

Data evaluation

Recordings were analyzed by custom-made programs in MATLAB® (The MathWorks, Natick, MA, USA). For each run, we calculated a value S, which quantifies the strength of the behavioral response to polarized light by taking the amplitude and the regularity of periodic changes in walking direction into account. Several measures have previously been used for this purpose (Brunner and Labhart, 1987; Herzmann and Labhart, 1989; Mappes and Homberg, 2004; von Philipsborn and Labhart, 1990). They were derived empirically and were defined in a slightly different way depending on the aim of the study. Our approach is based on the theoretical consideration that the behavioral data must show a periodicity of 180°. Developed in our laboratory, this idea was also taken up for recent experiments on locust orientation (Mappes and Homberg, 2007). We calculated the measure S in two steps: (1) a differentiation and (2) a Fourier transformation. (1) From the raw data (stimulus orientation and walking direction) (Fig. 1B), we computed the change in walking direction as a function of stimulus orientation, i.e. turning speed per degree. This differentiation step removes a generally observed linear offset (bias) in the raw data caused by a directional preference of the animal (see Fig. 1B). (2) After differentiation, the data were analyzed by a fast Fourier transformation (FFT). Given the 180° periodicity of the polarization signal, any responses to it should occur with a periodicity of 180°. Hence, we took the amplitude of the 180° component in the Fourier spectrum as a measure of the polarotactic response of the cricket. This value was called S (strength of response) (Fig. 1C).

If S was >200 and at least 2.5 times the mean of the amplitudes at 120° and 240°, a motivation control was regarded as positive (clear polarotactic response present). No signals are expected at 120° nor at 240°, and therefore the corresponding FFT amplitudes were chosen as references reflecting the strength of random noise in the Fourier spectrum.

Previous behavioral studies have shown that the readiness of the crickets to walk and to respond to polarized light varies considerably in the behavioral assay employed (Brunner and Labhart, 1987; Herzmann and Labhart, 1989). Data were therefore analyzed only if they met the following criteria: (1) The animal walked without interruption for at least three of the four 180° periods of a run and (2) a clear response to polarized light was present in both the preceding and the following motivation control. For statistical evaluations, we also corrected for daily or individual differences in responsiveness of the crickets by determining the strength of the polarotactic response relative to the mean response strength in the two motivation controls (S/S_{mot}). Unless mentioned otherwise, the statistics rely on Wilcoxon signed rank tests for Stimulus size and Haze experiments, and on Mann–Whitney tests for the Clouds experiment. Significance levels were corrected for multiple comparisons by Bonferroni-Holm.

Results

Motivation

In Stimulus size and Haze experiments, an entire test series with a positive motivation control at the beginning and at the end had to be recorded from an individual in one session. This implied that the cricket had to walk for at least 1–2 hours without interruption. Animals that accomplished this task showed no reduction in the strength of their polarotactic response in spite of the long walking time: responses in the first and last positive motivation control did not differ significantly from each other (P=0.93 and 0.44; compare gray triangles and diamonds in Fig. 3B and Fig. 4B, respectively). Two good performers actually kept on responding to the polarized light stimulus for over 8 h and were finally stopped by the experimenter. However, most of the individuals did not walk and respond continuously over an extended period of time (see also Brunner and Labhart, 1987; Herzmann and Labhart, 1989); in our study, 87% of the crickets never completed a series within one session and all of their data had to be discarded. For the Clouds experiment, we therefore adopted another testing protocol. We subjected the crickets to a motivation control before and after every single test run. Thus, all data recorded up to the last positive motivation control could be evaluated.

Stimulus size

In sun-exposed meadows, which is the preferred habitat of field crickets, sky visibility can be restricted by terrestrial objects, e.g. by grass and flowers (Fig. 3A), bushes or trees. To examine the influence of stimulus size on the polarotactic orientation behavior, we stepwise reduced the radius r of a strongly polarized stimulus (d=100%) presented at the zenith. For each individual, a complete series of runs was recorded in one session. If two or more series could be measured from the same individual (four cases), they were averaged to avoid a bias caused by multiple contribution of one individual to the data. The results from 11 individuals (16 series) are plotted in Fig. 3B–D. Test data ($2r$=48° to 1°; d=100%) are indicated by

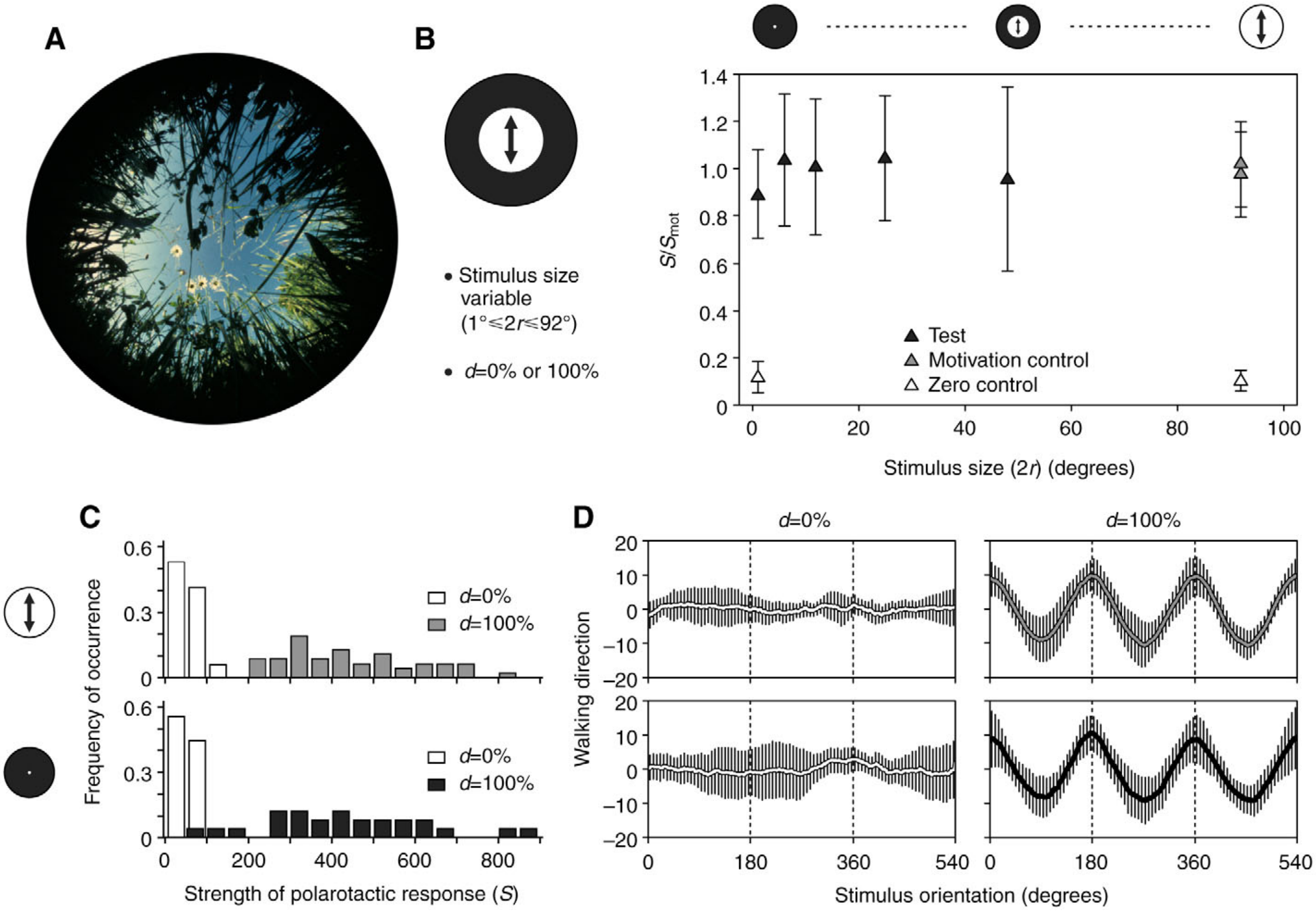

Fig. 3. Stimulus size experiment. (A) 180° fisheye view of the celestial hemisphere taken by a camera positioned in a meadow. A considerable part of the sky is obstructed by vegetation. (B–D) Polarotactic response as a function of stimulus size. The radius (r) of a zenithal stimulus was reduced from $2r$=92° to 1° with a degree of polarization (d) of either 100% or 0%. Tests ($2r$=1° to 48°, d=100%) are indicated by black, motivation controls ($2r$=92°, d=100%) by gray, and zero controls ($2r$=1° or 92°, d=0%) by white (16 series of 11 individuals). (B) Survey of results. The relative strength of the polarotactic response (S/S_{mot}, mean ± s.d.) is plotted against stimulus size. (C,D) Comparison between the largest (92°, top row) and the smallest (1°, bottom row) stimulus. (C) Distribution of S-values. (D) Walking direction of the crickets given by the number of dots that passed the detector (mean ± s.d.; positive and negative values indicate right and left turns, respectively) plotted *versus* stimulus orientation. Prior to averaging, data were standardized, i.e. the runs were phase-adjusted and corrected for an overall deviation from a straight walking path by subtraction of the inherent turning tendency. Note: a reduction in stimulus size to a diameter as low as 1° did not impair the polarotactic response.

black, motivation controls ($2r$=92°; d=100%) by gray, and zero controls ($2r$=92° or 1°; d=0%) by white (triangles in Fig. 3B, columns in Fig. 3C, lines in Fig. 3D).

Fig. 3B summarizes the relative strength of the polarotactic response (S/S_{mot}; mean ± s.d.) under all experimental conditions. A reduction of stimulus size down to $2r$=1° did not significantly influence the strength of the polarotactic response (P=0.41; Friedman test; see black triangles in Fig. 3B). However, for identical stimulus sizes, the response values dropped significantly if the degree of polarization was lowered to 0% (P<0.01 for $2r$=92° or 1°; see white triangles in Fig. 3B).

This overall behavior is further elucidated by the following details: Fig. 3C depicts the distribution of S-values (absolute strength of polarotactic response given by the amplitude of the 180° component in the Fourier spectrum) measured for the largest ($2r$=92°, upper diagram) and the smallest ($2r$=1°, lower diagram) stimulus. In spite of the discrepancy in stimulus size, the results are very similar. In both situations, the S-values for unpolarized (d=0%, white columns) and polarized light (d=100%, gray or black columns) differ clearly. For unpolarized light, S-values do not exceed 150, whereas for polarized light they are broadly distributed between 50 and 900, with two-thirds of all data between 300 and 650. S-values for the test situation (black columns) scatter slightly more than for the motivation controls (gray columns) as a consequence of our evaluation criteria: motivation controls had to be positive (clear polarotactic response present), otherwise the whole series was discarded, but for the tests no such screening took place. In Fig. 3D, the walking direction of the crickets (mean ± s.d.) is plotted *versus* stimulus orientation for the largest ($2r$=92°, top row) and the smallest ($2r$=1°, bottom row) stimulus. Before averaging, data had to be standardized. The runs were therefore corrected for an overall deviation from a straight walking path by subtraction of the inherent turning tendency and phase-adjusted if the *S*-value was higher than the 99% quantile of the zero control, i.e. if the presence of a polarotactic response was likely. For constant forward translation of the cricket, the curves in Fig. 3D can also be considered as normalized walking paths.

It is evident that the polarotactic response is not impaired if stimulus size is reduced from 92° to 1°: independent of stimulus size, the crickets' walking direction changes periodically with stimulus orientation for high *d*-values following a sinusoidal function (right column). Only under unpolarized light does this modulation of walking direction disappear (left column).

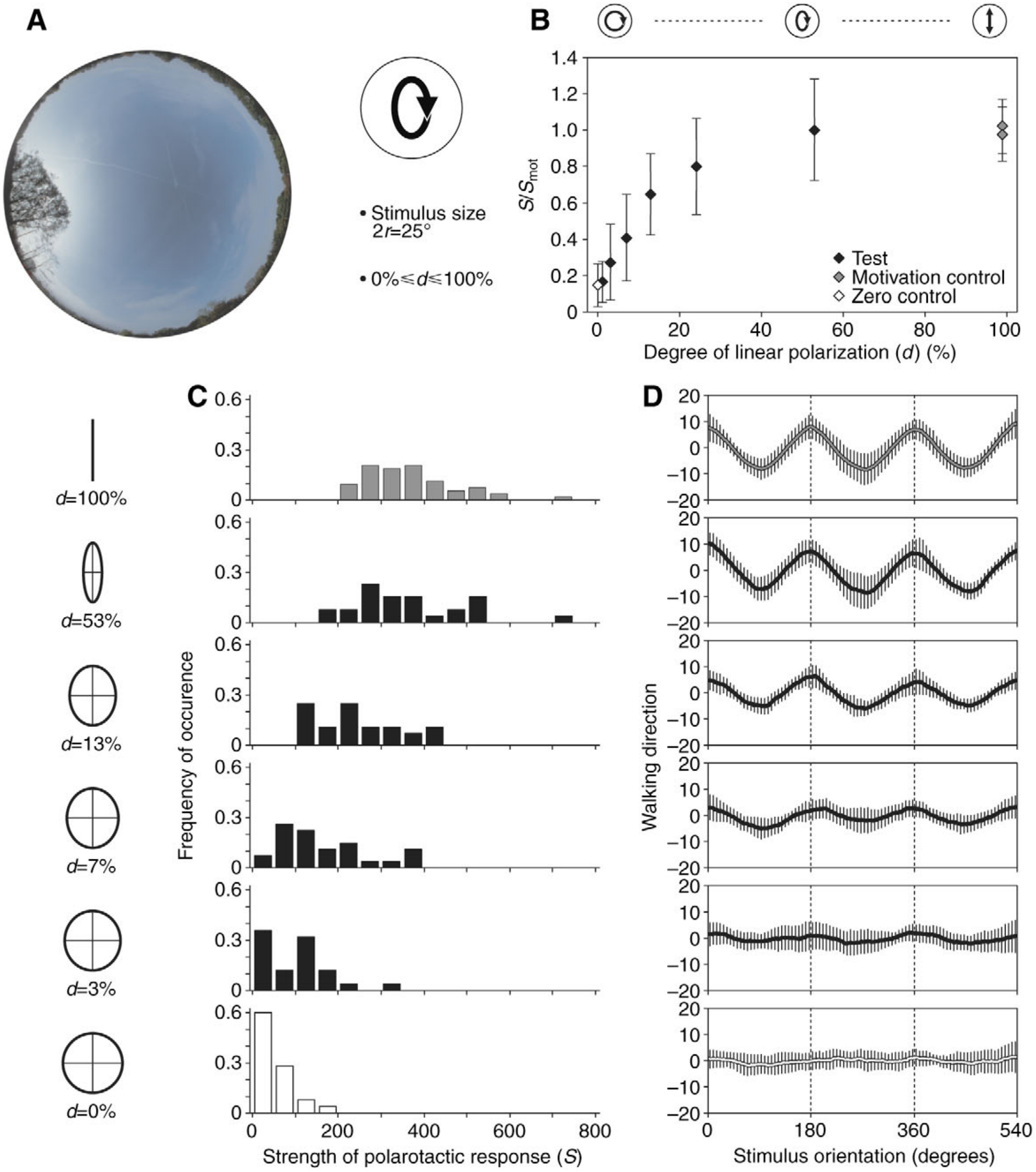

Fig. 4. Haze experiment. (A) 180° fisheye view of the celestial hemisphere on a hazy morning. Compared with clear atmospheric conditions, the degree of polarization across the whole sky is reduced. (B,C) Polarotactic response as a function of the degree of polarization for a uniform stimulus. The effective degree of linear polarization (*d*) of a medium-sized (25°) zenithal stimulus was reduced from *d*=100% to 0% by changing the ellipticity of light (see Materials and methods). Test data (*d*=1% to 53%) are indicated by black, motivation controls (*d*=100%) by gray, and zero controls (*d*=0%) by white (24 series of 17 individuals). (B) Survey of results. Relative strength of the polarotactic response (S/S_{mot}; mean ± s.d.) plotted against the effective degree of linear polarization. (C) Distribution of *S*-values and (D) modulation of walking direction with stimulus orientation for some of the polarization levels tested (see polarization ellipses to the left). Data in D are normalized and plotted as described in Fig. 3D. Note: a reduction in polarization to *d*=53% did not impair the polarotactic response. With lower *d*-levels, the response strength decreased. However, there was a statistically significant orientation to polarized light at least down to a *d*-level of 7% ($P<0.01$).

Haze

From the perspective of a field cricket in a meadow, the zenith is the part of the sky that is most often free of terrestrial objects (Fig. 3A) and that is therefore available for orientation. However, according to the law of Rayleigh scattering, the higher the solar elevation the lower the degree of polarization becomes in the zenith. Even at low solar elevations, which would allow high degrees of polarization in the zenith, d can be substantially reduced by the presence of haze (Fig. 4A). With this natural situation in mind, we investigated the polarotactic performance of crickets under a medium-sized ($2r$=25°) zenithal stimulus for which the degree of polarization was gradually lowered from 100% to 0% by changing the ellipticity of light. Data acquisition and evaluation were as described for Stimulus size. The results from 17 individuals (24 series) are plotted in Fig. 4B–D. Again, test data (d=1% to 53%) are indicated in black, motivation controls (d=100%) in gray, and zero controls (d=0%) in white (diamonds in Fig. 4B, columns in Fig. 4C, lines in Fig. 4D).

Fig. 4B resumes the relative strength of the polarotactic response (S/S_{mot}; mean ± s.d.) for all conditions investigated in this experiment. A reduction in polarization level to 53% had no significant effect on the strength of the polarotactic response (P=0.83). With lower degrees of polarization, response values declined ($P<0.01$ for $d\leqslant 24\%$), but a significant difference to the zero control (white diamond) was present at least down to d=7% ($P<0.01$). For d=3% the response values were also still higher than those of the zero control (P=0.044); however, this distinction was not significant after a Bonferroni-Holm correction for multiple comparisons.

More details are given in Fig. 4C,D. Fig. 4C shows the distribution of S-values, and Fig. 4D illustrates the modulation of walking direction with stimulus orientation for some of the polarization levels tested. The respective d-values are depicted by polarization ellipses to the left. With lower degrees of polarization, the distribution of S-values (Fig. 4C) gradually shifts towards the distribution of the zero control (bottom row). S-values decline since the modulation of walking direction (Fig. 4D) decreases in both amplitude and precision: maxima, for instance, become less prominent and do not occur every 180° at exactly the same stimulus orientation any more. Note again that a reduction in d to ~50% does not reduce the response (compare the first and second rows). Furthermore, a sinusoidal modulation with a periodicity of 180° is clearly present down to d=7% and is even faintly visible in the averaged run data for d=3%. Two of the 17 individuals tested under d=3% actually responded strongly (for an example, see Fig. 5); their runs even satisfied the strict criteria of positive motivation controls (see Materials and methods).

Clouds

Besides terrestrial objects, clouds can also obstruct parts of the celestial polarization pattern (Fig. 6A). In contrast to an opaque obstacle such as a tree, a cloud is often translucent. However, light passing through or reflected by a cloud is partly or totally unpolarized (Können, 1985). Together with the polarized light coming from areas of blue sky or from the air column between a cloud and the observer (Brines and Gould, 1982; Pomozi et al., 2001; Stockhammer, 1959), this results in a decrease of the overall degree of skylight polarization. We simulated such a situation by presenting a large ($2r$=92°) zenithal stimulus consisting of a strongly polarized centre (d=100%) and an unpolarized periphery (d=0%). By varying the ratio of the two components, we changed the mean degree of polarization ($\bar{d}$).

Results from 12 individuals are shown in Fig. 6B. Test data ($\bar{d}$=1% to 74%, number of runs N=17–19) are indicated by black, motivation controls ($\bar{d}$=100%, N=162) by gray, and zero controls ($\bar{d}$=0%, N=17) by white. The relative strength of the polarotactic response (S/S_{mot}; mean ± s.d.) is plotted against the mean degree of polarization for all conditions investigated. A reduction of $\bar{d}$ to 49% did not impair the polarotactic response of the crickets significantly (P=0.83). Below 17% polarization, response values declined ($P<0.01$). However, a significant difference to the zero control (white square) was present at least down to $\bar{d}$=10% ($P<0.01$). At $\bar{d}$=5% the polarotactic response was lost (P=0.30).

Fig. 7 compares the data of the two experiments in which the degree of polarization was gradually reduced; the relative strength of the polarotactic response (S/S_{mot}, mean ± s.d.) is plotted against the degree of linear polarization for the uniform stimulus simulating haze (black diamonds) and the compound stimulus simulating clouds (white squares). The results of the two experiments basically agree, indicating that the cricket polarization vision system is insensitive to the spatial structure of a polarized stimulus. In both cases, the mean strength of the orientation response to polarized light is a nonlinear function of d, with decreasing slope, closely resembling a root function (root index=2.75; R^2=0.92 for Haze and 0.86 for Clouds).

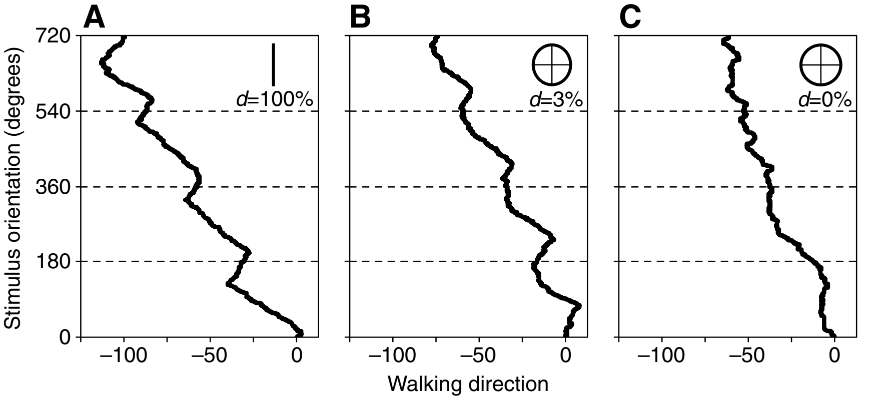

Fig. 5. Polarotactic behavior of an especially sensitive cricket under uniform stimuli of different degrees of polarization (d). (A–C) Rotational movements with d=100%, 3% and 0%, respectively (see polarization ellipses in the diagrams). Abscissa: walking direction (rotational component of the run) given by the number of dots on the ball that passed the detector; positive and negative values indicate right and left turns, respectively. Ordinate: stimulus orientation. Note that the periodic modulation of walking direction is almost as strong for 3% as for 100% polarization.

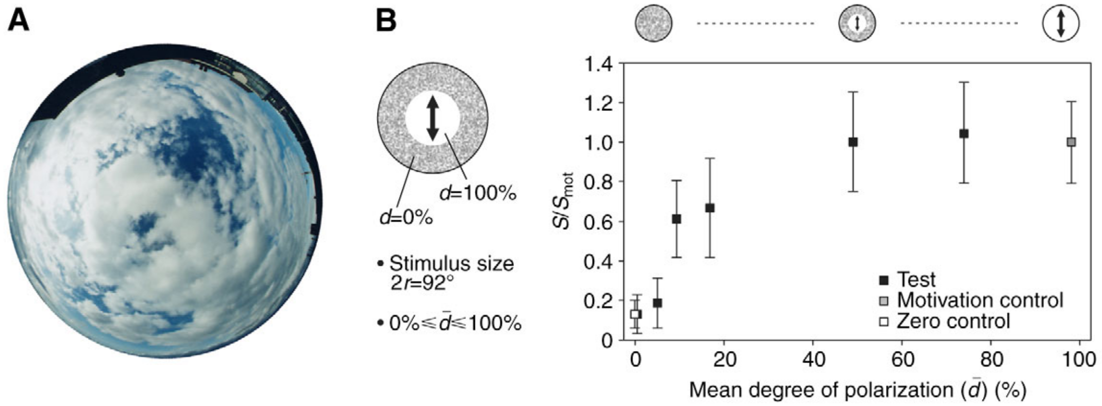

Fig. 6. Clouds experiment. (A) 180° fisheye view of the celestial hemisphere on a cloudy day. The mean degree of polarization is reduced since polarized light from patches of blue sky mixes with partly or totally unpolarized light from clouded sky regions. (B) Polarotactic response as a function of the mean degree of polarization ($\bar{d}$) for a compound stimulus. For a wide (92°) zenithal stimulus, $\bar{d}$ was reduced from 100% to 0% by changing the proportion of polarized to unpolarized light. Data are from 12 individuals. Tests are indicated by black symbols ($\bar{d}$=1% to 74%, *N*=17–19), motivation controls by gray symbols ($\bar{d}$=100%, *N*=162) and zero controls by white symbols ($\bar{d}$=0%, *N*=17). Note: a reduction in polarization to $\bar{d}$=49% did not impair the polarotactic response. With lower degrees of polarization, response values declined, but the orientation to polarized light was statistically significant at least down to a $\bar{d}$-level of 10% (*P*<0.01).

Discussion

Stimulus size

We have shown that field crickets clearly respond to a strongly polarized light stimulus in the zenith even if its size is reduced to just 1°. In the compound eye of adult field crickets, the DRA comprises ~600 upward-directed ommatidia and is 13–17 rows wide (Blum and Labhart, 2000; Brunner and Labhart, 1987; Labhart, 1988). The sampling frequency of the DRA is about one ommatidium per degree, the ommatidia have large acceptance angles of approximately 20° (Blum and Labhart, 2000), and both on- and off-axial polarization sensitivities are strong (Labhart et al., 1984). On the basis of these properties, we estimate that a 1° stimulus in the zenith stimulates at least one-third of all DRA ommatidia.

In our experiment, light intensity decreased with stimulus size. For a single photoreceptor in the cricket DRA, the threshold intensity for a reliable response to polarized light is in the order of 10^{10} quanta cm^{-2} s^{-1} (Labhart et al., 2001), which is about 10 times lower than the irradiance of our 1° stimulus. However, because of neural integration and polarization antagonism, POL neurons in the optic lobe show significant (half-maximal) responses at 10^{7} quanta cm^{-2} s^{-1} already (Labhart et al., 2001). Behavioral experiments yielded a similar threshold (Herzmann and Labhart, 1989). The intensity of our 1° stimulus was therefore approximately 10^{4} times higher than the threshold intensity of the cricket e-vector detection system.

For crickets walking in a meadow, the view of the sky is restricted by grass blades and other leaves. Could unpolarized light transmitted by leaves interfere with polarized skylight? Since chlorophyll strongly absorbs in the blue spectral range, the vegetation will appear dark against the blue sky for the blue-sensitive photoreceptors in the cricket DRA, and light stimulating the DRA will mostly be skylight. Hence, our experimental situation compares well with field conditions. Our data suggest that crickets are able to exploit even a minute patch of sky visible through dense vegetation given that the degree of polarization in this particular celestial spot is high enough.

There are but a few systematic studies on the minimum visual angle necessary for polarization vision in other insects. Data that are directly comparable to ours only exist for honey bees (*Apis mellifera*) (Edrich and von Helversen, 1976). The spatial threshold of polarization vision was tested by observing the waggle dances of foragers indicating the direction of a previously visited feeding site to hive mates on a horizontal comb. A strongly polarized light spot of variable size was presented at the zenith. Taking the scatter in the direction of waggle dances as an inverse measure for the degree of orientation, the conclusion was that the bees were able to orient by means of a polarized light stimulus of less than 1°. However, in contrast to crickets, the performance of the bees markedly decreased with stimulus size. Edrich and von Helversen suggested that the decreasing performance of the bees was primarily due to the decline in light intensity and was not caused by the small size of the stimulus (Edrich and von Helversen,

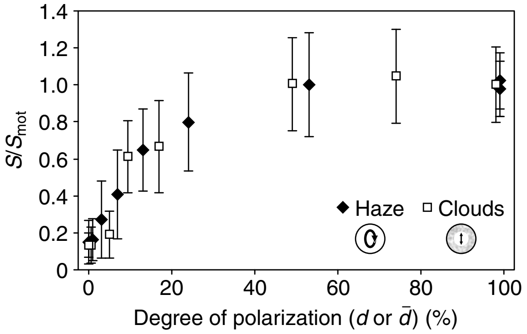

Fig. 7. Comparison between the Haze and Clouds experiments. The relative strength of the polarotactic response (S/S_{mot}; mean ± s.d.) is plotted against the degree of linear polarization (d or $\bar{d}$) for a uniform (black diamonds) and a compound stimulus (white squares). Note: the results are basically the same under both stimulus conditions.

1976). The polarization vision system of the strictly day-flying honey bees is 10^3–10^4 times less sensitive than that of field crickets (Herzmann and Labhart, 1989; von Helversen and Edrich, 1974), insects that are active by day and by night (Rost and Honegger, 1987). Furthermore, there is an essential difference in the dioptric design of the eye; as in crickets, the optics of the honey bee DRA is degraded. Although the corneal lenses are clear in the centre, they contain light-scattering pore canals at the margins (Meyer and Labhart, 1981). As a consequence, the angular sensitivity functions of the photoreceptors show a relatively narrow peak in the centre (average half-width ~5.5°) and a wide, flat brim in the periphery in which light sensitivity decreases only slowly (Labhart, 1980). The e-vector sensitivity of the UV receptors (mediating polarization vision in bees) is high even 20–30° off axis (Labhart, 1980). Assuming an inter-ommatidial angle of about 3° (Edrich and von Helversen, 1976), we conclude that at adequate light intensities a polarized 1° stimulus at the zenith stimulates a large fraction of the approximately 140 DRA ommatidia of the bee (Sommer, 1979). However, the light sensitivity of the DRA photoreceptors decreases sharply within a few degrees from the optical axis. For small stimuli, which tend to produce weak irradiances at the eye, the number of ommatidia delivering reliable information is therefore considerably reduced. In *Megalopta genalis*, a nocturnal bee featuring a DRA with corneal structures similar to those of the honey bee, angular sensitivity functions of photoreceptors are much broader (average half-width ~13.8°) probably due to the 6–7 times wider diameter of the rhabdom (Greiner et al., 2007).

Other studies on the influence of stimulus size on polarized light orientation in honey bees and desert ants (*Cataglyphis bicolor*) were designed to assess the size requirements for correct celestial e-vector navigation rather than the threshold for e-vector detection. Bees or ants were trained to a food source under the unrestricted natural sky and were tested under small windows admitting either skylight or artificially polarized light (Duelli, 1975; von Frisch, 1965; Zolotov and Frantsevich, 1973). In contrast to the previous bee study (Edrich and von Helversen, 1976), the performance of the animal was not measured by the degree of orientation but by the deviation of the observed dance or walking direction from the trained direction. The minimal extension of the celestial e-vector pattern necessary for compass navigation was 10–15° for honey bees (von Frisch, 1965; Zolotov and Frantsevich, 1973) and ~10° for desert ants (Duelli, 1975). It is difficult to compare these results to ours for the following reasons: The position of the stimulus in the visual field, its degree of polarization and its e-vector composition changed in the experiments. Studies on the rules applied by navigating insects have revealed that bees and ants rely on a rather generalized representation of the e-vector pattern in the sky (Brines and Gould, 1979; Fent, 1986; Rossel et al., 1978). This can cause navigational errors if the view on the celestial hemisphere differs for training and test situations. Under natural conditions, a dramatic change of sky visibility between an outgoing and an incoming run of a foraging desert ant will hardly ever occur. For the recruitment dances of honey bees, modifications do not matter as long as all workers interpret mistakes consistently. The results of the navigation studies mentioned above do therefore neither specify the lower limit of e-vector detection nor do they necessarily give the relevant spatial threshold in nature.

A systematic investigation on the minimal visual angle necessary for polarization vision would be particularly desirable for ants. In none of the ants investigated so far was the optics of the DRA degraded (Labhart and Meyer, 1999); in *C. bicolor* the acceptance angle (5.5°) (Labhart, 1986) is slightly smaller than the interommatidial angle (6°) (Zollikofer, 1981; Zollikofer et al., 1995), meaning that the visual fields are relatively narrow and separate. A 1° stimulus will thus stimulate just a few ommatidia. Therefore, spatial integration by POL neurons in the optic lobe of *Cataglyphis* must be based on neural integration alone (Labhart, 2000), and stimulus size may play an important role in *Cataglyphis* ants.

Haze and clouds

We have investigated the influence of the degree of polarization (d) on the polarotactic behavior of field crickets under two conditions: a uniform and a compound light stimulus presented at the zenith simulating a hazy and a cloudy sky, respectively. For both experiments, we obtained basically the same results (see Fig. 7). Considering the strong spatial integration by the e-vector detection system of the cricket, this is not surprising; since the celestial polarization signal is averaged by optical and neural mechanisms over a large area of sky (Labhart et al., 2001), it is irrelevant if a certain degree of polarization results from a mixture of polarized and unpolarized light as under a partly clouded sky or from an overall reduced degree of polarization as under a uniform haze cover.

Our data show that a zenithal stimulus with an astonishingly low d-value suffices for a field cricket to orient. Statistically, the behavioral threshold is located between 5% and 7% polarization, but two individuals even responded at 3% polarization (see Fig. 5). Electrophysiological recordings have demonstrated that POL neurons can signal e-vector information down to d-levels of ~5% (Labhart, 1996), which corresponds fairly well to the behavioral threshold. As previously noticed for the intensity threshold of polarization vision (Herzmann and Labhart, 1989; Petzold and Labhart, 1993), there is a close correlation between the absolute sensitivity of the POL neurons and the one for the whole organism.

Due to a presumed feedback mechanism, the response strength of polarization-sensitive neurons in the central complex of crickets is independent of d, at least down to d=18% (M. Sakura, personal communication). The same is true for the polarotactic behavior of crickets but only down to 50% polarization. Between 50% and 20% polarization, the behavioral response decreases only slightly although to a statistically significant degree. The slight divergence between electrophysiology and behavior may be explained by the following argument: while the signaling intensity remains constant, the signaling precision of central complex neurons at low d-values may be reduced, explaining the reduction in the behavioral performance.

In the field, crickets are frequently facing low degrees of polarization. Although under optimal conditions the degree of polarization measured in small patches of sky can reach 75% in the blue range of the spectrum (Coulson, 1988), spatial integration by the POL neurons over a large area of sky results in a considerably lower maximally experienced *d*-level (Labhart, 1999). This is because both e-vector orientation and degree of polarization vary across the sky (Coulson, 1988). Mean degrees of polarization in a celestial window similar in size to the visual field of cricket POL neurons reach 51–60% at most (Horváth and Wehner, 1999; Labhart, 1999; Lambrinos et al., 1997). Due to haze and clouds, and for high solar elevations, *d*-levels are often further reduced (Brines and Gould, 1982; Labhart, 1999; Pomozi et al., 2001). Measurements with an opto-electronic model of a cricket POL neuron under a variety of celestial conditions yielded *d*-levels of only 13% and 28% (medians) in the solar and anti-solar part of the sky, respectively (Labhart, 1999). Thus, the low detection threshold of the cricket polarization vision system is certainly justified. To be useful, weak celestial polarization signals must contain reliable directional information, i.e. they should indicate the same e-vector orientation as in clear skies. Measurements with the opto-electronic POL neuron model revealed that the precision of the directional signal in the sky was indeed high even under strong disturbances by clouds as long as the *d*-level was $\geqslant$5% (Labhart, 1999).

Concerning other insect species, the minimal *d*-level for polarization vision has only been investigated systematically in honey bees. By qualitative observations of dancing bees under a patch of blue sky, von Frisch determined a behavioral threshold of d~10% with a ‘transition range’ between 7% and 15% polarization (von Frisch, 1965). Quantitative measurements by Edrich and von Helversen under a zenithal polarized stimulus confirmed that bees can orient by a 10% stimulus (Edrich and von Helversen, 1987): lower *d*-values were not tested. However, it seems doubtful that honey bees, with their elaborate navigation system, are less polarization sensitive than crickets. We rather assume that differences in the testing procedure and evaluation method are responsible for the slightly higher threshold determined in bees.

Conclusions

Polarization vision in field crickets is an extremely sensitive and robust sensory system. It can deal with very low light intensities (Herzmann and Labhart, 1989; Labhart et al., 2001), low degrees of polarization (present study) and very small stimulus sizes (present study). Previous experiments have shown that crickets respond to polarized light at intensities that are even lower than the effective quantum flux under the clear, moonless night sky (Herzmann and Labhart, 1989). Here, we provide evidence that crickets exploit polarized stimuli down to $d<7\%$, which implies that skylight is useful for e-vector orientation even under unfavorable meteorological conditions or at high solar elevations (Pomozi et al., 2001). We also demonstrate that crickets are able to rely on a tiny spot of polarized light simulating a minute patch of sky visible through dense vegetation. In fact, our data suggest that, as a result of spatial integration (Labhart et al., 2001), there is no threshold concerning stimulus size at all, provided that the light intensity and the degree of polarization are high enough.

Crickets sitting in a meadow may often experience a combination of unfavorable stimulus conditions, such as a restricted view of the sky along with a low *d*-level. How does this affect the orientation performance? We believe that the minimal *d*-level for e-vector detection does not depend on stimulus size since a reduced stimulus size in itself does not make e-vector detection more difficult for a cricket (Fig. 3). The following findings support this view: although stimulus size in the Haze (25°) and Clouds (92°) experiments differed considerably, the strength of the polarotactic response was basically the same for a given degree of polarization, including the threshold level. This seems to be true for honey bees as well. When tested under a stimulus of 4.7° (Edrich and von Helversen, 1987), the bees did not show a higher threshold for the degree of polarization than under a 15° stimulus (von Frisch, 1965). In another study, the polarotactic orientation of bees under a variety of stimulus sizes did not improve noticeably if the degree of polarization was increased from 30–40% to 90% (Zolotov and Frantsevich, 1973). Thus, at least in crickets and bees, stimulus size and *d*-level do not seem to interfere with each other.

A reduction in stimulus size is usually accompanied by a decline in light intensity. However, the polarotactic response of crickets was previously found to be intensity independent above a critical light level (Herzmann and Labhart, 1989). This is based on the polarization-opponent properties of the POL neurons in the optic lobe (Labhart, 1988), by which information on light intensity is filtered out. We therefore propose that, above a critical level, light intensity has no influence on the threshold of the degree of polarization.

When haze, clouds or terrestrial obstacles reduce sky visibility, orientation by polarized skylight outplays orientation by the sun. Such situations might have driven the evolution of sensory systems for detecting skylight polarization and it therefore makes sense that the e-vector detection system of crickets can deal with low *d*-levels and spatially restricted stimuli.

List of abbreviations

d	degree of polarization (%), polarization level
$\bar{d}$	mean degree of polarization (%), polarization level
DRA	dorsal rim area
e-vector	electric vector of light
FFT	fast Fourier transform
N	number of runs
r	radius
S	strength of behavioral response to polarized light
S_{mot}	mean strength of response in motivation controls
POL neuron	polarization-sensitive neuron in the cricket optic lobe

We thank Franziska Baumann for assistance with the crickets, Hansjörg Baumann and Helmut Heise for technical support, Dr Stefan Schuster for advice on the evaluation method, Drs Lorenz Gygax and Adrian Roellin for statistical consulting and Dr Midori Sakura, Tobias Seidl and Martin Kohler for valuable discussions throughout the project. This research was supported by a grant of the ‘Studienstiftung des Deutschen Volkes’ to M.J.H.

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