“gating” proteins, which control the opening and closing of sodium ion channels in rod outer segments.

The significance of this postulated enzyme cascade in the transduction process is by no means confirmed. It is also not yet clear how this cascade is related to the calcium reactions in rod outer segments. The individual reaction steps investigated so far are not strongly calcium-dependent.

An enzyme cascade of this type could provide the basis for the explanation of many phenomena observed to be part of the excitation process, including, amplification and adaptation.

Selected References


Since the printing of this article, great advances have been made in our understanding of the phototransduction mechanism. These are summarized in:


15.2.4.2 Photoreceptor Optics—Structure and Function of Photoreceptors

RANDOLF MENZEL AND ALLEN W. SNYDER

a) Introduction

Photoreceptors are specialized sensory cells of animals. When photons are absorbed in the photoreceptive structure of these sensory cells, molecular processes are initiated which lead to a change in the electric potential difference between the inside of the sensory cell and the extracellular space. This electrical signal encodes the number of quanta absorbed in the photoreceptor and transmits the information via synaptic connections to adjacent neurons.

The change in the potential difference is maintained only so long as photons are absorbed. The electrical signal thus contains also information about the duration of the incident light stimulation. In highly evolved visual organs many photoreceptors lie densely packed in a retina. Since the individual photoreceptors of the retina are oriented toward different points in space, the signal from each photoreceptor contains also information about the direction from which the light stimulus comes. The photoreceptors in the retina may differ in addition in their light-absorbing photopigment. Some photoreceptors absorb for example more strongly in the blue (wavelength range around 450 nm), others in the green (around 520 nm), others in the red (around 650 nm). The electrical signal of the photoreceptor thus informs the adjacent neurons also about the wavelength range of the incident light. Some photoreceptors, certainly those of many insects and crustaceans, have in addition different sensitivity to different directions of oscillation of linearly polarized light.

The photoreceptors in the retina as a whole can thus encode and make available to the nervous system several parameters of the light stimulus: intensity, spatial and temporal distribution, wavelength region, and direction of the electric vector.

Phylogenetically highly evolved photoreceptors are particularly well adapted for these tasks. The elucidation of the mechanisms of this optimization of function is the subject of “Photoreceptor Optics”. The fundamental question is: How do the structural characteristics of photoreceptors — their arrangement, orientation, form, size, optical density, and membrane properties — make possible and influence the absorption of photons? More quantitatively, how do they determine their absolute, spectral, spatial, and polarization sensitivity?

The basis of this definition of the problem is the discovery that the visual pigments lie in a specialized region of the photoreceptor which has a higher index of refraction than its surroundings. As a result of the higher index of refraction this portion of the photoreceptor acts as a light guide, so that the photopigment is optimally exposed to the incident light. This phenomenon is the link between the various lines of research in photoreceptor optics. Biochemical investigations of photopigments and the biophysics of ion transport through the membrane contribute information which is fundamental to our considerations. This is discussed in Chapter 15.2.4.1. The effect of a light stimulus, that is the probability of absorption of a photon by a photopigment molecule, is decisively influenced by the structure of the photoreceptor. Therefore, in order to analyze thoroughly the molecular mechanisms of light reception in photoreceptors we have to understand not only the biophysics and biochemistry of the photoreceptive membrane, but also the interaction between light and the photoreceptive structure.
b) Structural Organization of Photoreceptors

To introduce the basic structure of photoreceptors we compare several anatomical characteristics of photoreceptors in vertebrates and invertebrates which make use of highly evolved visual systems (Fig. 15.114).

Photoreceptors of arthropods (insects, spiders, crustaceans), squids and vertebrates are specialized, elongated cells which lie tightly packed in the retina. A lens focuses an image of the surroundings on the retina. The higher the density of photoreceptive structures, the higher the spatial resolution of the photoreceptor mosaic. However, the number of photons that reach each photoreceptor decreases with the packing density. The evolution of the lens eye and of the compound eye, both with high spatial resolution, is thus necessarily coupled to the evolution of mechanisms which increase the probability of absorption in each photoreceptor. As we shall see, this has been achieved through structural elements on the molecular, the fine structure, and the coarse structure levels.

On the fine structural level the basis for high absorption is a many-layered membrane system in the light-absorbing part of the photoreceptor. In vertebrate rods this is the outer segment which is constructed of many hundred intracellular membrane disks containing the rhodopsin molecule. Cones contain fewer membrane disks than rods. In the cones the membrane stack consists of deep folds of the cell membrane, whereas in the rods the membrane stacks are intracellular and are formed at the transition to the inner segment (Fig. 15.114 upper part, Fig. 15.115c). The photoreceptors of arthropods and mollusces, the retinula cells, carry the photopigment in tightly packed, tubular protuberances of the membrane, the microvilli. All the microvilli of a retinula cell together are called a rhabdomere.

As a result of the tight membrane packing of disks and microvilli these photoreceptive structures have a higher index of refraction than their surroundings and therefore act as light guides, more precisely as optical wave guides. In vertebrate photoreceptors these are the outer segments and possible also those portions of the inner segments that are filled with mitochondria. In the invertebrates mentioned these are the rhabdomeres or the rhabdons (Fig. 15.114 center and lower part).

In most arthropods and mollusces the retinula cells are arranged in groups. The individual rhabdomeres of such a group constitute a rhabdom, a uniform light guiding and light-absorbing structure. Such
a group of cells is called an ommatidium. In the arachnid *Limulus*, for example, the ommatidium is composed of a variable number (9–14) of retinula cells and the rhabdom has a complicated, star-shaped form (Fig. 15.115a). Hymenoptera (i.e., ants, bees) always have nine retinula cells in one ommatidium, and the rhabdom has a simple round or square rodlike structure (Figs. 15.114, 15.115b). In the fused rhabdom of crustaceans successive packets of microvilli belonging to different retinula cells of the same ommatidium lie at right angles to one another (Fig. 15.114 lower). Flies, on the other hand, have an open rhabdom (Fig. 15.114, center), in which each of the six outer and the two central rhabdomeres together form a light-conducting structure. All eight rhabdomeres of one ommatidium look through one lens. The central rhabdomere of the retinula cells 7 and 8, which lie on top of one another, is thinner ($d=1 \mu m$) than the six peripheral ones ($d=2 \mu m$).

An important goal of photoreceptor optics is the determination of the influence of length, diameter, and form of the optical wave guide structure on the function of the receptor. Arthropod rhabdoms are particularly well suited for such an analysis, since they occur in a wide variety of shapes and sizes (Snyder and Menzel). The length of the rhabdoms or rhabdomeres covers the range from a few $\mu m$ to nearly 1000 $\mu m$. The diameter varies between 1 $\mu m$ and more than 50 $\mu m$. The form of the cross section may be round, square, rectangular, annular, or star-shaped. The variability is even further increased by the fact that the form of the rhabdom and the number of retinula cells involved in its construction may change along the length of the rhabdom. In addition, the length, diameter, and form of a rhabdom or rhabdomere may change upon illumination.

In the human eye, as we have known for a hundred years, rods and cones in different parts of the eye have different shapes and sizes. Fish,
amphibians, and birds frequently have double photoreceptors, in which one of the two receptors often contains a droplet of colored oil (Durkin). The part of the photoreceptor which is filled with mitochondria in fish and amphibians exhibits great variability in different species with different ecological adaptations.

All of the structural variability shows without doubt specific adaptations for the optimization of certain functional parameters. In the following we discuss briefly which factors play a role in this optimization.

c) Functional Organization of Photoreceptors

a) Physical Principles of Photoreceptive Optical Wave Guides

The photopigment molecules which absorb light are packed in long, thin cylinders, whose diameter is of the order of magnitude of the wavelength of light. The question, then is, what physical laws should be considered, if we wish to describe the propagation and absorption of light in such a structure.

Classical, Geometrical Optics View. As can be seen in Fig. 15.116, light is focused by the lens of the eye or of the ommatidium at the point P in the focal plane FP. It is a general rule that the distal end of the photoreceptor also lies in the plane FP. To simplify the general case we limit ourselves here to a parallel beam of monochromatic light and assume a circular cross section for the photoreceptor.

According to the laws of geometrical optics, parallel incident light is focussed at a point P which is removed from the optic axis by a distance X, which depends on the angle of incidence $\psi$. If $X$ is greater than the radius of the photoreceptor, no light reaches the photoreceptor; P is then outside the field of view of the photoreceptor, or outside the effective entrance aperture defined by the spatial extent of the photoreceptor. On the other hand, when P lies within the aperture of the photoreceptor, the rays of light can enter the photoreceptor and can then be guided along its entire length.

Whether or not light rays actually enter the photoreceptor and are guided within it by total internal reflection depends on the angle of incidence and on the indices of refraction according to the laws of reflection and refraction (Fig. 15.117a). Light incident at an angle $\Theta$ will be refracted toward the optical axis (or will be reflected) at the interface to a medium with a higher index of refraction ($n_0 < n_1$). The light beam will be totally reflected at the surface between the mediums with $n_1$ and $n_2$ if the ray coming from the medium with $n_2$ ($n_1 > n_2$) is incident at this surface at an angle $\alpha$ which is larger than the critical angle $\alpha_c$:

$$\sin \alpha_c = \frac{n_2}{n_1}.$$  \hspace{1cm} (15.25)

The fraction of the light which is propagated in the light guide depends on the number of rays starting from the
point P which fall within the critical angle. All the other rays will be refracted and will leave the photoreceptor again (Fig. 15.117b,c).

This simple, geometrical optics viewpoint suffices to show a fundamental optical property of photoreceptor structure, namely its light-guide nature. Many of the characteristics of photoreceptors to be discussed later (self-screening in long photoreceptors, optical coupling between parts of the wave-guide structure, dichroic absorption, birefringence) may be understood merely on the basis of this fundamental optical light-guide property. This description is sufficiently accurate under the assumption made here that the diameter of the light-guide structure is large compared to the wavelength of the light, which is the case for many photoreceptors.

**Diffraction of Light.** According to geometrical optics the photoreceptor in Fig. 15.116 should have a steplike change in spatial sensitivity as a function of the angle of incidence \( \theta \), since with each value of \( \theta \) the focal point \( P \) will lie either inside or outside of the distal end of the photoreceptor. This is not actually the case because of the wave nature of light, which makes it impossible for the lens to focus the light at a point. For example, take light which is sent through a very small hole with diameter \( d_h \). The smaller the ratio \( d_h / \lambda \) (\( \lambda \) = wavelength of the light), the greater the scatter of the transmitted light. A lens therefore does not produce a focal point, but a diffraction disk (Airy disk), whose diameter \( d_A \) is given by the following relation:

\[
d_A = 2.44 \left( \frac{\lambda}{d_h} \right) \sqrt{\frac{f}{n_0}} \quad \text{for} \quad d_A \ll f \quad (15.26)
\]

(\( \lambda \) wavelength of light, \( d_h \) diameter of the lens, \( f \) focal length of the lens, \( n_0 \) index of refraction of the medium between the lens and the focal plane).

For constant lens parameters \((f, d_h, n_0)\), \( d_A \) is proportional to \( \lambda / d_h \); the diffraction is stronger at longer wavelengths. When the diameter \( d \) of the photoreceptor is just equal to \( d_A \) at short wavelengths, then at long wavelengths significantly less light can reach the photoreceptor. The diffractive nature of the lens may thus have a primary influence on the spectral sensitivity of the photoreceptor.

It is easily seen that, due to the diffractive nature of the lens, the spatial distribution of the photoreceptor is not a step function, but a bell-shaped curve. We will omit a detailed formal derivation and illustrate the situation with Fig. 15.118 to convey an intuitive understanding. The degree of overlap (dark zone in Fig. 15.118) between the geometrical field of view of the photoreceptor and the Airy disk determines how much light can enter the photoreceptor. One sees immediately that the angle of acceptance of the photoreceptor decreases with the diameter \( d \).

The result of this effect may be given quantitatively in the spatial sensitivity function of a photoreceptor (Fig. 15.118). When a distant point source (parallel light) moves in an arc across a lens system and a photoreceptor, a bell-shaped curve is obtained for the spatial sensitivity function. The characteristic parameter \( \Delta \theta \), the half-width of the sensitivity curve, depends on the diffractive property of the lens and on the photoreceptor diameter:

\[
\Delta \theta = \left[ \left( \frac{\lambda}{d_A} \right)^2 + \left( \frac{d}{f} \right)^2 \right]^{1/2}.
\]

(15.27)
As we pointed out in the introduction, the more densely the photoreceptors are packed, that is the smaller the angle $\Delta \phi$ between the optical axes of adjacent photoreceptors, the greater the spatial resolution of a retina will be. Figure 15.118b indicates a simple, geometrical relationship in the compound eye. Since the compound eye consists of many small lenses, the angle $\Delta \phi$ between neighboring ommatidia decreases as the radius of the eye in that area increases.

$$
\Delta \phi = \frac{d}{R}.
$$

It is easily seen that a relationship must exist between $\Delta \phi$ and $\Delta \phi$ if the eye is to attain an optimal resolution of the image of its surroundings. An increase of $\Delta \phi$ makes the photoreceptor more sensitive, but reduces the spatial resolution of the eye if the spatial sensitivity curves of adjacent ommatidia overlap too much. Small $\Delta \phi$ therefore requires also small $\Delta \phi$, and that on the other hand reduces the quantum flux in the receptor. A critical factor is thus the noise level, or rather the signal-to-noise ratio in the photoreceptor. Sources of noise in the photoreceptor are first of all the random distribution of quantum absorptions in the photoreceptor and on the other hand, the differences in the magnitude of the signals produced by individual quantum absorptions. In the case of compound eyes it has been shown that for insects that are active in a bright environment the diffraction limit is nearly reached, whereas for insects that orient themselves visually in a dim environment the signal-to-noise ratio in the photoreceptor is the limiting factor. Such insects have larger diameter facets, and thus gather more light from their surroundings than would be expected from the diffraction condition. The manifold strategies in the construction of eyes and the great differences in the noise components of the photoreceptors and of the neurons of the visual system prohibit so far general conclusions. It has been shown, however, that there is no advantage for an eye to have $\Delta \phi$ smaller than

$$
\Delta \phi = \frac{1}{\sqrt{3}} \frac{\lambda}{d_n}.
$$

\section*{Beta) Lateral and Tiered Filters}

A type of structure found frequently in highly evolved photoreceptors is the packing together or stacking of photoreceptive units of different photoreceptors. Two examples are discussed here in detail: lateral and tiered filters in the fused rhabdoms of arthropods.

\textit{Lateral Filter Rhabdomeres in Fused Insect Rhabdoms.} In most insects, as shown in Fig. 15.114, several rhabdomeres are packed together to form a uniform, optical light-guide structure, a fused rhabdom. In certain insects we know that the individual rhabdomeres have different absorption characteristics for light of different wavelength (various photopigments) and electric vector ($E$) orientation. The merging in one uniform light guide leads to an optical coupling of the individual rhabdomeres, so that the absorption characteristic of each rhabdomere influences those of all of the others. What might be the advantage of such an optical coupling?

In the simple, geometrical optics, the model of a light pipe filled with an absorbing medium the absorbed energy $A$ is given by

$$
A = J_0(1 - e^{-\beta l})
$$

($\beta$ = absorption coefficient of the photopigment, $J_0$ = intensity of incident light, $e$ = concentration of the photopigment, $l$ = length of the photoreceptor).

The optical path $l$ of a light ray is longer than the length $l$ of the photoreceptor due to total reflection, and depends on the angle of incidence $\theta$ according to $l = l_l \cos \theta$. Equation (15.30) should be corrected accordingly. However, this correction may be neglected here since $n_l = n_l$ so that $\cos \theta = 1$ and $l = l_l$.

Due to the density of the packed membrane the absorption is quite high (order of magnitude 1% per micron). Since the rhabdons can be very long (up to 1000 $\mu$m in dragonflies), they achieve a high total absorption. For a bee rhabdom about 300 $\mu$m in length one can actually estimate the probability of absorption at 90%. Such a high absorption probability leads however to the phenomenon that the spectral absorption curve for the whole receptor differs markedly from that for a thin layer of the photopigment (Fig. 15.119a). The steep curve flattens out with increasing total absorption and the maximum is broadened. This effect may be understood by considering Eq. (15.30) as a function of $l_l$. One can picture this effect by imagining that the successive layers of photopigment act as identical color filters, so that the upper layers reduce the absorption probability of the deeper layers in the spectral absorption maximum first. The regions outside the absorption maximum are only affected deeper in the stack. This effect of high total absorption is thus sometimes called "self-screening".

Optical coupling counteracts the self-screening (Fig. 15.119b). The rhabdomeres containing different photopigments act on one another as absorption filters for different spectral regions. Since they are placed beside one another, we call them lateral filters. The optical coupling of three different photopigments with maximum absorption in the UV (340 nm), blue (420 or 440 nm), and green (510 nm) regions leads to the result that, although the spectral sensitivity of each receptor corresponds closely to the spectral extinction curve of its photopigment, the absorption probability of the entire rhabdom is very high over the whole spectral range.

The fused rhabdom of insects thus shows itself to be a structure which is adapted to give both high absolute sensitivity and sharp spectral distinction.

Color filter effects may also play a role within the photoreceptive structure of single visual cells. The occurrence of more than one photopigment in one visual cell has not yet been clearly established, but the possibility cannot yet be eliminated.

We know that in insects and squids the visual pigment does not bleach, as in vertebrates, but rather goes over into a stable state.
15.2.4.2 Photoreceptor Optics—Structure and Function of Photoreceptors

Fig. 15.119a,b. Self-screening: The effect of high total absorption in long rhodomeres on the spectral sensitivity of a photoreceptor. For small changes in the spectral sensitivity of the photoreceptor $S(\lambda)$ corresponds to the spectral extinction of the photopigment ($\beta_{\lambda},$ dotted curves for UV, blue, and green pigments). At higher total absorption, i.e., for $c_1 = 7$, the maxima flatten out and the $S(\lambda)$ curves are broadened. Lateral filtering: In a fused insect rhabdom composed of rhodomeres with different spectral absorption characteristics (i.e., a bee rhadom) the rhodomeres act on one another as absorbing color filters. Such a structure is identical with an arrangement in which each rhadomere is preceded by each of the two other types as color filters. As a result of the lateral filter effect of three different rhodomeres, the $S(\lambda)$ function of each photoreceptor corresponds rather well to that of its photopigment, although the total absorption in the long rhadom is high. The lateral filter effect thus counteracts self-screening.

Through this stacking of differently oriented microvilli an effect is produced similar to the lateral filter effect. In spite of high total absorption in the whole rhabdom, each rhadomere has the absorption characteristic of a thin layer of its photoreceptive membrane. Thus in the crustacean rhabdom the polarization sensitivity of a retinula cell is theoretically identical to the dichroic ratio of the absorbing membrane. Indeed, taking intracellular recordings of the retinula cells of crustaceans one finds a high polarization sensitivity: when $E$ is rotated, the sensitivity for the most effective orientation of $E$ is ten times larger than for the direction 90° away from it.

In insect ommatidia there are frequently special, short retinula cells whose rhodomeres lie beneath other rhodomeres. Examples are the eighth visual cell of the fly and the ninth visual cell of the bee (Fig. 15.114). If, for example, the distal cells which lie above these proximal cells have the same spectral absorption characteristics, but have their microvilli at right angles to those of the proximal cells, the distal cells serve as polarization filters and increase the polarization sensitivity of the short proximal cells.

The arrangement of rhodomeres in layers or of rhodomere sections with crossed orientation of micro-
villi emerges as a structural scheme for maintaining or amplifying polarization sensitivity while achieving simultaneously high absolute sensitivity.

Wave-guide Properties of Photoreceptors

Many animals with highly evolved visual systems have long, thin photoreceptive structures with a higher index of refraction than the surrounding medium. Such structures conduct light through total internal reflection (see above). This light-guide property has the advantage that adjacent photoreceptors are optically isolated from one another. Most important, however, is the property that a very high absorption is attained with a relatively small expenditure of photopigment. The photon absorption depends primarily on the length of the photoreceptor and relatively weakly on the diameter and form. The smallest possible diameter of a photoreceptor is determined by the optical wave-guide effect. Below a critical diameter less and less light is admitted to the interior of the wave-guide and thus the wave-guide becomes less and less effective. The wave-guide effects which are discussed below are actually by-products of the development of thin photoreceptive structures, which themselves arose in the process of optimization of photopigment expenditure and quantum absorption.

In the outer segments of vertebrate photoreceptors and in the rhabdomeres of insects are found light patterns which are recognized as wave-guide modes. Such patterns are associated with narrow optical wave-guides and are an indication of the wave-guide characteristics of the structure. These light patterns probably have no function in the light absorption process, although it is theoretically possible that some fused rhabdoms could differentiate between different modes on the basis of the geometry of their rhabdomes.

Optical wave guides have two particular properties which could play a role or at least set limits for the functioning of photoreceptors:

1. A fraction of the light energy which is distributed in modes is conducted inside the wave guide; the rest is propagated outside. This phenomenon results from the penetration of the electromagnetic field upon reflection during total internal reflection, and depends strongly upon wavelength.

2. Since light energy is propagated outside the photoreceptive structure as well as inside it the closely packed photoreceptors (e.g., in the vertebrate retina) are optically coupled with one another, though weakly.

The effects of wave-guide modes are best described using the parameter $V$:

$$V = \frac{d}{\lambda} \left( n_1^2 - n_2^2 \right)^{1/2} \tag{15.31}$$

where $d$ = diameter of the wave guide, $n_1$ = the index of refraction of the wave guide, and $n_2$ = the index of refraction of the surrounding medium. For example, the proportion $\eta$ of the optical energy inside the wave guide depends on $V$ and on the mode (Fig. 15.120). In this example we have assumed that the length of the wave guide is at least ten times greater than the diameter. In reality it is almost impossible to determine the parameter $V$ by the use of the formula Eq. (15.31) because the indices of refraction $n_1$ and $n_2$ cannot be determined experimentally with sufficient accuracy. A very accurate determination of these indices of refraction is necessary, however, since $n_1 \approx n_2$. It is also not possible to determine $V$ from the so-called cutoff characteristics of the modes, by measuring for which mode optical energy ceases to be carried in the wave guide, since we now know that modes do not exhibit an abrupt cutoff. The most accurate determination of $V$ so far was made by measuring the influence of the wave-guide mode on the birefringence. Such measurements in the thin rhabdomes of the fly ommatidium have led to a value $V \leq 2$. In these measurements a $n_{11}$ mode was excited. An important result of these measurements was the recognition that mode effects can influence measurements on photoreceptors only under certain conditions.

These conditions are primarily: (1) the diameter of the photoreceptive structure must be near or smaller than 1 µm, and (2) measurement of the spectral absorption and index of refraction must be made along the axis of the wave guide. Measurements perpendicular to the long axis of the photoreceptor are not influenced. Furthermore, the determination of the relative dichroic absorption (see below) is independent of mode effects.

1. Spectral Sensitivity of the Photoreceptor

For constant diameter of the photoreceptor $d$ and constant $(n_1^2 - n_2^2)$ we see from Eq. (15.31) that $V$ increases with decreasing wavelength of light. Thus for short wavelengths, a greater proportion of the energy is carried inside the wave guide. Since only light propagating inside the wave guide is absorbed by the photopigment, the spectral sensitivity of the photoreceptor is modified relative to the spectral absorption of its photopigment: (1) The absorption maximum in the visible wavelength region (400–700 nm) is shifted to shorter wavelength. (2) The relative sensitivity in the UV is increased. This effect may lead to an increase in
the spectral sensitivity in the UV region in the narrow fly rhodomers 7 and 8. The mode which is excited in the wave guide is also determined by the angle of incidence $\phi$. The more $\phi$ deviates from the optic axis, the higher the modes which contribute to the flow of energy in the wave guide. The resulting wavelength dependence due to the additional effectiveness of more modes between 450 and 500 nm leads to a change in the amount of energy flowing in the wave guide in this region. The spectral absorption maxima of photopigments having their absorption maxima in this region can thus be shifted to shorter wavelengths. The strength of this effect depends critically on $V$.

\section*{β) Effective Aperture of a Photoreceptor}

An important consequence of the wave-guide nature of the photoreceptor is that the effective aperture is larger than that determined by its geometrical diameter. The reason is the relationship between mode energy inside and outside of the wave guide. This means in effect that part of the light energy incident outside the photoreceptor can be absorbed by the photopigment. The magnitude of the effect depends on $V$ and on the conditions of illumination (size of the Airy disk relative to the diameter of the photoreceptor). If, for example, $V=2$ and the Airy disk has twice the diameter of the photoreceptor, then 90\% more light reaches the wave guide than geometrical optics considerations would predict.

\section*{γ) Form, Length, and Packing of Photoreceptors}

It is well known that the shape and packing pattern of human photoreceptors depends on location on the retina. With increasing distance from the fovea, for example, the cones become shorter, thicker, and more conical, and their index of refraction decreases. This may possibly be understood on the basis of wave-guide effects. Peripheral cones could have the double function of (1) increasing the sensitivity of the rod system in the sketopic visual region by acting as antennas for light waves and guiding these onto the cones, and (2) absorbing light in the photopic visual region and thus allowing color vision also in the peripheral areas.

Experimental evidence for this hypothesis is not yet available. The length of tightly packed photoreceptors in the retina of vertebrates must be limited, since otherwise the energy carried outside the wave guides could go over to adjacent photoreceptors, so that the photoreceptors would be optically coupled. This mode effect develops only after a certain pathlength in the wave guide, so that the packing density of short photoreceptors can be greater than for long ones. It is an interesting open question whether cone density and length in the fovea of the human eye are adapted according to these criteria. In fly ommatidia the rhodomers lie close together at the distal end and then spread apart within the first few microns. This arrangement suggests that optical coupling between rhodometers, particularly between the central and peripheral ones, is avoided. Invertebrate eyes in particular show a wealth of differently formed photoreceptive structures which doubtless represent special adaptations to their particular tasks. It remains for further research activity in this area of photoreceptor optics to clarify these relationships.

e) Photoreceptor Optics and the Structure of the Photoreceptive Membrane

The photoreceptive membrane is anisotropic and has dichroic as well as birefringent properties. By dichroism we mean the dependence of the absorption of light on the direction of the electric vector $E$. We designate individual molecules which absorb dichroically as dipole absorbers in the following discussion. The absorption axis of a dipole absorber is then the direction in the molecule parallel to which $E$ must oscillate for linearly polarized light to be maximally absorbed. The dichroic ratio gives the ratio between the maximal and minimal absorption upon rotation of $E$.

For a photoreceptive membrane the dichroic ratio describes the degree to which such absorbing dipoles are lined up parallel. Birefringence describes the dependence of the index of refraction on the direction of the electric vector $E$ and is a measure of the order in the membrane structure, or of the "crystallinity" of the membrane.

\section*{a) Functional Basis of the Orientation of Dipoles in the Membranes of Different Photoreceptors}

The chromophore group 11-cis-retinal in the rhodopsin molecule is a dipole absorber since the $r$-electron clouds of the conjugated double bonds lie in a plane on either side of the slightly zig-zag carbon chain (see Chap. 15.2.4.1). The absorption axis of the chromophore group lies parallel to the membrane surface. In the disk membranes of vertebrate photoreceptors and most probably also in the microvilli of fly rhodomers the dipoles in the membrane surface are randomly oriented (see Chap. 15.2.4.1). This can be directly measured in rod outer segments: illumination of single outer segments from the side yields a dichroic ratio of 6.5; illumination along the physiological axis, the long axis of the outer segment, yields no dichroic absorption. The reason for the random orientation of the dipoles in the membrane is free rotation about an axis perpendicular to the membrane surface and the lateral motion of the rhodopsin molecule due to thermal (Brownian) motion.

In contrast to this, the dipoles in the fused rhodopsins of crustaceans and insects must be largely parallel, since these visual cells show a high polarization sensitivity.

However, it is not clear how such an alignment of the rhodopsin molecule is brought about. The various models suggested up to now are untested.

For example, one might imagine that the membrane of these microvilli is much "stiffer" than the disk membrane and does not allow free motion of the rhodopsin molecules once they have been oriented.

Another model relies on the Brownian motion itself to explain the orientation of the rhodopsin molecules. If a "liquid membrane" such that of the disks is rolled into a microvillus (diameter about 50 nm), the rhodopsin molecules will move preferably along the length of the microvillus. Any motion perpendicular to the axis, along the strong curvature, is hindered by a radial force directed towards the center axis of the microvillus. If the rhodopsin molecules in the surface of the membrane are not circularly symmetric, but oval or otherwise asymmetric, then the preferred direction of motion along the long axis of the microvillus should produce a nearly parallel alignment of the rhodopsin molecules. A third possibility assumes a cytoplasmic skeleton in each microvillus which fixes the membrane-bound rhodopsin molecules in an ordered arrangement. This model is supported by recent findings on the interaction between membrane and fibrillar structures of the cytoplasm.


The absorption of light is greatest when the absorption axes of all the dipole absorbers are perpendicular to the direction of propagation of the light, since E oscillates perpendicular to the direction of propagation. Since the chromophore group is built into its protein carrier in such a way that its long axis is parallel to the membrane surface, the photoreceptive membrane in all highly-developed photoceptors is oriented perpendicular to the direction of incidence of light. A flat photoreceptive membrane (disk) has the greatest absorption probability for unpolarized light if the absorption axes of the dipole absorbers are randomly distributed in the surface. The same is true for the rhabdomeres of open rhabdoms (of flies, for example). In fused rhabdoms, on the other hand, the orientation of the dipoles for optimal absorption of unpolarized light depends on the structure of the whole rhabdom. In the type found in crustaceans and bees (Fig. 15.114) the greatest absorption of unpolarized light in the whole rhabdom is achieved when the dipole absorbers in the variously oriented microvilli are strictly parallel within each microvillus.

These findings and their interpretation are the basis for a hypothesis according to which the dipole absorbers in a photoreceptive structure are in each case so arranged as to give the highest sensitivity for unpolarized light. The dichroism of most rhabdomere photoceptors would then be a secondary result of this mechanism and not a special property for the detection of polarized light.

Apparently, the resulting polarization sensitivity of visual cells is not necessarily a desirable side product; there are some insects with twisted rhabdoms in which the polarization sensitivity is canceled out. However the polarization sensitivity of special retinula cells is maintained or even amplified and forms the basis for the development of orientation mechanisms using the polarization pattern of the blue sky.

b) Crystallinity of the Photoreceptive Structure

The high degree of order of the lipoidal molecules in the parallel membranes is the source of the birefringence of photoreceptive structures which was observed long ago. Since many such membranes are in a tightly packed, parallel arrangement, the birefringence observed for the entire structure (i.e. rod outer segment, rhabdomere) is a sum of the birefringence of the membrane ($\Delta n_1$, intrinsic birefringence) and form birefringence ($\Delta n_2$).

Measurements of the birefringence of the membrane yield similar values for rod outer segments and for fly rhabdomeres: $\Delta n \approx 5 \times 10^{-3}$ ($\Delta n_1 = n_1 - n_2$, where $n_1$ and $n_2$ are the indices of refraction for linear polarized light parallel to the two optical axes of the birefringent membrane). This means that rhabdomeres and disk photoceptors show about the same crystallinity.

If the birefringent structure is a wave guide, then the effective indices of refraction ($\langle \Delta n_1 \rangle$, $\langle \Delta n_2 \rangle$), which are influenced by the wave-guide properties, are determined from experiments, and not the indices of refraction of the material ($\Delta n_1$ and $\Delta n_2$) alone. It may be shown that the measured birefringence is a product of structural birefringence and $\eta$. Since $\eta$ defines the waveguide parameter $\Gamma$, this parameter may be determined indirectly from the wavelength dependence of the effective birefringence. $\Gamma$ was determined in this way for the fly rhabdomeres. For the thin rhabdomere $7$ the values $\Gamma \approx 2$ at 300 nm and $\Gamma \approx 1$ at 650 nm were found.

i) Conclusions and Prospects

The structures of living organisms have an evolutionary history. Their effectiveness in improving the chances of survival and reproduction of their species are under the control of external factors. For visual organs the influence of such factors is immediately obvious. High absolute light sensitivity allows optical orientation even at very low illumination; at dusk, at night, deep in the forest or in caves. This can open new sources of food to exploitation, and can offer better protection from enemies. The development of greater spatial and temporal resolution of the complete visual organ becomes possible, and mechanisms that allow detailed perception even in fast flight. Photoceptors with visual pigments having different spectral absorption are the precondition for color vision, an orientation mechanism which opens additional dimensions of the optical surroundings and can be of decisive importance for the acquisition of food, the location of sexual partners, and the discriminating recognition of orientation markers.

Our discussion concentrated on the question of how the spatial structure of the light-absorbing portion of a photoceptor determines its function, aside from the biochemistry of the visual dyes. Since we have considered only highly evolved visual organs, we can properly assume that their structure is to a large extent adapted to specific tasks. At the level of the "photoreceptive membrane unit" it was shown that the orientation of the dipole absorber molecules perpendicular to the direction of propagation of the light beam, the random distribution of dipole absorbers in disk photoceptors and unfused rhabdomeres, the parallel orientation thereof in fused rhabdoms, and the dense packing of absorbing membranes perpendicular to the incident light, all are optimal for achieving the goal of greatest light sensitivity.

The dense stacking of membranes has the additional result that the light-absorbing structure guides the light waves so that the photopigment molecules are maximally exposed to the light. Quantitative analysis of the functional structures show that the geometrical optics description does not suffice due to the small diameter of these optical wave guides, and that mode effects in optical wave guides can play an important role. As a result, shape parameters such as length, cross section and shape of cross section of the wave guide, assembly out of differently absorbing sections or sectors, and distance from adjacent wave guides are of great significance for the functioning of photoceptors.

The analysis of the functional structure of photoceptors is just in its beginnings. Only the general lines of understanding have been worked out so far. The whole multiplicity of photoreceptive structures in the
animal world and of their relationship with their respective specific tasks is still but little understood. The concepts presented here can be a fruitful starting point for further exploring this field.

Selected References


15.2.4.3 Information Transmission and Representation in the Nervous System: The Neurophysiology of Vision as an Example

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a) Introduction

Biological organisms dissect the physically continuous stimulus field around them and relevant to them into a raster, whose single points represent a specific location in space and a specific quality. The location in space is given by the anatomical location of the receptor on the body surface, within the body, or within a sensory organ. The information on quality is determined by the biophysical properties of the receptor (e.g., sensitivity to chemical, thermal, photic, or mechanoreceptors) as well as by its relation to certain stimulus-receiving structures (e.g., mechanoreceptors in the skin or in the inner ear). Thus, the excitation of a given receptor will produce only that sensory quality for which the receptor is specialized, no matter whether this excitation is brought about by the specific stimulus or by an artificial, e.g., an electrical stimulus (law of specific sensory energy of Max von Müller).

The excitation of single receptors or of groups of receptors is transmitted on individual conduction channels (nerve fibers) to neural networks at higher levels of the central nervous system (CNS), where the excitations of these different conduction lines are combined and computed in a characteristic manner. As a result of these network circuits, certain temporospatial sequences of receptor excitations may excite the network effectively, others not or only little, so that they will not be transmitted to the next levels of the CNS. In this respect, these networks serve as multidimensional filters. The task of these filters is to transform information about the environment into such a code, which at the final level elicits spatiotemporal patterns of excitation in the effector structures of the nervous system, i.e., the motor systems which enable the organism to behave reasonably in its environment. These principles of transformation of the physically defined stimulus field into neuronal excitatory patterns can be illustrated in the visual system.

b) The Retina

1) Anatomical Organization of the Retina

(Figs. 15.121-15.123)

At the receptor level of the retina in the eye light energy of a certain wavelength is being transformed into electrical activity (see Chap. 15.2.4.1). In the human retina, the receptor cells have a diameter of about 3–4 µm and form a dense sheath (Fig. 15.121). The single receptors are connected via specialized contacts (synapses) to a second layer of cells, the bipolar cells, and these again with the ganglion cells of the retina, which send their processes (axons) into the central nervous system. The retinal receptors are of two types, the rods and the cones. The rods contain rhodopsin as light-sensitive chromophore, with a maximal sensitivity to light of 505 nm wavelength and a range of about 380–650 nm. They are responsible for achromatic vision in the scotopic range, i.e., at low light levels (seeing in the dark). The cones contain one of the three known pigments which are responsible for color vision: erythrob (maximal sensitivity at 570 nm, range 430–720 nm), chlorob (maximum at 535 nm, range about 400–630 nm), and cyanob (maximum at 445 nm, range 380–530 nm). Their relative and absolute density is not evenly distributed across the retina; blue-sensitive cones with cyanob as pigment are missing in the fovea (the center of the visual field) but are present in the parafoveal regions; green- and red-sensitive cones (with chloro- and cyanob as pigments) are found in the fovea as well as in the parafoveal regions. Toward the periphery of the retina (and thus, of the visual field) the density of the various color-sensitive cones decreases steeply, and 1° outside the fovea only few cones are found. Therefore, color vision is essentially restricted to the central region of the visual field. Since the maximum sensitivity of rods is at 505 nm and that of all cones together at 555 nm, the maximum sensitivity of the eye is at 555 nm in the light-adapted state (photopic sensitivity), and is shifted toward 505 nm in the dark-adapted state (scotopic sensitivity). This shift of spectral sensitivity toward shorter wavelengths during dark adaptation is called the Purkinje shift.

In addition to the vertical connections in the retina from receptor to ganglion cells there is a horizontal organization, which is localized at the level of contacts between the various vertical elements, that is in the outer and inner plexiform layers (layers 5 and 7 in Fig. 15.121d). This horizontal organization is due to divergent and convergent connections of lateral branches of the various vertical transmission channels, and to lateral interaction between these channels via horizontal cell systems at the level of the synapses.

The light reaches the receptors only after passage through the nearly 300 µm thick layer of tissue, which