BIOPHYSICS ON PHOTORECEPTORS

Kuno Kirschfeld

Max-Planck-Institut für biologische Kybernetik, Tübingen

Photoreceptors are cells specialised for the detection of quanta of light. The problems these cells have to deal with are considerable in many respects: they should exhibit low internal noise in order to be able to detect individual quanta of light and they should absorb these quanta with high probability. They should also be capable of measuring mean rates of quanta (or changes in rate) when they are being hit by millions of quanta per second. They should be sensitive in different ranges of the sun spectrum in order to allow for colour vision. In arthropods in addition they should be capable of responding to linearly polarised light depending upon the orientation of its electric vector. Furthermore these receptors should be small so that they can be densely packed into a retina to enable high spatial resolution. And finally photoreceptors should respond rapidly in order to be capable of triggering fast reactions of an animal if necessary.

Different parameters are decisive in different respects: high absorption probability is due to a high density of membranes in those parts of photoreceptors that contain visual pigment molecules (rod and cone outer segments, rhabdomeres), and these molecules are densely packed into the membranes. In addition small accessory pigment molecules can be incorporated between the visual pigment molecules. These molecules can act as "sensitizing pigment", absorbing light and transferring the energy to the rhodopsin. This energy transfer is most likely mediated via Förster-type dipole-dipole interaction. Absorption probability can thus be enhanced and the spectral range of the receptors sensitivity extended, e.g. in the case of the photoreceptors of the fly, into the ultraviolet.

The minimal size of photoreceptors in highly evolved eyes is not dictated by cytological factors - e.g. the space needed for the biochemical machinery - but by the wave nature of light: they have been reduced e.g. in the human fovea, to the size that is still just capable of working sufficiently well from an optical point of view. Smaller receptors could no longer guide light effectively because these tiny structures act as waveguides, guiding the light in discrete "modes". Part of the mode energy travels outside the geometrical boundary of the receptor as an evanescent wave. This part is not absorbed by the visual pigment located inside the receptor and hence absorption efficiency is reduced. Furthermore the evanescent wave can penetrate into neighbouring receptors and cause deleterious optical crosstalk.

The waveguide properties are improved by a high refractive index of the receptors. Due to their lipid content biological membranes exhibit high refractive indices. Therefore a high membrane density in these receptors not only allows for high visual pigment concentration but also for a maximal refractive index and hence for optimal waveguide properties. The wave nature of light not only limits the angular resolution of eyes because of diffraction, but it also determines the minimal size of photoreceptors. In addition, it can be shown that from the constraints on receptor size the minimal size of lens eyes is also fundamentally limited by the wave nature of light.

Compared to most other receptor cells, in photoreceptors the time that elapses between the stimulus and the electrical response of the cell (late receptor potential) is rather long, from several to more than 100 milliseconds, depending upon stimulus conditions and species. On the contrary, e.g. mechanoreceptors can react without detectable latency. The origin of the long photoreceptor latency is not yet fully understood. In fly photoreceptors it is not the time needed to transform the visual pigment molecule rhodopsin into its other stable state, metarhodopsin. This reaction is completed within fractions of a millisecond. Most likely the timeconsuming steps are: 1. the activation of an enzyme-like molecule that is needed to produce an internal transmitter, and 2. the accumulation time of this internal transmitter to such a concentration that a threshold is reached to open channels for sodium ions.

Besides the late receptor potential, at sufficiently strong light intensities an electrical response without detectable latency can also be observed, the early receptor potential (ERP). This potential is not due to permeability changes of the cell membrane but to changes of the dipole moment of the visual pigment molecules. The ERP which monitors visual pigment transitions does not appear to have evolved as a physiologically relevant signal carrier, although in principle this is possible, since the ERP is also able to trigger the synapse that connects the photoreceptor cell with its second order neuron. Insofar the realised photoreceptors with their long latency are not the optimal solution that could be thought of from a physical point of view.