Large variation among photoreceptors as the basis of visual flexibility in the common backswimmer

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The common backswimmer, Notonecta glauca, uses vision by day and night for functions such as underwater prey animal capture and flight in search of new habitats. Although previous studies have identified some of the physiological mechanisms facilitating such flexibility in the animal’s vision, neither the biophysics of Notonecta photoreceptors nor possible cellular adaptations are known. Here, we studied Notonecta photoreceptors using patch-clamp and intracellular recording methods. Photoreceptor size (approximated by capacitance) was positively correlated with absolute sensitivity and acceptance angles. Information rate measurements indicated that large and more sensitive photoreceptors performed better than small ones. Our results suggest that backswimmers are adapted for vision in both dim and well-illuminated environments by having open-rhabdom eyes with large intrinsic variation in absolute sensitivity among photoreceptors, exceeding those found in purely diurnal or nocturnal species. Both electrophysiology and microscopic analysis of retinal structure suggest two retinal subsystems: the largest peripheral photoreceptors provide vision in dim light and the smaller peripheral and central photoreceptors function primarily in sunlight, with light-dependent pigment screening further contributing to adaptation in this system by dynamically recruiting photoreceptors with varying sensitivity into the operational pool.

1. Introduction

The visual system of Notonecta glauca, the common backswimmer, must provide for numerous challenges arising from the insect’s diverse visual environments and behavioural demands. Backswimmers prefer to live in freshwater ponds, preying upon aquatic organisms as well as terrestrial insects of suitable size that have fallen into the water. They are active around the clock, and use their vision for underwater hunting as well as during flight in search of new habitats. Because of its interesting behaviour and ecology [1–4], the backswimmer’s vision has been broadly studied.

The backswimmer compound eye is an acone-type open-rhabdom apposition eye with corneal structure optimized for creating sharp images in both air and water [5–7]. There are two zones of high acuity in each eye, ventral and dorsal, with 75% of ommatidia viewing a binocular visual field [6]. Each ommatidium consists of two fused central rhabdomeres surrounded by a ring of six detached different-sized peripheral rhabdomeres [8], and an adjustable pigment aperture is present in front of the rhabdom [9]. Rhabdomeres of two central photoreceptors are situated close to each other, with one of them located more proximally than the other, as in the fly [8]. Microspectrophotometric studies found three visual pigments in the rhabdomeres: peripheral rhabdomeres contain a pigment with an extinction maximum at 560 nm (coinciding with the intensity maximum of scattered background light in turbid phytoplankton-rich water [10]) and with sensitivity to red light, whereas
2. Material and methods

(a) Patch-clamp recordings from photoreceptors in dissociated ommatidia

Adult backswimmers (N. glauca) were collected locally (Oulu, Lund) or purchased from Blades Biological (UK). Dissociation of ommatidia (electronic supplementary material, figure S1) and electrophysiological recordings were performed as described previously [26–28]. In brief, an Axopatch 1-D patch-clamp amplifier and pCLAMP v. 9.2 software (Axon Instruments/Molecular Devices, CA, USA) were used for data acquisition and analysis. Patch electrodes (made from borosilicate glass; World Precision Instruments, Sarasota, FL, USA) had resistance of 3–8 MΩ. Bath solution contained (in mM): 120 NaCl, 5 KCl, 1.5 CaCl₂, 10 N-Tris(hydroxymethyl)-methyl-2-amino-ethanesulfonic acid (TES), 25 proline and 5 alanine, pH 7.15. Patch pipette solution contained (in mM): 140 KC1, 10 TES, 2 MgCl₂, 4 Mg-ATP, 0.4 Na-GTP and 1 NAD, pH 7.15. All chemicals were purchased from Sigma Aldrich (St. Louis, MO, USA). The liquid junction potential (LJP) between the bath and the normal intracellular solution was −4 mV. All voltage values cited in text were corrected for the LJP. Series resistance was compensated by 80%. All cells had resting potentials of −44 mV or lower (the average resting potential was −54.9 ± 8.6 mV; n = 23); if photoreceptor condition deteriorated during recordings to give a resting potential of −44 mV or higher, voltage recordings were discontinued.

(b) In vivo intracellular single-electrode recordings

In vivo intracellular single-electrode recordings were performed as described previously [29]. In brief, for intracellular recordings, backswimmers were maintained in reversed 12–12 illumination conditions with a subjective ‘night’ period matching the actual day (regimen 2; see below for details). Photoreceptor responses were recorded using microelectrodes (aluminosilicate glass; Harvard Apparatus, UK) manufactured with a laser puller (P-2000; Sutter Instrument, USA) and filled with 2 M KCl solution to a final resistance of 80–110 MΩ. Signals were amplified with an intracellular amplifier (SEC-05L; NPI, Germany). Before recording the angular sensitivity, the optical axis of the photoreceptor was determined by changing the polar and azimuthal angles of the light source while recording light responses in a Cardan-arm system. Then the V-log(I) curve was plotted to obtain the stimulus intensity eliciting the half-maximum response. This light intensity (and a 10-fold higher intensity) was used to measure the receptive field of the photoreceptor by changing the polar angle. Voltage responses, measured at different angles, were converted to angular sensitivity after the correction for the azimuthal angle. The angular diameter of the light source was approximately 1°.

Recordings were performed mainly but not exclusively from the central part of the eye; no notable differences in photoreceptor properties were observed between different parts of the eye. All cells used for analysis had resting potentials of −45 mV or lower, showed single angular sensitivity peaks and demonstrated transient depolarization with the zero attenuation filter of at least 22 mV in amplitude (at least 35 mV at the maximal light intensity); in addition, in current-clamp experiments involving current injections to determine capacitance, only cells showing strong rectification without any recording artefacts were used to ensure that capacitance was not overestimated due to electrode blockade.

Light stimulation was performed as described previously [28]. In brief, a computer-controlled custom-made voltage-to-current driver for light-emitting diodes (LEDs) was used to drive 10 (in patch-clamp experiments) or 13 (in intracellular experiments) monochromatic LEDs (Roithner Laser Technik, Austria), covering a range from 355 to 639 nm, which were used in combination with neutral density filters (Kodak, New York, NY, USA). In
patch-clamp experiments, full-field stimuli were delivered to
dissociated ommatidia through the inverted microscope objective.

(c) Pupil sizes and rhabdomere migration
For experiments with pseudopupil adjustment and rhabdomere
migration, half the population was maintained under normal
12–12 illumination conditions (regimen 1), whereas the rest lived
in regimen 2 so that animals in both night and day pupil adap-
tation states [2] could be studied during day-time. To test
adaptation to bright sunlight, the regimen 1 animals were placed
in direct sunlight for 3 h. To obtain fully dark-adapted animals,
another sample of backswimmers maintained under regimen 2
was placed in a dark box for the same period. Animals adapted
to laboratory light were obtained in similar way. Following the
exposure, backswimmers were killed and their heads were fixed
in 4% paraformaldehyde in phosphate-buffered saline sup-
plemented with 3% sucrose. After rinsing, dehydration and
embedding in Spurr’s embedding medium, 4 μm sections were
cut and mounted with Entellan (Merck, Germany).

(d) Data analysis
Information rates were analysed using the Shannon method [30]
as described previously [28,31]. In brief, to measure photo-
receptor performance, a computer-generated 90 s light contrast
series, made of 30 s long steady light pre-pulse followed by a
test pulse consisting of 30 repetitions of a 2 s Gaussian randomly
modulated (white-noise, WN) sequence with a cut-off frequency
of 200 Hz was used to obtain information rates (IRs). Analysis of
responses to WN stimulation was performed by estimating the
2 s signal S(f) by averaging voltage responses to thirty 2 s long
segments of the stimulus. The noise was then obtained by sub-
tracting the signal estimate from the original (noise-containing)
sequences. The signal-to-noise ratio (SNR(f)) was obtained in
the frequency domain as SNR(f) = |S(f)|^2/N(f)^2, where |S(f)|^2
is the estimated response signal power spectrum and N(f)^2 is
the estimated noise power spectrum. The contrast gain of voltage
responses |T(f)| was calculated by dividing the cross-spectrum of
photoreceptor input (WN contrast, C(f)) and output (photo-
receptor signal) S(f)C*(f) (the asterisk denoting complex
conjugate) by the autospectrum of the input C(f)C*(f) and
taking the absolute value of the resulting frequency response
function T(f): T(f) = |S(f)C*(f)/C(f)C*(f)|. The Shannon IR for
WN modulated responses was calculated according to the equation
IR = ∫[log₂(|S(f)|/|N(f)| + 1)]df within a frequency range from
1 Hz to a frequency where the value of SNR equalled 0.5.

All values are means ± s.d. Spearman’s rank correlation co-
efficient (ρ) was calculated as described previously [32]. Spearman’s
ρ was considered significantly different from zero when the
p-value calculated by using the large-sample approximation test
in MATLAB was less than 0.05.

3. Results
(a) General properties of backswimmer photoreceptors
Basic features of photoreceptor function were first investigated
with the patch-clamp method in isolated ommatidia. Figure 1a
shows examples of action spectra obtained in patch-clamp
recordings. Of 34 photoreceptors, two cells demonstrated
responses to UV light only (figure 1a, represented by violet
trace); two cells had a response maximum at 435 nm (blue
trace); one cell had a response maximum at 470 nm (cyan
trace); the remaining cells exhibited strongest responses to
LEDs with maxima between 490 and 591 nm (green and
dark yellow traces), and with an average response maximum
at 535 nm. Figure 1b shows examples of microscopic current
responses, the quantum bumps elicited by 1 ms flashes of light
with enough intensity to evoke responses with approxi-
mately 50% success rate. The average quantum bump
amplitude was −47.2 ± 19.2 pA (n = 26). In patch-clamp, vol-
tage bumps were present in all photoreceptors at rest upon
stimulation by steady low-intensity light. Voltage bump
amplitude usually varied from 0.5 to 2 mV.

Figure 1c shows macroscopic voltage and light-induced
current (LIC) responses to a naturalistic stimulus. Figure 1d
quantifies transient and sustained depolarization during
light responses of dark-adapted photoreceptors to steady light of increasing intensity in patch-clamp and intracellular experiments. The differences in depolarization amplitudes were apparently caused by dissimilar illumination conditions (side-on stimulation of dissociated ommatidia in vitro versus natural illumination through optics with intact pigment screening in intracellular experiments).

Consistent with previous studies documenting significant differences in the size of individual rhabdomeres [8], backswimmer photoreceptors exhibited large variation in whole-cell capacitance. Capacitance was measured both in vitro, in voltage-clamp experiments (patch-clamp) by calculating the charge under the capacitive transient following a small voltage step, and in vitro, in intracellular current-clamp experiments involving current injections (figure 1c), from the time constant. In patch-clamp experiments, whole-cell capacitance varied from 107 to 907 pF with a median of 247 (190–369) pF (interquartile range) \( (n = 38) \), whereas intracellular recording capacitance varied from 262 to 1120 pF with a median of 379 (303–507) pF \( (n = 36) \) (figure 1f).

In Notonecta photoreceptors, the depolarizing effects of LIC were opposed by two K\(^+\) currents, a rapidly activating and inactivating \( (I_{A}) \), and a very slowly inactivating delayed rectifier current \( (I_{DR}) \) (electronic supplementary material, figure S2). \( I_{DR} \) showed almost no inactivation within the physiological voltage range \((\text{approx. between } -70 \text{ and } -20 \text{ mV})\). \( I_{A} \) was sensitive to 4-AP and in most cells could be completely abolished by a 2 s inactivating pre-pulse to \(-34 \text{ mV}\). Peak conductances and half-activation potentials \( (V_{1/2}) \) determined by fitting the data points with a Boltzmann function) of these currents were of similar magnitude (electronic supplementary material, figure S2d). The values of \( V_{1/2} \) were \(-25.2 \pm 3.7 \text{ mV} \) for \( I_{A} \) and \(-23.8 \pm 6.3 \text{ mV} \) for \( I_{DR} \) \((n = 7)\).

**Absolute sensitivity**

We found a large variation in absolute sensitivity among green photoreceptors. Sensitivity was measured in patch-clamp experiments by counting voltage bumps evoked by continuous stimulation at light intensities dim enough to elicit less than 10 bumps s\(^{-1}\) (less than 5 bumps s\(^{-1}\) on average) in order to avoid overlapping bumps. For each photoreceptor, sensitivity to light was defined as a reciprocal of the light intensity that would induce 1 effective photon s\(^{-1}\) (i.e. 1 bump s\(^{-1}\)). The relative light sensitivity was then calculated as a fraction of sensitivity of the most sensitive cell in the sample. Strong correlation was found between sensitivity and the corresponding capacitance value \( (p = 0.76, p = 0.00011; \text{figure 2})\).

**Photoreceptor performance in bright light**

To evaluate photoreceptor performance and information processing, we used a 90 s WN contrast sequence to stimulate photoreceptors over a range of light intensities from a sensitivity threshold to a saturating intensity (figure 3). Responses to WN modulated light are shown in figure 3. Photoreceptor depolarization increased, bump noise decreased and contrast resolution improved with increasing light intensity, up to the level of bright light \((\text{around } 400,000 \text{ effective photons s}^{-1} \text{ in figure 3d})\). Consistent with these changes, contrast gain and information rate also increased (figure 3b,c). The maximal gain was \(15.0 \pm 4.4 \text{ mV} \) per unit of contrast with an average 50% cut-off frequency of \(14.1 \pm 5.0 \text{ Hz} \) \((n = 11)\). The maximal average IR \( (\text{IR}_{\text{max}}) \) was \(87 \pm 42 \text{ bits s}^{-1} \) \((n = 23)\). In still brighter light, photoreceptor performance deteriorated again, reflecting saturation of transduction units in bright light as a consequence of stimulating dissociated ommatidia deprived of optical adaptation mechanisms [33,34]. This decrease in the IR in very bright environments is very similar to that observed in photoreceptors of dissociated stick insect, cricket and water strider ommatidia [28,31,35], and consistent with the saturation effects observed in white-eyed blowflies and *Drosophila* [36,37].
The functional importance of photoreceptor size and its variation, already demonstrated in the correlation between sensitivity to light and whole-cell capacitance (figure 2), was supported by two additional observations: larger and more sensitive backswimmer photoreceptors had higher $IR_{\text{max}}$ values than their smaller and less sensitive counterparts ($\rho = 0.57$, $p = 0.0045$ for the correlation between capacitance and $IR_{\text{max}}$; $n = 23$ cells; $\rho = 0.70$, $p = 0.0024$ for the correlation between the relative sensitivity and $IR_{\text{max}}$; $n = 16$ cells; figure 3d,e), which might be a useful development considering the relatively small number of photoreceptors capable of seeing in very dim environments.

(d) In vivo recordings: capacitance, angular sensitivity and absolute sensitivity

While patch-clamp experiments allow characterization of biophysical properties of photoreceptors without the bias introduced by ommatidial optics, functional interpretation of the discovered variations in the key properties of backswimmer photoreceptors (capacitance, absolute sensitivity and performance) is compromised by the fact that our patch-clamp preparation required side-on illumination, which is non-physiological for photoreceptors, and does not take into account angular sensitivity.

To determine whether larger photoreceptors, characterized by higher absolute sensitivity in the in vitro experiments, have higher absolute and angular sensitivities than their smaller counterparts in vivo, intracellular recordings were performed from backswimmers maintained under reverse illumination conditions (to maximize the expected variation in acceptance angles). The above-cited capacitance values (figure 1a) calculated from voltage responses tended to be higher than capacitance values obtained in voltage-clamp experiments, possibly due to underestimation of the cellular resistance, caused by an electrode-induced leak, leading to overestimation of capacitance. Also, in vitro capacitance can be underestimated due to the loss of axonal membrane or space-clamp error. However, as anticipated on the basis of the patch-clamp recordings and previous hypotheses, there was large variation in acceptance angle values among photoreceptors (figure 4a,b), from 2.88° to 12.43° pF with a median of 4.9° (4.0–6.0°) ($n = 41$). A moderate positive correlation was found between capacitance and acceptance angle values ($\rho = 0.45$, $p = 0.038$, $n = 21$; figure 4c, open circles). A slightly higher correlation was found in a different sample with a 10-fold higher stimulus intensity, which produced wider acceptance angles ($\rho = 0.61$, $p = 0.01$, $n = 17$; figure 4c, closed circles).

To determine the absolute sensitivity in intracellular recordings, we first attempted to calculate it directly, by counting voltage bumps, as in patch-clamp experiments. However, it was not feasible to resolve individual bumps regularly enough due to the relatively high noise and the small bump amplitude. Therefore, we used a more indirect measure of steady-state depolarization in dim light. Figure 4d demonstrates the experimental steady-state depolarization curves with red dashed lines illustrating the types of thresholds that we used to determine the correlation between acceptance angles and absolute sensitivity. Statistically significant positive correlations were found between acceptance angle and light intensity at which the photoreceptor depolarized by 0.5 or 1 mV (the values were obtained from fitted parameters; correspondingly, $\rho = 0.63$, $p = 0.0024$ and $\rho = 0.61$, $p = 0.0034$, $n = 21$; figure 4e).

As in patch-clamp experiments, sensitivity varied more than 100-fold, depending on the threshold used. Also, there were significant correlations between the acceptance angle and steady-state depolarization at a specified light intensity threshold ($\rho = 0.73$, $p = 0.0002$ for the attenuation ‘–3’; and $\rho = 0.49$, $p = 0.025$ for the attenuation ‘–2’, $n = 21$; figure 4f). However, it should be noted that the depolarization level depends on bump frequency, quantum bump size, membrane gain (determined by input resistance, affected, for example, by the voltage-activated conductances), voltage-dependence of gain (determined by voltage-dependencies of ion channels) and voltage bump amplitude. Because all these parameters may vary from cell to cell, these steady-state depolarization metrics probably underestimated the correlation between acceptance angles and absolute sensitivity of backswimmer photoreceptors.

(e) Central rhabdomeres

Two central photoreceptors in each ommatidium contain either a UV- or a blue-sensitive pigment [38]. Because they seem to
perform a different function than the green peripheral photoreceptors, being responsible for colour vision (e.g. [39]), we compared their electrophysiological properties. Only five UV-, violet- and blue-sensitive photoreceptors were successfully patched, due to their difficult position within the ommatidium. No differences between green photoreceptors and the small sample of UV and blue cells were found in terms of capacitance, ionic currents or information rates. Three intracellular recordings of blue cells were made from intact retinas. All were characterized by relatively small acceptance angles (around 5°) and low absolute sensitivities.

(f) The pupil in light microscopy
To see which photoreceptors receive light in different illumination conditions, we used light microscopy to examine backswimmer retinas adapted to different conditions. Anatomically, it appears that in bright light (figure 5a, d), screening pigment acts as a pupil and may restrict light to the small central rhabdomeres, whereas in dark-adapted eyes (figure 5c, e) the pigment moves away so that light can enter all rhabdomeres. Specifically, in the light-adapted eye, a light-guiding tract about 5–8 μm in diameter and 10 μm long is formed between heavily pigmented pigment cells (figure 5d). In the dark-adapted state, the tract is completely absent and the rhabdomeres are about 40 μm closer to the cornea than in the day-adapted eye, and indent into the cone cells (figure 5a). These movements may have an intrinsic diurnal rhythm as well, as can be seen in the intermediate position of the pigments in the dark-adapted state during subjective day when compared with the dark-adapted pupil during subjective night (figure 5b, c). Adjustment of the pupil implies that the central and peripheral rhabdomeres have performance optima at different light levels.

4. Discussion
In this work, we studied the electrophysiological properties of backswimmer photoreceptors in an attempt to determine the mechanisms that allow the animal to use vision under dramatically different illumination conditions, such as those experienced during day and night. Our results, documenting large variations among individual photoreceptors in capacitance, absolute sensitivity to light and angular sensitivity, with substantial positive correlations between these properties, are fully consistent with the previously reported variation in the size of individual rhabdomeres in backswimmer ommatidia [5, 8]. Although the general anatomical design of the backswimmer eye is optimized for vision in well-lit backgrounds (open-rhabdom apposition eye), the presence in each ommatidium of two large peripheral green-sensitive rhabdomeres with wide acceptance angle (the angle subtended by the photoreceptor entrance aperture), and hence a small F-number, and with relatively high absolute sensitivity, can be considered as an adaptation for vision in the dark. One puzzling issue was the apparent scarcity of very large photoreceptors in our experiments. A reason for that could be that large peripheral photoreceptors differ in rhabdom length (and therefore capacitance), or that there is variation in photoreceptor size across the eye resulting in relatively smooth experimental capacitance distribution.

As the large variation in absolute sensitivity and its correlation with capacitance are central to our argument, these findings must answer three main questions: (i) whether the variation in absolute sensitivity and its correlation with capacitance are real; (ii) whether the variation in absolute sensitivity has any functional importance; and (iii) whether it is possible to explain variation in absolute sensitivity largely or fully by variation in other presently determined factors (e.g.
that (i) sensitivity of the diurnal findings reported in this article.

These results reinforce the validity of the water strider. This pattern implies that the variation in absolute sensitivity in sensitivity like those observed in the water strider. This pattern function very much like the highly sensitive photoreceptors of the backswimmer and cockroach. Interestingly, shielding of peripheral photoreceptors not only protects the peripheral photoreceptors from bright light, but also enables them to function at otherwise saturating back-lighting levels. The equation for the cockroach, 0.0088 for the backswimmer, 0.0092 for the stick insect and 0.0139 for the water strider (although in the latter case there were two classes of peripheral photoreceptors, blue and green, characterized by different absolute sensitivities and average capacitances) [31].

Our estimates made from micrographs of backswimmer ommatidia [8] indicate that the cross-sectional area of the largest pair of rhabdons is three times greater than that of the smallest pair. However, in vivo sensitivity depends, among other factors, on the product of two probabilities: the probability of a photon entering the rhabdom (which increases with the cross-sectional area of the rhabdom, especially at the distal end) and the probability that rhodopsin absorbs a photon entering the rhabdom (which depends on the length of the rhabdom). In dark, the latter probability seems to be more important, while in bright light it is the entrance aperture size that determines sensitivity. As sensitivity is proportional to the rhabdom membrane area, the threefold difference between the largest and smallest rhabdones means that either the wide rhabdones should be substantially larger than their narrow counterparts (to accommodate more microvilli) or that other factors, such as those listed above, should disproportionately boost the sensitivity of the largest rhabdones or reduce the sensitivity of the smallest ones.

Backswimmers generally prefer to swim or rest on the water surface, often in direct sunlight. To prevent photoreceptor saturation in such conditions, their light attenuation mechanisms must be sufficiently strong. One such mechanism is the dynamic screening by pigment cells situated at the distal end of the ommatidium and forming the pupil [2]. Figure 5 shows cross-sections of the backswimmer pupill in three adaptation states: dark-adapted during night, light-adapted to laboratory illumination during the day and light-adapted to sunlight. The pigment diaphragm is fully open in the dark, partially closed in laboratory light and completely shields the peripheral rhabdones in sunlight. Note that the pigment cell movement was accompanied by proximal migration of rhabdones (figure 5d,e). These observations on rhabdomere and pigment cell movement mirror findings made in the giant water bug Lethocerus [41]. The sensitivity range of the backswimmer pseudopupil is very large, about 7 log units during the day and 6 log units during night, with the total range reaching 8 log units [2]. For comparison, the diurnal blowfly has a pupil dynamic range of 3 log units [34], and the strictly nocturnal moth Hyalophora cecropia has a range of 4 log units [42]. Obviously, such a large range reflects the need to use vision both during the day and at night in the backswimmer. Interestingly, shielding of peripheral photoreceptors not only protects the peripheral photoreceptors from bright light, but also enables them to function at otherwise saturating backgrounds, as evidenced by the finding that peripheral
photoreceptors can mediate optomotor responses even in bright light, when they are shaded by the pigment diaphragm [25]. (Although the attenuation strength of shielding pigment filtering in the backswimmer is not known it might be similar to that in diurnal flies, i.e. between 2 and 3 decades [33].) The proximal rhabdomere migration should also act as a pupil, providing additional attenuation, although its strength was not evaluated in this study.

Overall, combining previous studies with our results suggests that the backswimmer’s retina can be functionally separated into at least two photoreceptor subsystems. The first would consist of the largest and most sensitive peripheral photoreceptors. These are sensitive to green and allow the backswimmer to see in dim light. The second subsystem would consist of the smaller peripheral and central photoreceptors, and would be used for vision in bright light and during flight. Even though the operational ranges of these subsystems are expected to overlap substantially, such a classification could be merited by consistent differences in several respects: large green-sensitive photoreceptors are generally also more sensitive to light, and have larger acceptance angles, slower membrane responses and higher IR$_{max}$ than the smaller photoreceptors. Even though little is known about the properties of central photoreceptors, it appears that they are similar to the properties of peripheral ones, but because pigment screening cannot shield them even in the brightest light, they should have lower sensitivity to light than peripheral photoreceptors in order to avoid saturation in sunlight. In this context, it is interesting that the rhabdom of one of the two central photoreceptors is always situated proximally to the other [8], which necessarily entails lower sensitivity to light due to a lower photon flux. This raises the possibility that the functions of the central rhabdomeres are also optimized to different backgrounds—the proximal rhabdomere may continue to function when the distally situated rhabdomere is already saturated.

Data accessibility. The data supporting the article are available in the electronic supplementary material.

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