On Optical Crosstalk between Fly Rhabdomeres

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W. Wijngaard* and D. G. Stavenga**

Abstract

In a fly retinula light may be transferred among the rhabdomeres. It is estimated that the light from a point source imaged on the axis of a rhabdomere may eventually be transferred completely to a neighbouring rhabdomere. However, the effect on the sensitivity of this latter rhabdomere will remain small, owing to the fact that the light transfer occurs only proximally. This result is in accordance with the neural superposition theory of fly vision.

Introduction

Visual photoreceptors of flies, the rhabdomeres, act as optical waveguides (De Vries, 1956). This has been clearly established by the observation of mode patterns (Franceschini and Kirschfeld, 1971a).

Usually it is supposed that fly rhabdomeres can be regarded as separate units (cf. Kirschfeld, 1971). In an anatomical sense this is certainly true, however, it is less obvious whether or not the same holds from an optical point of view, since it has been found that optical cross-talk exists between rhabdomeres within a fly retinula (Kirschfeld, 1972).

Recently optical cross-talk between optical waveguides has been investigated extensively (Jones, 1965; Snyder, 1972; Wijngaard, 1973; McIntyre and Snyder, 1973, 1974). Basing ourselves on these studies we shall here derive quantitative estimates for the leak of light between fly rhabdomeres. To that end we shall first describe the essentials of the anatomy of a fly retinula. After calculating explicit values for the light-power transfer between rhabdomeres its consequences will be discussed in connection with the neural superposition theory of fly vision; in that theory the optical distinctness of the rhabdomeres is essentially taken for granted (see Trujillo-Cenóz, 1972).

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Anatomy of the Fly Retinula

The organization of the dipteran visual system has recently received considerable attention (for reviews see Kirschfeld, 1971; Seitz, 1971; Trujillo-Cenóz, 1972; Braitenberg and Strausfeld, 1973). Boschek (1971) has extensively investigated the retina of the housefly *Musca domestica*.

A fly retinula, i.e. the set of eight visual sense cells served by one facet lens, consists of six peripheral cells and two central ones. Each sense cell on one side bears a pile of protrusions, the rhabdomere, the cross-section of which is more or less circular.

Boschek (1971) has found that the peripheral six rhabdomeres taper from the distal to the proximal end, the radius decreasing from about 1.0 to 0.5 μm. The central two rhabdomeres are uniform cylinders with a radius of about 0.5 μm. Noteworthy is that these latter rhabdomeres are situated on top of one another, such as to build together one functional waveguide, which is just as long as the peripheral ones.

The gross morphology of most fly eyes is identical, but minor interspecies differences in rhabdomere radius may occur. Yet, the length of the rhabdomeres can deviate substantially and may vary from 70 μm for *Drosophila* to 350 μm for *Calliphora*. Furthermore, rhabdomere length depends rather on eye region; e.g. from Braitenberg (1967) it can be deduced for the housefly *Musca domestica* that rhabdomere length is frontally about 200 μm and laterally about 150 μm.

However, in the next section it will appear that in considerations regarding optical cross-talk between rhabdomeres, the most critical parameter is the relative distance of rhabdomeres a/ϱ, where ϱ is the radius of the rhabdomeres and a is the distance of their axes. From Boschek (1971, Fig. 5) we derive that a lower limit for the relative distance mainly is $a/\varrho = 3$. Electronmicroscopic photographs available in the literature (Langer, 1966; Trujillo-Cenóz and Melamed, 1966; Melamed and Trujillo-Cenóz, 1968) also generally show relative distances exceeding the value 3.

Only one clear exception has to be made, namely for the most distal part of the retinulae, where $a/\varrho \simeq 2.5$.

The extent of optical cross-talk between fly rhabdomeres will be investigated next.

Transfer of Lightpower Among two Optical Waveguides

Light propagates along rhabdomeres in patterns called modes. A discussion of modepropagation with regard to fly rhabdomeres has been presented by Snyder and Pask (1973). We recall that circle-cylindrical dielectric waveguides are characterized by the cutoff parameter

$$V = \frac{2\pi\varrho n_1}{\lambda_0}\sqrt{\delta} \qquad (1)$$

and

$$\delta = 1 - \frac{n_2^2}{n_1^2}. \qquad (2)$$

Here ϱ is the radius of the waveguide, n_1 and n_2 are the refractive indices of the inside and outside medium respectively ($n_1 > n_2$) and λ_0 is the vacuum wavelength of the incident light. For $V < 2.405$, only the fundamental $HE_{1,1}$ mode can be guided along the rhabdomere. For $V < 3.832$ a point source imaged on the axis of the rhabdomere will exclusively excite the $HE_{1,1}$ mode and a radiation field. For fly rhabdomeres with $\lambda_0 = 0.5\ \mu m$ V is probably less than 3.8, therefore we shall restrict our discussion to the transfer of lightpower among the $HE_{1,1}$ modes of the different rhabdomeres.

To obtain an estimate of the relevance of this kind of power transfer we will first consider the case of two parallel circle-cylindrical dielectric rods (optical waveguides), which are taken to guide the light without loss. It will be assumed that the $HE_{1,1}$ mode of one of the rods is excited with unity power at $z = 0$; the power in the $HE_{1,1}$ mode of the other rod at $z = 0$ is assumed to be zero (z is the coordinate along the axis of the rod). The power is transferred from the excited rod into the unexcited one and back again. The power P_2 in the $HE_{1,1}$ mode of the latter rod can generally be given by (McIntyre and Snyder, 1973):

$$P_2(z) = F_{21}\sin^2\left(\frac{\pi}{\lambda_B} z\right), \qquad (3a)$$

with

$$F_{21} = \frac{1}{\left|\dfrac{C_{12}}{C_{21}}\right| + \dfrac{(\beta_1 - \beta_2)^2}{4|C_{21}|^2}}, \qquad (3b)$$

and

$$\frac{\pi}{\lambda_B} = |C_{21}|\sqrt{\frac{1}{F_{21}}}. \qquad (3c)$$

C_{12} and C_{21} are mutual coupling constants; β_1 and β_2 are the propagation constants of the $HE_{1,1}$ modes of the excited and unexcited rod respectively (the phase velocity of the wave is ω/β, if ω is the angular frequency). The maximum value of F_{21} is 1, this value is obtained when $\beta_1 = \beta_2$, for example in the case that the two waveguides are identical. The distance between the successive light intensity maxima in the rods, called the beatlength, then is

$$\lambda_B = \pi/|C| \qquad (4)$$

with $C = C_{12} = C_{21}$.

For two identical rods, when $\delta \ll 1$, $\sqrt{\delta}/(\varrho|C|)$ only depends on V and a/ϱ; for numerical values see Fig. 5 in Snyder (1972). In Fig. 1 $\lambda_B\sqrt{\delta}/\varrho = \pi\sqrt{\delta}/(\varrho|C|)$ is presented as a function of V with independent parameter a/ϱ (continuous curves).

Power transfer between identical rods of length L is clearly determined by L/λ_B [see Eq. (3a)]. To determine the power transfer for the real case of fly rhabdomeres Fig. 1 can be utilized by putting in the normalized length $L\sqrt{\delta}/\varrho$. As an example we take for the length of the rhabdomeres $L = 300\ \mu m$, a mean radius ϱ of $0.75\ \mu m$ and a wavelength $\lambda_0 = 0.5\ \mu m$. The length L has been chosen fairly large because we are mainly interested in an upper estimate for the power transfer. Reliable values for the refractive indices are $n_1 = 1.365$ and $n_2 = 1.339$ (Stavenga, 1974a, b). The cutoff parameter in this instance is $V = 2.5$, whereas $L\sqrt{\delta}/\varrho = 77.7$; this situation is indicated by Point A in Fig. 1. From Fig. 1 the ratio L/λ_B may be obtained. When the normalized distance between the rhabdomeres is $a/\varrho = 3.0$ then $L/\lambda_B = 0.31$ and accordingly $P_2 = \sin^2(\pi L/\lambda_B) = 0.68$. Similarly it follows that at $a/\varrho = 4.0$ the power transfer P_2 is less than 0.02.

Further insight can be gained from Fig. 1 by changing one by one the parameters in the present example. The resulting values of $L\sqrt{\delta}/\varrho$ are indicated by a dot at the end of each dashed line radiating from Point A. The respective values of λ_0, ϱ and n_1 are inserted near the dots. For $a/\varrho = 3.0$, L exceeds λ_B when $\varrho = 0.5\ \mu m$ and hence in this case light-power transfer will be abundant, on the other hand when $\varrho = 1.0\ \mu m$ the transfer of light is negligeable.

The relevance of this discussion is not at once evident because the peripheral rhabdomeres taper from a radius of $1.0\ \mu m$ distally to $0.5\ \mu m$ proximally. Apart from this, since the rhabdomeres contain the absorbing visual pigment the supposition that the waveguides function without loss is not fulfilled. Fortunately though, absorption and tapering can be accounted for together.
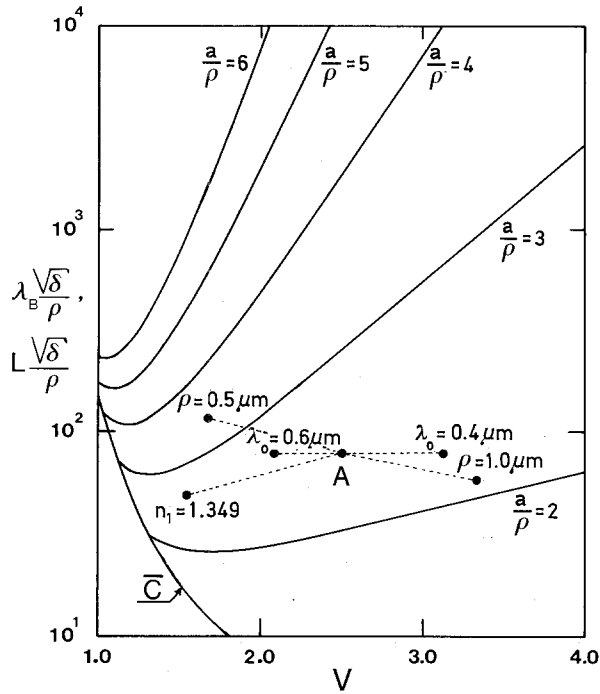
Fig. 1. Continuous curves: The normalized beatlength $\lambda_B\sqrt{\delta}/\varrho$ for the $HE_{1,1}$ modes of two identical circle-cylindrical dielectric rods, as a function of the cutoff parameter V defined in Eq. 1. ϱ is the radius of the rods and a is the distance between their axes ($\delta \ll 1$). Curve $\bar{C}$ is a cutoff curve (see Wijngaard, 1973). Point A presents the normalized length $L\sqrt{\delta}/\varrho$ of a hypothetical rhabdomere pair of circular cross section and equal radius, which is assumed to be constant throughout the retinula. Point A was calculated with $L = 300$ μm, $\varrho = 0.75$ μm, $n_1 = 1.365$, $n_2 = 1.339$ and $\lambda_0 = 0.5$ μm. The dots at the ends of the dashed lines were obtained in the same way, but by changing one of the parameters ϱ, λ_0 or n_1. The value of the changed parameter is indicated near the dot in question
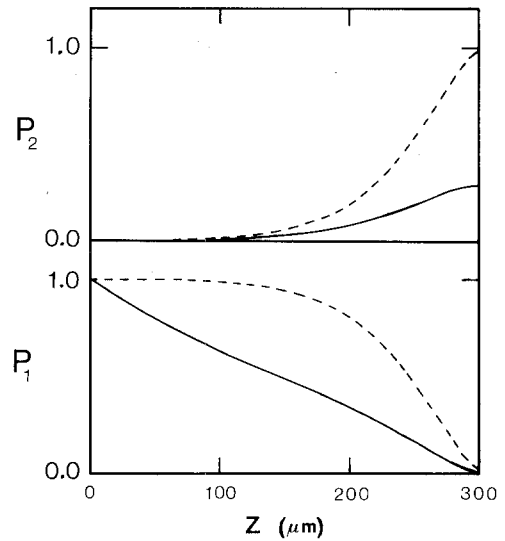

Fig. 2. Lower figure: The power P_1 in the $HE_{1,1}$ mode of the excited rhabdomere of a pair of tapering rhabdomeres. Upper figure: The power P_2 in the $HE_{1,1}$ mode of the nonexcited rhabdomere. The dashed and continuous curves represent the case where $\kappa L \ll 1$ and $\kappa = 0.005$ μm^{-1} respectively; κ is the absorptioncoefficient of the rhabdomere-medium and L the length of the rhabdomeres. The taper is linear with $\varrho = 1.0$ μm distally and $\varrho = 0.5$ μm proximally. $L = 300$ μm, $n_1 = 1.365$, $n_2 = 1.339$, and $\lambda_0 = 0.5$ μm. The relative distance a/ϱ is assumed to be 3.0 throughout the retinula

Consider the case of two identically tapering and identically absorbing waveguides of which one is excited, then the part of the power in de $HE_{1,1}$ mode of the unexcited rhabdomere is given by (McIntyre and Snyder, 1974):

$$P_2(z) = \sin^2\left[\int_0^z C(z')\,dz'\right]\exp\left[-\int_0^z \kappa\eta(z')\,dz'\right]. \quad (5)$$

Here κ is the absorptioncoefficient of the rhabdomere medium and $\eta(z)$ the part of the power of the $HE_{1,1}$ mode guided inside the rhabdomere.

To achieve $\int_0^z C(z')\,dz'$ quantitatively we assume that the taper is linear and that a/ϱ is constant throughout the retinula as is suggested by Fig. 5 of Boschek (1971). When $|C(0)|$ at $z = 0$, where $\varrho = 1.0$ μm, is much smaller than $|C(z)|$, for $\varrho < 1.0$ μm, we can advantageously use the relation (derived in the Appendix)

$$\int_0^z C(z')\,dz' = \frac{zC(z)}{\{V(0) - V(z)\}\,\{1.146\,a/\varrho - 1.479\}}. \quad (6)$$

For $z = L = 300$ μm, $\lambda_0 = 0.5$ μm, $n_1 = 1.365$ and $n_2 = 1.339$ we obtain at $a/\varrho = 3.0$ from Eq. (6) that $\int_0^L C(z')\,dz' = 0.306\ L\cdot C(L)$ when the radius of the guides tapers from 1.0 μm distally to 0.5 μm proximally. It will be noted that $L\cdot C(L)$ is equal to $\int_0^L C(z')\,dz'$ in the case of guides with a constant radius $\varrho = 0.5$ μm.

In conclusion, when for the peripheral rhabdomeres $|C(0)|$ is much smaller than $|C(L)|$ and the taper is linear with a/ϱ constant, the transfer of light is determined by the properties of the rhabdomeres for $z = L$. However, in the example considered above the power transfer occurs only over some 30% of the length of the rhabdomeres.

The exact course of the transfer of light along the axial coordinate z is depicted in Fig. 2. In this figure the power P_1 of the $HE_{1,1}$ mode of the excited rhabdomere and the power P_2 of the $HE_{1,1}$ mode of the nonexcited rhabdomere are given. The power P_2 was obtained by use of Eq. (5) and P_1 was obtained from a similar expression with the sine function replaced by the cosine function (see McIntyre and Snyder, 1973, 1974). The integrals in Eq. (5) were evaluated numerically.

Two separate cases are considered in Fig. 2. First, negligeable absorption, or $\kappa L \ll 1$, is represented by the dashed curves. Secondly, the continuous curves

give the results for $\kappa = 0.005\ \mu m^{-1}$ (cf. Kirschfeld, 1969).

In our example ($a/\varrho = 3$) light is transferred almost completely. However, of more physiological relevance is the total absorption of light by the unexcited rhabdomere. This absorption is given by $\int_0^L \kappa \eta(z)$ $\cdot P_2(z)\,dz$. Similarly the absorption by the excited rhabdomere is $\int_0^L \kappa \eta(z)\,P_1(z)\,dz$. $\eta(z)$ may be obtained from Biernson and Kinsley (1965). In our example $\eta(z)$ does not change much over the length of a rhabdomere (compare, however, Snyder and Pask, 1973; Stavenga, 1974a). Therefore the area below the curves in Fig. 2 is approximately proportional to the light absorbed by the photopigment. From the evaluation of these areas in Fig. 2 we obtain for $\kappa L \ll 1$ that of the total absorbed light power about 21% is absorbed by the unexcited rhabdomere. On the other hand, taking $\kappa = 0.005\ \mu m^{-1}$ approximately 13% of the total amount is absorbed by the unexcited rhabdomere.

The light transfer between two identical model rhabdomeres represents an upper estimate, for small differences in propagation constant of the $HE_{1,1}$ modes of the rhabdomeres may substantially diminish the transfer of light. To illustrate this effect we consider the hypothetical case of two rhabdomeres with constant but unequal radius throughout the retinula. For $a/\varrho = 3$, and $V = 2$ a radius difference of only 8% is sufficient to diminish the maximum light transfer to half the value resulting with identical rhabdomeres. Yet, differences in radius become unimportant if $\pi L/\lambda_B < \frac{1}{2}\pi$.

In conclusion we considered two peripheral Rhabdomeres A and B of one retinula. When the Gaussian image of a point source of light is situated on the axis of Rhabdomere B only the $HE_{1,1}$ mode of this rhabdomere will be excited. It has been assumed that the diffraction pattern does not excite the $HE_{1,1}$ mode of Rhabdomere A. However, the $HE_{1,1}$ mode of Rhabdomere B excites the $HE_{1,1}$ mode of Rhabdomere A. The sensitivity of Rhabdomere A for light incident axially on B is therefore partly due to the power transfer from Rhabdomere B to Rhabdomere A. We estimated above that this part of the sensitivity of A in that direction is less than approximately 25% of the maximum sensitivity (see Kirschfeld, 1972).

Discussion

In considering the light leak between fly rhabdomeres we made a number of assumptions and we have to investigate in how far these are justified.

First, the applied relations hold for waveguides having a circular cross-section. It may be argued that,

although this condition is not fulfilled for fly rhabdomeres (cf. Boschek, 1971) this is no serious problem, since in optical waveguides having a non-circular cross-section $HE_{1,1}$ like modes can be guided, with a propagation constant that does not differ seriously from the propagation constant of a $HE_{1,1}$ mode of a circle-cylinder with a cross-section of equal area. (Yeh, 1972). Therefore it should be permitted to use the equivalent radius as calculated by Boschek (1971) for Musca rhabdomeres.

Secondly we treated optical cross-talk between two rhabdomeres. However, within a fly retinula seven waveguides are present. Since the central rhabdomeres have a uniform radius throughout, whereas the peripheral rhabdomeres taper, transfer of light-power from central to peripheral rhabdomeres and vice versa must be small compared to the exchange of light between the peripheral rhabdomeres (cf. Jones, 1965). Hence it is sufficient to consider the more or less hexagonal array of the six peripheral rhabdomeres in some detail.

Each rhabdomere looses power to all other rhabdomeres. Most power transfer will occur to the nearest neighbours. To give an example, in the proximal part of the Musca retinula (Boschek, 1971; Fig. 5) the distance between Rhabdomeres 2 and 3 is smaller than the distance between Rhabdomeres 1 and 2; so, light incident at Rhabdomere 2 will leak mostly to Rhabdomere 3. The effect of the other present rhabdomeres will be a reduction of the distance over which complete power transfer occurs. According to Eq. (3) in the case of two rods this distance is $\lambda_B/2 = 0.5\pi/|C|$. It can easily be shown for a hexagonal array of identical rods placed at the same relative distance a/ϱ that complete power transfer from one excited rod occurs at a distance of $0.38\ \pi/|C|$, where C is again the coupling constant for the two rod case (Wijngaard, unpublished). Thus in a hexagonal array the distance of complete power transfer is reduced with a factor of about 1.3.

Thirdly, the tapering of fly rhabdomeres is not linear. Along the complete rhabdomere length the radius exceeds the value expected for a linear taper (Boschek, 1971). Hence the leak of light will be smaller than derived for the example of the previous section.

There remains an uncertainty about the absorption coefficient of fly rhabdomeres. The value $0.005\ \mu m^{-1}$ inferred for Musca by Kirschfeld (1969) seems to be reliable since a similar estimate follows for Calliphora (Stavenga, unpublished). We remark here that we supposed the medium surrounding the rhabdomeres to be without loss. It is well known that flies have a pupil mechanism active especially in the peripheral cells. Pigment granules migrate towards and away
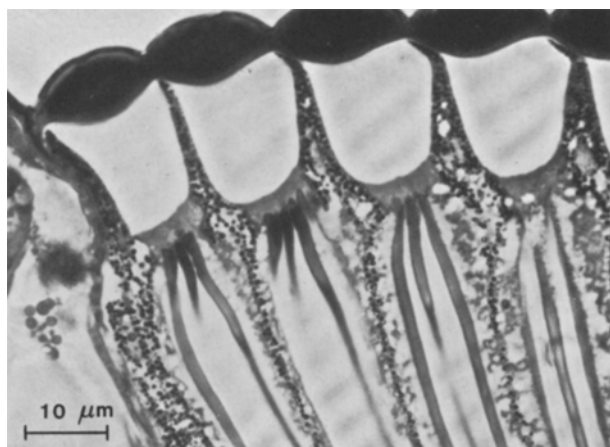
Fig. 3. Light microscopical section of a Drosophila eye approximately parallel to the axes of some ommatidia. Note the sudden divergence of the rhabdomeres from the distal end towards more proximal

Fig. 4. Oblique section of a Drosophila retina

from the rhabdomeres depending on light or dark adaptation (Kirschfeld and Franceschini, 1969; Stavenga et al., 1973). The supposition of an external medium without loss thus concerns light intensity levels below pupilthreshold only.

Evidently, most crucial to the amount of the effective light transfer is the value of the relative distance a/ϱ. However, it is not clear how the parameter a/ϱ should be interpreted for non-circular cross-sections. Instead of using a/ϱ where a is the distance between the rod axes, it may be better to use $(b/\varrho)+2$, where b is the distance between the boundaries of the rods. For identical rods with circular cross-section it holds that $a/\varrho=(b/\varrho)+2$. Use of $(b/\varrho)+2$ instead of a/ϱ does not change the picture significantly; according to Fig. 5 of Boschek (1971) for Musca $(b/\varrho)+2$ is equal to 3.0 or larger.

We have observed that a/ϱ should exceed 3.0 in order to restrict the change in sensitivity due to light-power transfer to neighbouring rhabdomeres up to a few percent. This condition is fulfilled in the already amply documented case of Musca in the whole retinula except most distally where a/ϱ is about 2.5. The rhabdomeres from distally to proximally curve outwards and further on they approach each other again, in accordance with the approximately constant value of a/ϱ of the tapering rhabdomeres.

The curving of the rhabdomeres is shown in Figs. 3 and 4 for the case of Drosophila. Clearly for a short distance only the relative distance is smaller than $a/\varrho=3$. It may be called remarkable that the particular retinula structure to which we are pointing has already several times been observed resulting in the schematical
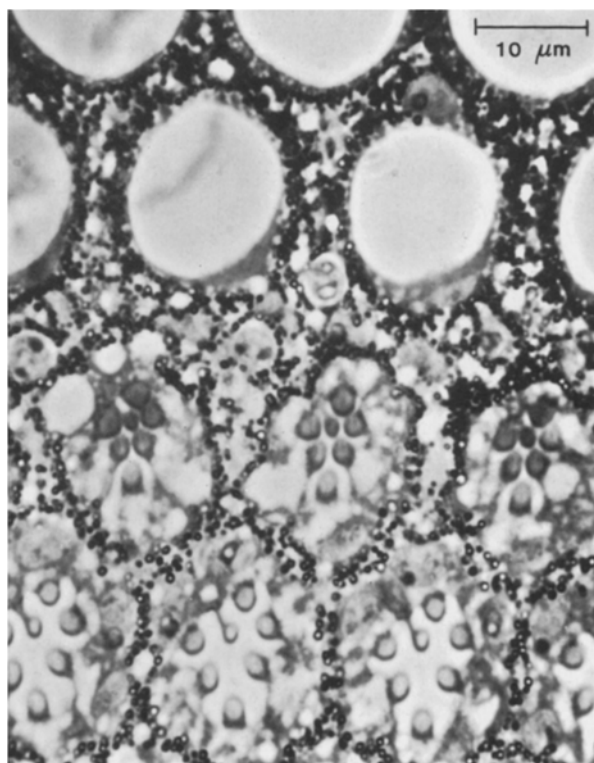
pictures of Waddington and Perry (1960, Fig. 4, which also shows the tapering!) and of Burkhardt et al. (1966, Fig. 1). Yet we have not been able to find a specific account of this striking rhabdomere architecture.

An interpretation concerning the outward curving of fly rhabdomeres seems to be given best in terms of the well-established neural superposition theory for fly vision (see for example Kirschfeld, 1971). According to this theory the peripheral cells of a fly retinula are individual units each having a distinct visual field. This field is among other things determined by the optical properties of the rhabdomere.

Actually our calculations concerning the transfer of light between rhabdomeres within a fly retinula reinforce the neural superposition theory since we can regard a change in sensitivity of some percent as acceptable.

There are, however, proceeding from the neural superposition theory, several more requirements for the optical construction of the eye of flies, namely the angle between the visual axes of retinula cells equaling the angle between neighbouring ommatidia (see e.g. Franceschini and Kirschfeld, 1971 b; Braitenberg and Strausfeld, 1973) and the peripheral rhabdomeres having a high light gathering power (Kirschfeld, 1971).

In view of the latter demand it may be expected that the caps of the rhabdomeres (Boschek, 1971) are approximately placed in the focal plane of the facet lenses (Kuiper, 1966; Kirschfeld and Franceschini, 1968; Seitz, 1968) and that they are situated close together, in order to build an efficient receiver system for incident light. The consequence of the distal intimate connection certainly will be some lightpower transfer, but this will remain of minor importance, owing to the rather abrupt separation of the rhabdomeres more proximally. So after all, fly rhabdomeres can indeed be regarded as independent optical waveguides.

The results given above are of interest not only for the neural superposition theory, but also for those studies in which the optical independence of the rhabdomeres is assumed explicitly. We refer to the spectrophotometrical investigations on fly visual pigment (Langer, 1966; Stavenga et al., 1973) and the birefringence measurements on thick retina sections (Seitz, 1969). Waveguide optics remains of prime importance to the latter studies, as will be discussed in a future paper (cf. also Stavenga, 1974a).

In conclusion we claim that a fly retinula is a well constructed assembly of visual photoreceptors, functioning sufficiently independently.

Appendix

We calculated $\int_0^z C(z')\,dz'$ for two identical tapering dielectric rods with a/ϱ constant. It is assumed that the taper is linear and that $|C(0)|$ is much less than $|C(z)|$. We define a normalized beatlength

$$\gamma(z') = \frac{\delta n_1}{2\lambda_0} \cdot \frac{\pi}{|C(z')|}$$ (Wijngaard, 1973), it follows that

$$\int_0^z |C(z')|\,dz' = \frac{\pi\delta n_1}{2\lambda_0} \int_0^z \frac{1}{\gamma(z')}\,dz' .$$

The cutoff parameter V is a function of z' given by $V(z')$ and, for a linear taper, $\dfrac{dV(z')}{dz'} = \dfrac{V(z) - V(0)}{z}$.

The curves for γ as a function of V, given by Wijngaard (1973), may be approximated by

$$\gamma(V) = 5.2 \exp\left[(1.146\, a/\varrho - 1.479)\, V - 0.877\, a/\varrho\right].$$

From $|C(0)| \ll |C(z)|$ it follows that $\dfrac{1}{\gamma(V(0))} \ll \dfrac{1}{\gamma(V(z))}$, therefore

$$\int_0^z |C(z')|\,dz' = \frac{-z}{\{V(z) - V(0)\}\{1.146\, a/\varrho - 1.479\}} \frac{\delta n_1}{2\lambda_0} \frac{\pi}{\gamma(V(z))} .$$

$C(z)$ does not change sign with changing z and therefore we finally obtain

$$\int_0^z C(z')\,dz' = \frac{z\, C(z)}{\{V(0) - V(z)\}\{1.146\, a/\varrho - 1.479\}} .$$ (6)

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