Properties of Single Cells in Posterior Lateral Eyes of Jumping Spiders

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Z. Naturforsch. **33 c**, 156–158 (1978);
received November 8, 1977

Jumping Spiders, Receptors, Spectral Sensitivity, Angular Sensitivity, Absolute Sensitivity

Properties of single cells in the posterior lateral (PL) eyes of the jumping spider *Plexippus validus* are described. Only one spectral class of cells was encountered and the spectra sensitivity was indistinguishable from that measured from the ERG, both peaking at ca. 535 nm. Angular sensitivity (width of angular sensitivity function at the 50% level) averaged .89° ± .12°, the smallest value being .77°. Absolute sensitivity (reciprocal of the number of quanta of peak wavelength, on axis required to generate a 50% response) averaged $1.43 \pm 2.5 \times 10^{-11}$ $q^{-1} \cdot cm^2 \cdot s$. All cells studied were sensitive to the plane of polarised light. The performance of receptors in the PL eyes is compared with that of receptors in the compound eyes of diurnal insects. It is concluded that the single lens eye system of spiders is inherently superior in design to the insect compound eye.

The visual system of wolf spiders and jumping spiders has attracted considerable attention in recent years. The large anterior median (AM) eyes have been most studied and found to be important in pattern recognition [1] and possibly colour vision [2, 3]; in addition there is a limited amount of physiological data concerning the receptors to back up the behavioural findings [4–6]. The function of the posterior lateral (PL) eyes has also been investigated behaviourally [7, 8]. They have been shown to be important in detecting peripheral motion, and with these eyes, spiders are capable of detecting and orienting towards movements as small as 1°. The anatomy of the PL eyes is also known, and the retina consists of a uniform hexagonal array of receptors with paired rhabdomeres [9, 10]. Our knowledge of the physiology of the receptors, however, is virtually non-existent, being restricted to ERG measurements in *Menemerus confusus* [6]. In the present work properties of single cells are reported for the first time.

Jumping spiders (*Plexippus validus*) were collected in and around Canberra. After being lightly etherised they were mounted intact and immobilised in low melting point wax. The only surgery was a tiny hole in the carapace behind the lens, which was punched with an etched tungsten needle [11]. Into this hole was lowered a fine glass micropipette (resistance 100–200 megohm when filled with 3 M K Acetate). The eye was stimulated with a point source using a 900 Watt Xenon arc lamp and quartz optics described elsewhere [12].

Penetration of cells was indicated by a 30–70 mV drop in potential and the appearance of depolarising light-evoked responses of up to 70 mV (Fig. 1). These resembled in waveform those reported from the AM eyes of *Menemerus* [6]. Confirmation of the intracellular location of the electrode was given by the sharp angular sensitivity function, a 5–10 megohm resistance decrease during response to light (measured by bridge imbalance), the noisy nature of the response to light of low intensity and sensitivity to the plane of polarised light. The small size of the receptor cells (3–5 μm in diameter) meant prolonged stable recording was very difficult and at most, cells could be held stably for only 30 minutes. In all, data were collected from 19 cells.

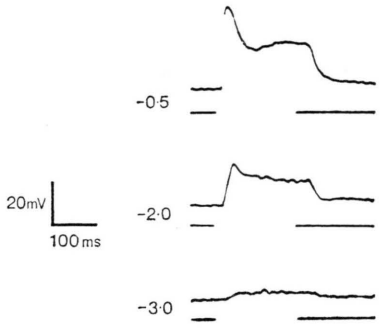

Fig. 1. Typical response waveforms from receptors in PL eyes of *Plexippus*. Stimulation was by 200 ms flashes of monochromatic light at 572 nm. Numbers indicate log relative intensity.

Spectral sensitivity was measured by delivering isoquantal flashes at each of 16 wavelengths and referring the responses to the response intensity (V-log I) function of the same cell. Spectral data were collected from 10 cells, all showing the same spectral sensitivity, with a single peak at ca. 535 nm (Fig. 2). In addition, the other 9 cells (in which other parameters were measured) all responded well to light at 572 nm, demonstrating, at least, that they were not pure UV sensitive cells. The spectral sensitivity of the ERG was measured similarly and found

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to be indistinguishable from that of the 10 cells (Fig. 2).

Angular sensitivity was measured by moving the point source in 1/4 degree steps through the cell's visual field and again referring the responses to the V-log I function to calculate sensitivity (Fig. 3). $\Delta\varrho$ values (width of the angular sensitivity function at the 50% level) all fell between .77° and 1.1° and averaged .89° ± .12° (1.0 S.D.) for a sample of 7 cells (two determinations being made on each cell).

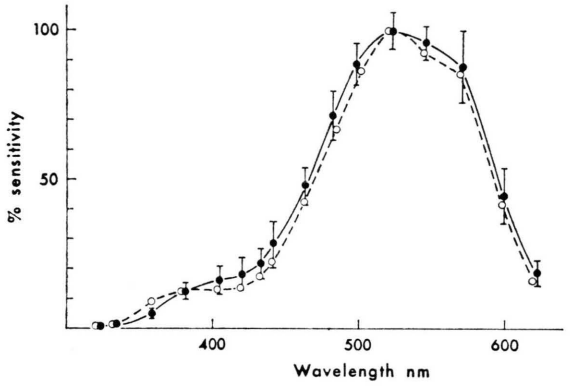

Fig. 2. Spectral sensitivity function from intracellular recording (filled circles, solid line), and ERG (open circles, broken line) in *Plexippus* PL eye. The curve for the single cells is the average of ten units. Error bars indicate ±1.0 S.D. For clarity error bars have been omitted from the ERG curve (average of six determinations).

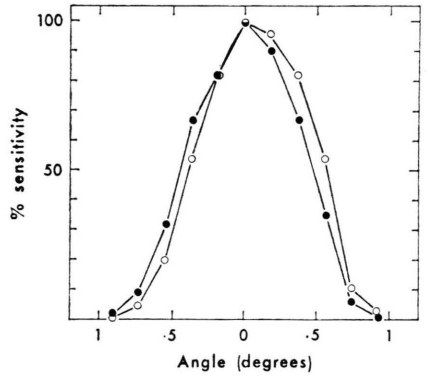

Fig. 3. Representative angular sensitivity function of a PL eye receptor. Results of two runs in the horizontal plane on one cell are shown. Correction has been made for the error due to vertical deviation from the equatorial plane. The widths of the functions at the 50% level (= $\Delta\varrho$) for the two runs were .96° (open circles) and .92° (filled circles).

The absolute sensitivity of the 7 best cells (judged as such on size of response and stability of recording) was measured by estimating the reciprocal of the number of quanta of peak wavelength, on axis, required to generate a 50% response (*i. e.* the axial peak sensitivity at the 50% level, or APS50, of Laughlin [13]). The average value was $1.43 \pm 2.5 \times 10^{-11}\,q^{-1}\cdot cm^2\cdot s$.

All cells studied were found to be moderately sensitive to the plane of polarised light, and polarization sensitivity (ratio of sensitivity at the most effective ε vector orientation to sensitivity at the least effective) averaged 2.33 ± .83 in the 12 cells tested for this parameter [14].

Although earlier ERG measurements in *Menemerus* PL eyes showed no evidence for more than one spectral class of cells [6], this is by no means proof of such a limitation. Indeed, original recordings of the ERG from the AM eyes of jumping spiders, including attempted selective spectral adaptation, failed to reveal the existence of more than one colour receptor [15]. However, subsequent intracellular recordings revealed the existence of at least two receptor types in AM eyes of *Phidippus regius* [5], and four different colour receptors have been reported in AM eyes of *Menemerus confusus* [6]. In the present investigation the discovery of only one spectral class of cells, and the matching of its spectral sensitivity to that of the ERG argues strongly for the existence of only one spectral class in the PL eyes.

The other parameters investigated (angular and absolute sensitivity) also appeared uniform, and showed no obvious relation to the visual axes of the cells in either the vertical or horizontal planes.

The PL eyes are functionally specialised to the task of detecting and localising moving objects [8]. Their large visual fields are registered by a regular array of anatomically [9, 10], and, according to the present results, physiologically, remarkably similar units – a situation that arguably reflects their functional specialization.

The sharp angular sensitivity function ($\Delta\varrho$ = .89°) agrees well with the optical properties of the PL eyes of the related *Metaphidippus*, where the angular divergence of adjacent receptors is estimated at ca. 1° [16] and also the behavioural data, where a 1° movement of a .7° spot is sufficient to initiate a turning reaction [7].

It is interesting to compare the performance of receptors in the PL eyes with that of receptors in compound eyes of diurnal insects. In terms of acuity (judged by $\Delta\varrho$ values) the receptors of the PL eyes are sharper than any published results of insect eyes, including: fly [12] ($1-2^\circ$), bee [17] (2.5°), locust [18] (2.5°), and dragonfly [19] (1.4°). In terms of interreceptor spacing (an anatomical measure of resolution) the PL eyes are also better than the majority of insects. It is true that a few high acuity insect eyes have denser spacing (*e. g.* $.5^\circ$ in dragonfly [20]), but this is only achieved in a limited foveal region, whereas the 1° receptor spacing in *Metaphidippus* [16] is maintained over the whole eye [7]. At the same time the receptors of the PL eyes maintain an absolute sensitivity (APS50) which is approximately the same as for the fly [12], and greater than in dragonfly [13] (the only high acuity insects where this parameter has been measured to our knowledge). This performance is achieved by an eye containing ca. 8000 receptors [10] but which has a lens equivalent in size to about 100 facets of a compound eye. In addition the radius of the PL eyes is also small – (only 174 μm in *Metaphidippus* [16]) compared, for instance, with ca. 600 μm for the eye of *Musca*. This exceptional performance can be largely attributed to the inherently superior design of a single lens eye, where light for each photoreceptor can be collected over a much larger area than is possible with a single facet of a compound eye. Not only does this result in more available quanta, and hence greater potential absolute sensitivity, but, as diffraction is reduced by the greater lens aperture, acuity can be increased simultaneously. It has been suggested that the advantage of compound eyes in small animals is a consequence of the fact that, when diffraction limited, the resolution of a single lens eye increases in direct proportion to the radius of the eye, but in compound eyes it increases only as the square root of the radius [21] – compound eyes thus being favoured in smaller animals. However, the results presented here demonstrate that in terms of both acuity *and* absolute sensitivity, the performance of the tiny PL eyes outstrips any known compound eye, and it thus becomes necessary to conceive of a different evolutionary advantage of the compound eye system. The superiority of the single lens system of spiders is further emphasised when one recalls that the PL eyes described here function solely as a "peripheral" visual system, and, judging from the available optical data [16], the receptors of the "foveal" AM eyes are likely to perform even better.

We would like to thank Drs. A. D. Blest and S. B. Laughlin for making valuable comments on the manuscript.

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