

Adaptations for vision in dim light: impulse responses and bumps in nocturnal spider photoreceptor cells (*Cupiennius salei* Keys)

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Abstract The photoreceptor cells of the nocturnal spider *Cupiennius salei* were investigated by intracellular electrophysiology. (1) The responses of photoreceptor cells of posterior median (PM) and anterior median (AM) eyes to short (2 ms) light pulses showed long integration times in the dark-adapted and shorter integration times in the light-adapted state. (2) At very low light intensities, the photoreceptors responded to single photons with discrete potentials, called bumps, of high amplitude (2–20 mV). When measured in profoundly dark-adapted photoreceptor cells of the PM eyes these bumps showed an integration time of 128 ± 35 ms ($n = 7$) whereas in dark-adapted photoreceptor cells of AM eyes the integration time was 84 ± 13 ms ($n = 8$), indicating that the AM eyes are intrinsically faster than the PM eyes. (3) Long integration times, which improve visual reliability in dim light, and large responses to single photons in the dark-adapted state, contribute to a high visual sensitivity in *Cupiennius* at night. This conclusion is underlined by a calculation of sensitivity that accounts for both anatomical and physiological characteristics of the eye.

Introduction

Animals active in dim light typically have large eyes with wide pupils and large photoreceptor cells with wide visual fields and long integration times (Warrant 2004). These adaptations improve photon capture, but compromise resolution. However, eyes with high resolution are not useful if there is not enough light to produce a reliable visual signal. In nocturnal animals, high sensitivity tends to be favoured over fine resolution.

The spider *Cupiennius salei* is a nocturnal hunter that hides in monocotyledons during the day (Barth and Seyfarth 1979; Barth 2002). According to previous investigations, its visual system is well developed (Barth et al. 1993; Strausfeld and Barth 1993; Strausfeld et al. 1993; review in Barth 2002). The lenses of the anterior median (AM) eyes provide the retinae with images of good optical quality (Land and Barth 1992). By recording electroretinograms, Barth et al. (1993) calculated a retinal illuminance of 5.9×10^9 photons/cm²/s, a value implying that vision is possible in moonlight.

Considering these prior investigations the question arises: how are single photoreceptor cells of *Cupiennius* adapted to vision in dim light? On a moonless night the light intensity is over 100 million times lower than on a bright sunny day (Land and Nilsson 2002). Hence, the eyes of the spider need to collect sufficient photons to support reliable vision. Not only well developed sensitivity but also appropriate temporal resolution is an important characteristic of a nocturnal eye (Warrant 2004). In the present paper we hypothesize that the physiological properties of the photoreceptor cells of *C. salei* are adapted to night vision in regard to both temporal resolution and absolute sensitivity. We expect dark-adapted photoreceptor cells to have long integration times and poor temporal resolution in

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order to improve the reliability of vision in dim light. To test this, an electrophysiological analysis was undertaken on dark- and light-adapted photoreceptor cells in the spider anterior and posterior median eyes. The photoreceptors in the anterior median (AM) and posterior median (PM) eyes are compared and discussed in reference to other diurnal and nocturnal spiders.

Material and methods

Animals

Adult females of *C. salei* (Ctenidae) from our breeding stock at the University of Vienna were taken to Lund University for the electrophysiological experiments. The spiders were kept under a light regime of 12 h light and 12 h dark with the change to darkness occurring at 2 PM so that experiments with dark-adapted eyes could be performed in the afternoon.

Electrophysiology

The spider was mounted on a plastic cylinder that was fixed with a ball joint on a magnet stand. This ball joint allowed movement of the animal in different hemispherical directions. The spider was attached to the cylinder with a small amount of bee's wax mixed with violin resin (1:1). The prosoma, opisthosoma, the eight legs and the pedipalps were fixed with small strips of tape. Wax was used to immobilize the chelicerae. Borosilicate glass microelectrodes filled with 2 M potassium acetate were used for the recordings. A grounded silver wire was inserted into the opisthosoma and served as the indifferent electrode. Since the cornea of these spiders is hard and thick a small hole was cut with a sharp piece of razor blade near the margin of the eye to introduce the microelectrode into the retina. The magnet stand, with the spider, was placed on a vibration-free table. The animal was oriented so that the axis of the eye was aligned with the light stimulus, to allow entry of the glass electrode perpendicular to the axis of the eye. The position of the spider was manipulated until its eye was at the center of curvature of a goniometer holding the light stimulus.

The recordings were done in a laboratory with 20°C room temperature on average. For experiments in the dark-adapted state the photoreceptor cells were dark-adapted for about an hour. There was no dark adaptation necessary between the pulses as the stimulus used was extremely brief and very dim. Experiments in the light-adapted state were conducted in room light, as soon as the preparations were made. Full dark-adaptation was recognized by the appearance of "bumps" (responses to single stray photons).

White light from a xenon arc lamp (Nikon XPS-100) passed through a series of quartz neutral density filters (to control light intensity) and reached the animal through a narrow quartz light guide. It provided a point-source stimulus subtending an angle of 0.05° at the eye. A high speed Uniblitz shutter was used to produce light flashes. A goniometer held the light guide at its end and allowed the precise positioning of the stimulus within the visual field of the examined eye.

Measurement of impulse responses and bumps

The ability of an eye to detect moving objects—the eye's temporal resolution—can be defined by the response of a photoreceptor to a brief and dim flash of light, also known as the impulse response. The half-width of the impulse response is the integration time (Δt), the time within which light is absorbed (Warrant 2004). The time-to-peak (τ_p) is the time taken for the impulse response to attain maximum voltage amplitude (Fig. 1b).

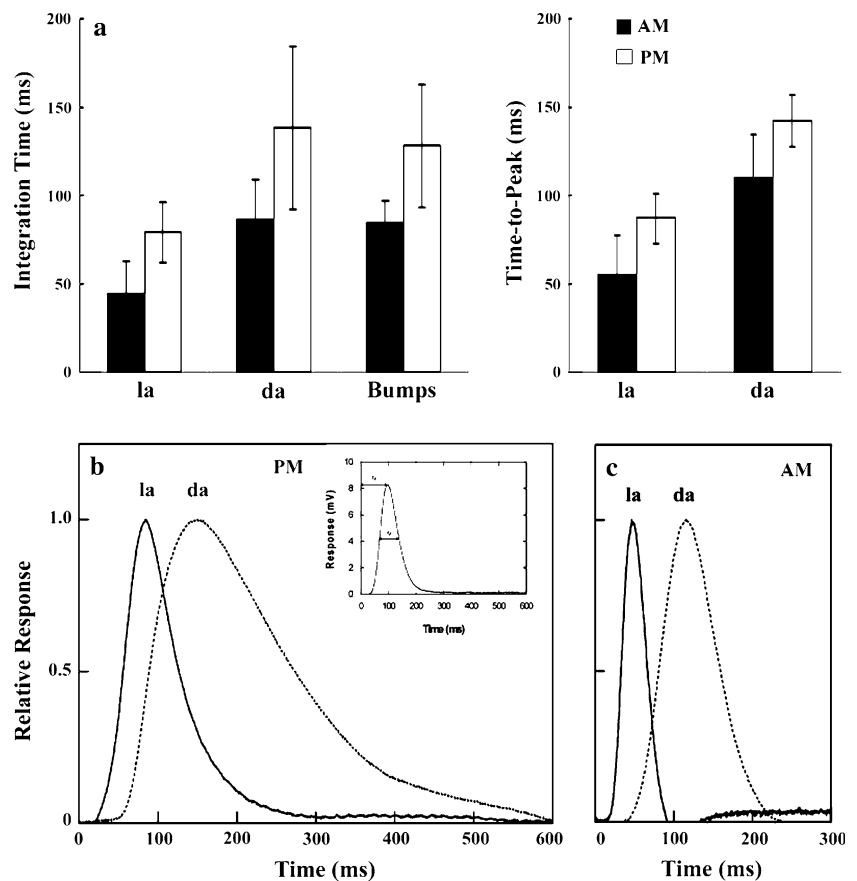
To measure the temporal resolution of the photoreceptors, the duration of the stimulus was set at 2 ms and its intensity was reduced to the minimum response amplitude possible (not greater than 9 mV). One hundred light pulses, with 1 s between two pulses, were delivered and the cell's responses were recorded and averaged to obtain the "impulse response".

When the cell was profoundly dark-adapted and produced large bumps, it was not possible to record the impulse response in the manner described above. The bumps, which occurred randomly, interfered with the response of the photoreceptor cell and the difference became unclear. Instead a series of bumps were recorded and the integration time was calculated from the half-width of each bump.

Theory

Kirschfeld (1974) and Land (1981) developed a model that predicts the optical sensitivity (S) of an eye based on its anatomy and optics. This model was applied to *C. salei* by Grusch et al. (1997). However, this model does not account for the physiological characteristics of the eye, including the electrophysiologically measured value of the acceptance angle $\Delta\rho$ and the visual integration time Δt , and the parameters that respectively characterise the spatial and temporal resolution of the eye. A modified model, taking these physiological parameters into account, was later developed by Warrant and colleagues (Warrant and Nilsson 1998; Kelber et al. 2002; Warrant 2004). In this model, the number of photons N absorbed by a photoreceptor with an acceptance angle $\Delta\rho$ (radians) and a rhodopsin absorption spectrum $R(\lambda)$, from a light source with an

Fig. 1 **a** The mean time-to-peak and mean integration time, with standard deviations of the mean of bumps and impulse response recordings in dark-adapted (da; PM: $n = 6$ and AM: $n = 5$) and light-adapted (la; PM: $n = 10$ and AM: $n = 4$) photoreceptor cells in the posterior median (PM) and anterior median (AM) eyes. **b** Relative responses to light pulses of 2 ms duration in photoreceptors of the posterior median (PM) eyes (**b** τ_p : 148 and 85 ms) and anterior median (AM) eyes (**c** τ_p : 116 and 46 ms) of *C. salei* in the dark-adapted state (da) and the light-adapted state (la). The inset in **b** shows how the integration time (Δt) and the time to peak (τ_p) are defined using the response of a light-adapted PM photoreceptor cell as an example



intensity spectrum $I(\lambda)$ (photons per nm) within one visual integration time Δt (s), is:

$$N = 1.13 \left(\frac{\pi}{4} \right) A \rho^2 A^2 \kappa \tau \Delta t \int \left(1 - e^{-k R_i(\lambda) l} \right) I(\lambda) d\lambda. \quad (1)$$

Here, A (μm) is the diameter of the lens, κ is the quantum efficiency of transduction, τ is the transmission of the optics, l (μm) is the length of the photoreceptor, and k (μm^{-1}) is the peak absorption coefficient of the visual pigment. $I(\lambda)$ is taken as the quantal reflection spectrum of green foliage at night (Warrant et al. 2004).

Inspection of Eq. 1 shows that long integration times and wide acceptance angles both result in greater photon capture and therefore improve the sensitivity of the eye. In the present study, this equation is used to look for differences in sensitivity between AM and PM eyes of the night active spider *Cupiennius*, and to compare these eyes with those of other diurnal and nocturnal arthropod species.

Results

Temporal resolution

The temporal properties of a photoreceptor cell are specified by the integration time (Δt) and the time to peak (τ_p) of

the photoreceptor's impulse response (Fig. 1b). Δt is defined as the half-width of the impulse response and τ_p is the time taken for the response to attain maximum voltage amplitude.

Recordings were made from six dark-adapted photoreceptor cells in the PM eyes and from five dark-adapted photoreceptor cells in the AM eyes. In the light-adapted state, recordings were made from ten photoreceptors in the PM eyes and from four in the AM eyes. In the dark-adapted state, the mean and the standard deviation of the time-to-peak (τ_p) and the integration time (Δt) of photoreceptors in the PM eyes were found to be 142 ± 15 ms ($n = 6$) and 138 ± 46 ms ($n = 6$), respectively, and in the AM eyes 110 ± 24 ms ($n = 5$) and 86 ± 23 ms ($n = 5$), respectively (Fig. 1a). Intracellular recordings in the light adapted state revealed values of 87 ± 14 ms ($n = 10$; time-to-peak) and 79 ± 17 ms ($n = 10$; integration time) in the PM photoreceptor cells and 55 ± 22 ms ($n = 4$; time-to-peak) and 44 ± 19 ms ($n = 4$; integration time) in the AM photoreceptor cells (Fig. 1a). The value n indicates the number of photoreceptor cells of the corresponding eye type. The recordings were made for a total of nine spiders.

In terms of the time-to-peak and the integration time, both pairs of eyes have significantly slower photoreceptors in the dark-adapted than in the light-adapted state (PM eyes τ_p : Mann–Whitney $U = 0$, $P < 0.001$; Δt : Mann–Whitney

$U = 6$, $P < 0.05$; AM eyes τ_p : Mann–Whitney $U = 1.5$, $P < 0.05$; Δt : Mann–Whitney $U = 2$, $P < 0.01$). In the light-adapted state the time-to-peak and the integration time of the AM photoreceptors were significantly shorter than those of the PM photoreceptors (Fig. 1a, b, c; τ_p : Mann–Whitney $U = 6$, $P < 0.05$; Δt : Mann–Whitney $U = 2$, $P < 0.01$). Recordings of the impulse responses of the AM and PM photoreceptors in the dark-adapted state were not significantly different ($P > 0.05$) but the values of time-to-peak in the AM eyes consistently showed lower values than in the PM eyes (Fig. 1a, b, c; $P = 0.05$).

Bumps

Bumps—the responses of the photoreceptor to single photons of light—could commonly be recorded in the dark-adapted state in both the AM and PM eyes (Fig. 2a). Their amplitude increased with the extent of dark-adaptation, eventually reaching a maximum amplitude (data not shown). The maximum amplitude of the bumps varied between 2 and 20 mV and the variation was the same for both pairs of eyes. By recording a large number of bumps it was possible to determine their integration times by measuring the half-width of the bump. Like photon arrivals, bumps occurred at random.

In the photoreceptors of the secondary (PM) eyes, bump amplitude varied between 3.0 and 8.8 mV, while in the principal (AM) eyes it varied between 3.2 and 7.5 mV (Fig. 2a). Integration times (Δt) differed between each pair of eyes (Δt : Mann–Whitney $U = 8.5$, $P < 0.05$; Fig. 2b). The average integration time (and standard deviation of the mean) for bumps in the PM eyes was 128 ± 35 ms ($n = 7$) and in the AM eyes 84 ± 13 ms ($n = 8$). The scatter plot of the bump integration times shows that, while there is some overlap, the two eyes fall in two reasonably clear groups (Fig. 2b).

Sensitivity

When the responses of a photoreceptor cell to a series of increasing light intensities are measured, one obtains a response-intensity, or a V -Log I , curve (Fig. 3). This curve describes the range of light intensities that excites the photoreceptor. Even though the cells shown in the figure all have different maximum response amplitudes, most saturate at an intensity about 100 times dimmer (i.e., at Log $I = -2$) than the brightest we could produce. The cells respond to light over a roughly 2-log unit range, and the largest responses recorded were in the vicinity of 70 mV amplitude. The lowest intensity, measured with white light, that resulted in a response in a dark-adapted PM

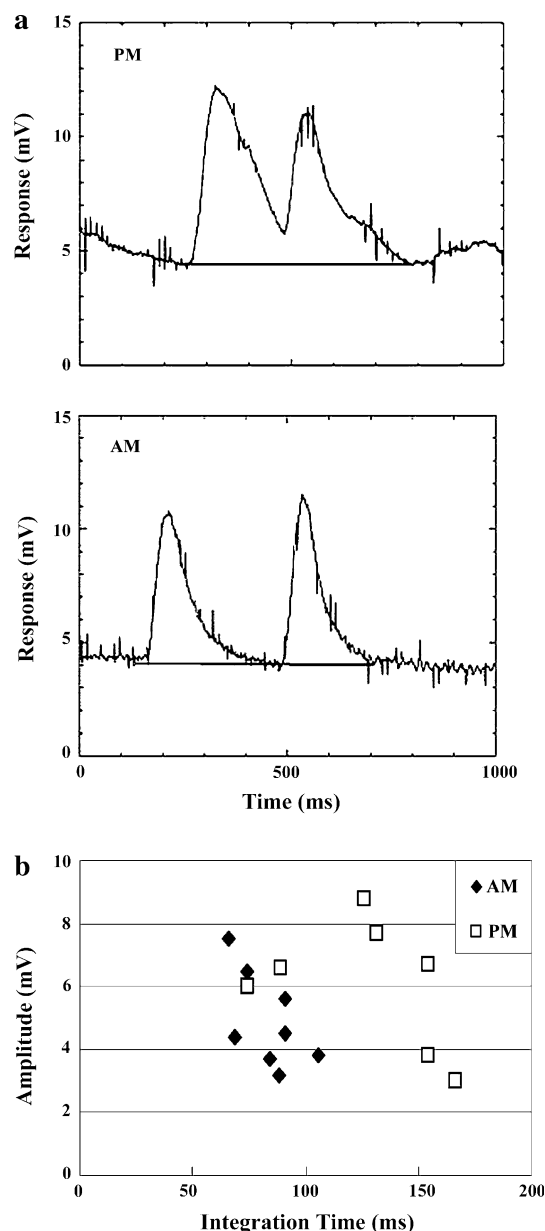


Fig. 2 **a** Bumps recorded from a dark-adapted photoreceptor cell in a PM eye and an AM eye of *C. salei*. PM eyes: the amplitudes of the bumps are 6.6 and 7.7 mV and the integration times Δt 131 and 89 ms; AM eyes: amplitude of bumps 6.5 and 7.5 mV, integration times Δt 66 and 74 ms. Higher frequency spikelets are noise artefacts from the microelectrode amplifier. **b** The integration time and amplitude of bumps recorded from seven dark-adapted photoreceptor cells in two PM eyes and eight dark-adapted photoreceptor cells in one AM eye. Mean integration times from bumps in PM and AM photoreceptor cells are significantly different (Mann–Whitney $U = 8.5$; $P = 0.02$)

photoreceptor was at -6.5 log units. This value is about one order of magnitude smaller than that previously calculated for the entire retina from ERGs (Barth et al. 1993).

The ability of the photoreceptors of the AM and PM eyes to capture photons was calculated using Eq. 1 for the

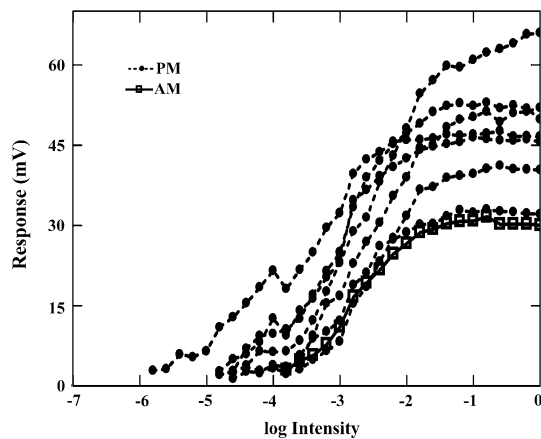


Fig. 3 V-Log I curves of eight photoreceptor cells in seven dark-adapted PM eyes (dotted lines) and one dark-adapted AM eye (solid line) of *C. salei*. The lowest threshold of the PM eye photoreceptor was at ca. Log I -6.5 and of the AM eye photoreceptor at ca. log I -5 (maximum intensity at log I = 0)

profoundly dark-adapted state and compared with calculations for the diurnal jumping spider *Phidippus johnsoni* and the nocturnal bee *Megalopta genalis* (apposition eyes).

The various parameters that were used to calculate the number of photons absorbed (N) are listed in Table 1. *C. salei* is active well after sunset when it has become almost totally dark for the human eye (Barth and Seyfarth 1979, Barth 2002). A moonlight intensity at which *C. salei* is active, corresponds to approximately 0.1 photons/ $\mu\text{m}^2/\text{s}/\text{sr}$

at 540 nm and this value was therefore used for the calculations.

Discussion

In this paper we demonstrate that single photoreceptors in the median eyes of *C. salei* are adapted to vision in dim light. This is revealed by measurements of the integration times of dark- and light-adapted photoreceptors in PM and AM eyes, and by calculations of sensitivity in photoreceptor cells. The occurrence of large, slow bumps in both pairs of median eyes supports the argument that the photoreceptors are adapted to night vision.

Temporal resolution

As seen from their response to a light pulse, dark-adapted photoreceptor cells of *C. salei* are significantly slower than light-adapted photoreceptor cells, a property seen in the photoreceptors of many other animals, irrespective of the light level in which they are normally active (Howard et al. 1984). Long integration times improve the visual signal-to-noise ratio in dim light and thus the reliability of vision (Land 1981). However, compared to most insects (which have dark-adapted times-to-peak of around 40–60 ms: Howard et al. 1984), the dark-adapted photoreceptors of

Table 1 Physiological, anatomical and optical parameters of the eyes of the nocturnal spider *C. salei*, the diurnal jumping spider *Phidippus johnsoni* and the nocturnal halictid bee *Megalopta genalis*

Parameter	<i>C. salei</i> (AM) ^{d,e}	<i>C. salei</i> (PM) ^{d,e}	<i>P. johnsoni</i> (AM) ^f	<i>M. genalis</i> ^g
Acceptance angle, $\Delta\rho$ (radians)	0.0949	0.035	0.0026 ^c	0.0978
Diameter of aperture, D (μm)	396	629	380	36
Integration time, Δt (s)	0.084 ^a	0.128 ^a	0.042 ^c	0.032
Quantum efficiency of transduction, κ	0.5	0.5	0.5	0.5
Transmission fraction of the optics, τ	0.8	0.8	0.8	0.8
Absorption coefficient, k (μm^{-1}) ^b	0.0067	0.0067	0.0067	0.0067
Rhabdom length, l (μm)	59	49 (98)	23	300
Facets illuminating one rhabdom, n	—	—	—	1
Temperature (in laboratory), $^{\circ}\text{C}$	20	20	—	20
Photons absorbed, N	133	105	0.020	1.4

The random length in the PM eyes of *C. salei* (in parentheses) is doubled because of the reflecting tapetum.

^a Values derived from bumps

^b Generally taken as 0.0067 μm^{-1} for arthropods (Land 1981)

^c Values derived from approximations (integration time of *P. johnsoni* is taken as half that of the dark-adapted *C. salei* AM eye, since times-to-peak are known to differ by a factor of two; acceptance angle \approx rhabdom diameter/focal length)

^d Grusch et al. (1997)

^e Land and Barth (1992)

^f Land (1981)

^g Warrant et al. (2004)

C. salei, with times-to-peak that well exceed 100 ms, are very slow. In this respect, the PM eyes of *Cupiennius* resemble the camera eyes of the night-active toad *Bufo bufo*. Due to an integration time of up to 1.5 s, dark-adapted toad rods subserve very slow vision, well adapted to enable the toad to catch small and slowly moving prey at night (Aho et al. 1988). Similarly long “exposure times”, and the resulting low temporal resolution could prove fatal for fast-flying nocturnal animals. For example, the nocturnal insect *Megalopta* (Table 1) requires sufficient temporal resolution to be able to perform nocturnal foraging flights. However, toads and *Cupiennius* are both sit-and-wait hunters, which can afford to sacrifice temporal resolution in favour of absolute sensitivity.

The slow impulse responses found for the visual cells of *Cupiennius* (average time-to-peak in PM eyes: $\tau_p = 142$ ms) are very similar to those described for photoreceptors in the PM eyes of *Dinopis* ($\tau_p = 150$ ms), another night-active spider that hunts using a sit-and-wait strategy (Laughlin et al. 1980). By comparison, the responses of photoreceptors in the PL eye of the day-active jumping spider *Plexippus validus* are considerably faster (τ_p ca. 70 ms) (Hardie and Duelli 1978; Laughlin et al. 1980). As the vision of the diurnal spider is not limited by a scarcity of photons, it can afford to invest in temporal resolution at the cost of sensitivity. Similarly, in the day-active housefly *Musca domestica*, integration times are only about 1/20 of those in nocturnal spiders (Dubs 1981). In the day-active butterfly *Asterocampa leilia*, integration times are only about 1/5–1/8 as long as in *Cupiennius* (Rutowski and Warrant 2002).

Bumps and absolute sensitivity

In the dark-adapted state the visual cells of *Cupiennius* produce bumps of considerable amplitude (up to 20 mV). Such large bumps indicate high sensitivity to low light intensities, supporting earlier findings from ERG measurements that in *C. salei* vision is possible under moonlight conditions; according to V-Log I curves the absolute corneal illuminance thresholds were clearly below 0.01 lx (Barth et al. 1993). In the night-active spider *Dinopis*, bumps had mean amplitudes as high as 18 mV (Laughlin et al. 1980). In the present study a very dim light source immediately increased the number of bumps and the noise, thus disturbing recordings from cells in the profoundly dark-adapted state. “Dark bumps” (i.e., bumps not associated with photon capture) are exceptionally rare in invertebrate photoreceptors, and in practice do not limit sensitivity in the same way as they do in vertebrates (where the rate of dark bumps is vastly greater).

In the nocturnal spider *C. salei* the photoreceptors of both pairs of median eyes are clearly adapted to dim light conditions. According to sensitivity calculations (Eq. 1) for the dark-adapted eyes of *Cupiennius* 133 photons are absorbed per integration time in the AM photoreceptor cells and 105 in the PM photoreceptor cells. In comparison, the value for photoreceptors in the AM eyes of the diurnal jumping spider *P. johnsoni* is lower by about four orders of magnitude: 0.020 photons absorbed per integration time. As mentioned above, during the day photon catch is usually not limited. Consequently, diurnal animals do not have to invest in high sensitivity, but instead develop eyes with high spatial or temporal resolution.

Another nocturnal arthropod—the tropical bee *M. genalis*—has apposition compound eyes, a design of relatively low sensitivity that is common in diurnal insects. A calculation of sensitivity (again at a light intensity of 0.1 photons/ $\mu\text{m}^2/\text{s}/\text{sr}$ at 540 nm, moonlight) shows that photoreceptors of *M. genalis* capture only 1.4 photons per integration time (Warrant et al. 2004). That is, the photoreceptor cells collect 95 times fewer photons than the photoreceptors of the principal eyes of *Cupiennius*, which points to the superior nature of the camera eye design for vision at night. However, it is very likely that *Megalopta* employs spatial summation to improve photon capture at night (Greiner et al. 2004).

In order to exploit the advantages of living at night, the senses of animals—their vision, audition, olfaction and mechanoreception—have evolved adaptations that allow a nocturnal lifestyle. This is particularly the case for vision (Warrant 2004). The wandering spider *C. salei* leaves its retreat after sunset and therefore avoids the heat of the day and low humidity outside the retreat (Barth and Seyfarth 1979). Competition for resources and predation are also often lower at night. The intracellular recordings presented in this study suggest that in *Cupiennius* the photoreceptor cells of both pairs of median eyes are adapted for vision in dim light by having large and slow responses to single photons, and a very high sensitivity.

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