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Photoreceptor Optics, Theory and Practice

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1 Introduction

According to Snyder and Menzel (1975b), the goal of photoreceptor optics is to explain the structural basis of a photoreceptor's absolute, spectral, directional, and polarization sensitivities. This review will concentrate, however, on the directional sensitivity, as this is the quality, together with the absolute sensitivity, most influenced by photoreceptor optics and most thoroughly investigated both theoretically and experimentally. For other reviews on related topics see Snyder 1975, 1979; Snyder and Love 1983; and Horowitz 1981.

The optics of well-developed eyes in general consists of two parts: the first part, forming an image of the surroundings, funnels the light collected into the second part of the optical system, the light-sensitive structures. These structures usually consist of lightguides containing visual pigment. Absorption of light by this pigment eventually leads to electrical signals transmitted to the brain. The most common design, and the one theoretically best understood, is the combination of lens and waveguide. Many variations on this theme are found, though (see the reviews of Land and Nilsson this Vol.). The lens-waveguide system is found in many compound eyes, but also in camera-type eyes, such as those of vertebrates.

Although physiological optics is not a new discipline (e.g., Exner 1891), only quite recently has it received an impetus from wave optics. Several investigators noted the fact that the size of the lens(es) imposes a constraint on the resolution an eye can reach, due to diffraction (Mallock 1922, Barlow 1952, de Vries 1956). Toraldo di Francia (1949) was the first to compare the directional sensitivity of a visual lightguide to the receptive field of an antenna, and suggested that the visual lightguide functions as a dielectric waveguide. Snitzer and Osterberg (1961) developed mathematical expressions for waveguide modes, and observed them in small glass fibers. Enoch (1961, 1963) observed modes in retinae of vertebrates.

Photoreceptor optics received a great impetus through the theoretical work of Snyder (1969a,b), who developed approximations for waveguide modes that were more convenient to handle, and applied concepts from waveguide optics to eyes (e.g., Snyder and Pask 1973). The beginning of the 1970's witnessed a blooming of this area, culminating in a conference in 1974 entirely devoted to photoreceptor optics (Snyder and Menzel 1975a). As sometimes happens, theory was ahead of experiment for some time. Only recently has experimental work partly caught up through work on fly and butterfly (van Hateren 1984, 1985; Nilsson et al. 1984, 1988; van Hateren and Nilsson 1987).

2 Methods

Physiological optics is blessed with a wide variety of theoretical and experimental methods. Below we will see how these methods can be applied to the best-investigated system, a lens with a waveguide in its focal plane, but many of the results are valid for other designs as well.

2.1 Theoretical Methods

In the next sections we will use several of the following theoretical approaches. *Geometrical optics* uses light rays to explain optical phenomena, such as imaging by a lens and guiding of light in a lightguide. It can deal with more complicated structures through the method of ray tracing, but it fails on a scale smaller than a few wavelengths of light, i.e., about a micrometer. Then we enter the realm of (*vectorial*) *wave optics*, which is closely related to Maxwell's equations for the electromagnetic field. Problems tend to be difficult to handle, due to the vectorial nature of the electromagnetic field. Fortunately, vectorial wave optics has a simpler approximation, *scalar wave optics*, where a single scalar quantity, called the amplitude of the field, replaces the electric and magnetic field vectors. The intensity of the light is proportional to the squared modulus of this amplitude. Scalar wave optics gives accurate results if the refractive indices vary only slightly over distances in the order of the wavelength of light. It explains diffraction at a lens, and the emergence of waveguide modes in a waveguide, but it cannot always deal successfully with polarization. A most useful approach based on scalar wave optics is *Fourier optics* (Goodman 1968). This approach decomposes amplitude distributions into plane waves, which explains diffraction in a very natural way. Furthermore, it leads to a simple and basic understanding of how lenses work.

2.1.1 The Lens

Depending on the viewpoint a lens is: (1) a device that focuses light rays (geometrical optics, Fig. 1a), (2) that converts an incoming plane wave into part of a spherical wave, propagating into a diffraction pattern (wave optics, Fig. 1b), or (3) that yields Fourier transforms of amplitude distributions (Fourier optics, Fig. 1b and c).

As the geometrical optics of a lens (Fig. 1a) will be familiar to all readers, we will turn right away to wave optics. Figure 1b shows that a lens converts an incoming plane wave into part of a spherical wave. If this spherical wave were complete, it would produce a small spot of maximum intensity in the center with roughly the size of a wavelength. But information is lacking because there is only part of a spherical wave, with the result that the small spot in its center is enlarged to a diffraction pattern. The smaller the diameter of the lens (with the same focal distance), the smaller the part of the spherical wave, and the larger the diffraction pattern that results. A circular lens thus produces the well-known Airy diffraction pattern.

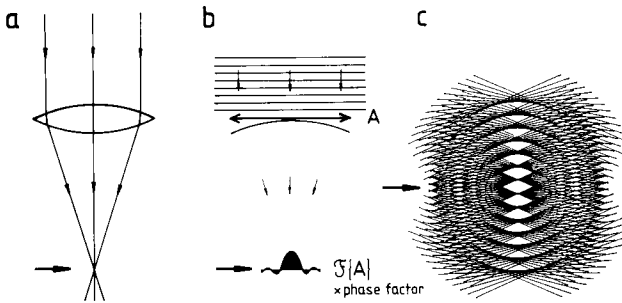


Fig. 1a-c. Optics of a lens. *a* Geometrical optics: a lens focuses light rays. *b* Wave optics: a lens converts a plane wave into part of a spherical wave. The resulting Airy diffraction pattern is the Fourier transform of the lens aperture, times a phase factor. *c* Fourier optics: a diffraction pattern can be decomposed into a set of plane waves with an angular distribution filling the lens aperture exactly. Arrows indicate the focal plane

Fourier optics considers lenses as devices that yield Fourier transforms. The Fourier transform of the aperture of a lens (e.g., circular or square) yields the amplitude of the diffraction pattern, apart from a phase factor (see Goodman 1968). Another way of putting this Fourier relationship is that the diffraction pattern can be thought of as being composed of a distribution of plane waves with directions filling the lens aperture exactly. Figure 1c illustrates how a superposition of plane waves produces a spherical wave front at the lens and a diffraction pattern at the focus.

2.1.2 The Waveguide

Geometrical optics explains the guiding of light in a lightguide by total reflection of light rays (Fig. 2a, left); a light ray is totally reflected if $n_1 > n_2$ and the angle α is sufficiently small [$\alpha \leq \arccos(n_2/n_1)$, with n_1 and n_2 the refractive indices inside and outside the waveguide respectively]. This explanation fails, however, for lightguides with diameters in the order of the wavelength of light (about $0.5 \mu\text{m}$), which is often the case for visual lightguides. Wave optics must be used for describing light propagation in these small lightguides, then called waveguides. Interference of the waves inside a waveguide leads to waveguide modes, stable patterns of light travelling along the waveguide. They are the only way light can propagate through it.

The modes of a cylindrical waveguide can be obtained directly from the Maxwell equations (vectorial wave optics). This leads to modes designated as HE_{11} , TM_{01} , etc. (Snitzer and Osterberg 1961). These modes are exact solutions for a waveguide, fully describing the vectorial nature of the electromagnetic field. Snyder (1969a, b) introduced a more convenient approximation, assuming that the refractive indices inside and outside the waveguide are only slightly different — which is usually the case in visual waveguides. This approximation leads to a scalar wave equation, and thus belongs to scalar wave optics (see Marcuse 1974). This yields modes which are designated as LP_{01} , LP_{11} , etc. LP means Linearly Polarized:

the modes are linearly polarized superpositions of the exact modes, which are not linearly polarized (apart from HE_{11} , which is identical to LP_{01}). As the scalar approximation is much simpler to handle and understand, we will use it in the following.

Figure 2a (right) shows an LP_{01} travelling in a waveguide. When it leaves the waveguide, it will radiate away with a certain angular amplitude distribution, which is, far away from the waveguide aperture, called the far field radiation

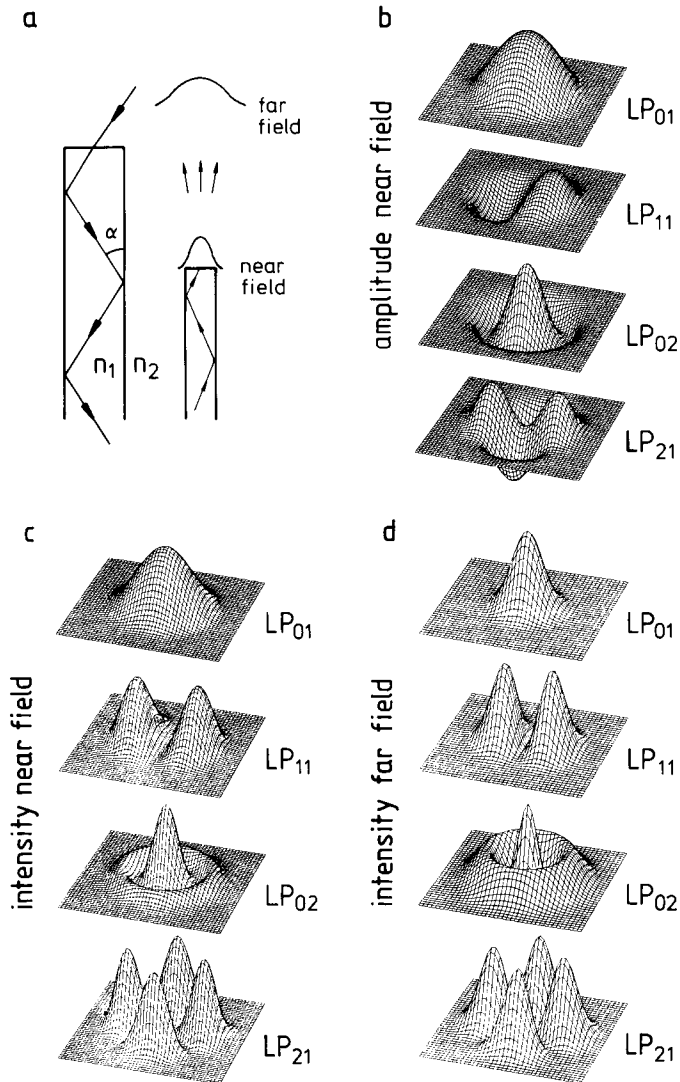


Fig. 2a-d. Optics of a waveguide. a Left light guiding by total reflection of light rays. Right near field pattern of a mode LP_{01} radiates away to its far field pattern. b Amplitude distributions of the near field patterns of the first four modes. c Near field intensity distributions of the first four modes d Far field intensity distributions of the first four modes

pattern. Figure 2b shows the amplitude distributions of the first four waveguide modes (called the near field to distinguish them from the far field distributions), Figure 2c shows their intensity distributions, and Figure 2d the intensity distributions of their far field radiation patterns. The indices designating each mode have a simple interpretation: the first digit is half the number of maxima in the intensity distribution encountered azimuthally, the second digit the number of maxima encountered going from the center toward infinity. How many modes can propagate in a waveguide is determined by an important parameter, the V-number:

$$V = \frac{2\pi b}{\lambda} \sqrt{n_1^2 - n_2^2}$$

with b the radius of the waveguide, λ the wavelength of the light, n_1 the refractive index inside, and n_2 outside the waveguide. If $V \leq 2.4$, only LP_{01} can propagate, if $V \leq 3.8$ both LP_{01} and LP_{11} , if $V \leq 5.1$ all four modes shown in Fig. 2b, and if $V > 5.1$ other modes as well. As an example, fly photoreceptors (R1-6) have $n_1 \approx 1.36$, $n_2 \approx 1.34$ (Stavenga 1974, 1975; Beersma et al. 1982), and $b \approx 0.9 \mu\text{m}$ (Horridge et al. 1976), which yield $V = 2.2$ for $\lambda = 600 \text{ nm}$, and $V = 3.3$ for $\lambda = 400 \text{ nm}$ (Kirschfeld and Snyder 1976). Thus at 600 nm only LP_{01} can exist in fly photoreceptors, whereas at 400 nm LP_{11} also exists.

Fourier optics is useful for waveguides because it relates any amplitude distribution to its far field radiation pattern: these are Fourier transforms of each other. Thus the near field of a mode is related to its far field in a simple way: their amplitudes are each other's Fourier transforms. We will show in the next section that this notion can give us insight into how a lens-waveguide system works.

2.1.3 The Lens-Waveguide System

Figure 3a shows how geometrical optics explains a lens-waveguide system. Light rays coming from the lens and entering the lightguide will be trapped inside the fiber through total reflection if the angle α is sufficiently small. Ideally, the lens aperture should be matched to the maximum α allowing total reflection. The angular sensitivity of the photoreceptor, i.e., its receptive field, is the projection of the fiber aperture to infinity. Thus the fiber aperture determines the width of the angular sensitivity. This shows the weakness of this model: geometrical optics does not take diffraction at the lens into account, and this is only accurate if the fiber aperture is much larger than the diffraction pattern of the lens.

Figure 3b shows a more realistic picture of how light enters the waveguide: an incoming plane wave is first diffracted by the lens, and the resulting diffraction pattern subsequently excites waveguide modes in the waveguide, which are finally absorbed by the visual pigment (see Sect. 2.1.4). How strong the various modes are excited depends on how well their amplitude distributions fit with the exciting amplitude distribution, in this case the Airy diffraction pattern produced by a distant point light source. This goodness of fit depends, of course, on the relative position of diffraction pattern and waveguide aperture, and thus on the angular position of the stimulus. For example, on-axis illumination will only excite

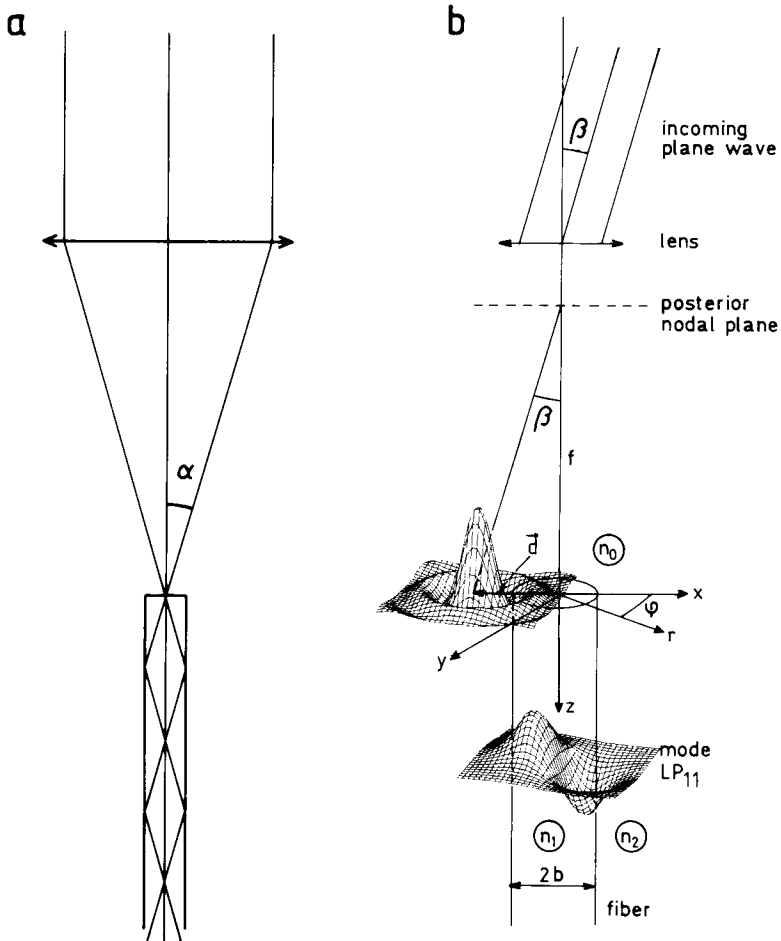


Fig. 3a,b. Optics of a lens-waveguide system. *a* Light rays focused by the lens are totally reflected inside the lightguide. *b* Wave optics: a diffraction pattern excites modes in a waveguide. The waveguide shown is large enough to support LP_{11} (thus LP_{01} is also present, not shown)

azimuthally symmetrical modes (LP_{01} , and LP_{02} etc.) because the positive and negative parts of the azimuthally asymmetrical modes cancel each other with symmetrical illumination. Off-axis illumination, on the other hand, may also excite asymmetrical modes like LP_{11} – if the waveguide dimensions allow their existence. The excitation of the modes as a function of the stimulus position thus leads to the angular sensitivity of the system. In mathematical terms it is for each mode the convolution of mode and diffraction pattern.

Fourier optics is most illuminating when used with an extremely useful method, both theoretically and experimentally, namely reversal of the light direction. From the reciprocity theorem of Helmholtz (see, e.g., Born and Wolf 1965) it follows that the sensitivity of a photoreceptor to light travelling in the

normal direction (orthodromic light) is similar in shape to the intensity distribution obtained when the light direction is reversed (antidromic light). Some care when applying this reciprocity theorem is necessary, however, because it only applies to each mode separately if the modes are absorbed independently (see Sect. 2.1.4). We will now illustrate the power of this method.

Suppose an LP_{01} is travelling through the waveguide in the antidromic direction. After leaving the fiber aperture it transforms gradually from near field pattern to far field pattern (the Fourier transform the mode). At the lens we thus find in good approximation the far field radiation pattern of LP_{01} , with its phase front spherical with the fiber aperture as its center. Just as a lens converts a plane wave front into a spherical one, it will convert a spherical wave front into a plane one. Therefore, the light emerging from the facet lens has a plane phase front, and an amplitude distribution equal to the far field pattern of the waveguide, but limited (cut off) by the lens aperture. This light will subsequently radiate toward infinity, which means another Fourier transform (see end of Sect. 2.1.2). Consequently, the pattern we find at infinity is the Fourier transform of the Fourier-transformed mode (the far field of the mode) restricted by the lens aperture. A mathematical theorem states that the Fourier transform (actually the inverse Fourier transform, but this leads only to a reflection of coordinates which we will ignore) of the product of two functions, in this case the Fourier-transformed mode and the lens aperture, equals the convolution of their (inverse) Fourier transforms, in this case the mode and the diffraction pattern. This is the same result as we mentioned above for the angular sensitivity. Thus

$$R = F\{F\{M\} \times L\} = F\{F\{M\} \times F\{D\}\} = M * D = S,$$

where R is the far field radiation pattern of the system (or, from Helmholtz's reciprocity theorem, the angular sensitivity S), F denotes a Fourier transform, M the mode pattern, L the lens aperture, D the diffraction pattern, and $*$ convolution. Efficient excitation of a mode by the diffraction pattern depends on how well they fit, and we have just shown that this is equivalent to how well the far field pattern of the mode matches the lens aperture. Details and formulas can be found in van Hateren 1984 and 1985.

Van Hateren and Nilsson (1987) show that in butterflies this matching of mode pattern and diffraction pattern is even better than in conventional lens-waveguide systems, resulting in an improved resolution and sensitivity. They suggest that this is accomplished by the cone stalk of the butterfly through matching the diffraction pattern with a combination of LP_{01} and LP_{02} and subsequent coupling of these modes. The cone stalk is an optically very complicated structure, showing the properties of a strong lens (Nilsson et al. 1984, 1988, van Hateren and Nilsson 1987).

2.1.4 Absorption of Modes

When modes are excited in a waveguide, they will travel along it, and be absorbed by the visual pigment it contains. An important notion is the following: although the modes are coherent, their absorption is independent, which means that the intensity of each mode determines how strongly it is absorbed (see van Hateren and Nilsson 1987). This independent absorption is caused by the fact that the modes

beat with each other due to different wave velocities (see, e.g., Bernard 1975). Because the beat period is typically in the order of 10–20 μm , thus much shorter than most visual waveguides, the modes appear to be absorbed independently. The reverse is true for another kind of beating, namely of the vectorial modes that compose the LP modes. These vectorial modes also have slightly different wave velocities, but their beat period is typically in the order of 5–10 mm, thus much longer than a typical visual waveguide. Therefore, the absorption of these modes is in effect not independent, which is the reason why the LP modes describe absorption accurately. An experimental technique introduced by Nilsson et al. (1984) for the butterfly, however, looks at light that is depolarized during passage through the waveguide. For explaining this effect one needs the vectorial modes, and the fact that they are beating (Nilsson and Howard in prep.).

Modes can also be absorbed by the longitudinal pupil of the photoreceptors. In bright light this pupil closes, i.e., pigment granules in the photoreceptor cells move close to the waveguide (Kirschfeld and Franceschini 1969). As only part of the power of a mode is propagated inside the waveguide (this fraction is called η , see Snyder 1975) the remaining part, travelling alongside the waveguide, can be absorbed by the pigment granules. The fraction η is different for different modes (higher order modes have a smaller η than lower order ones), thus the pupil affects higher order modes more. One consequence of this is that the pupil can influence the angular sensitivity of the photoreceptors (Smakman et al. 1984; Nilsson et al. 1988). For a theoretical discussion of absorption by the pupil see Snyder 1975.

2.2 Experimental Methods

2.2.1 Physiological Methods

Physiological methods for studying physiological optics are defined here as those methods that use the sensitivity of the photoreceptor cells, either directly or indirectly. Indirect methods use higher-order neurons or the behavior of the animal. For example, the halfwidth of the angular sensitivity of housefly photoreceptors was inferred from behavioral experiments (Götz 1965; Buchner 1976). Another example is the psychophysical determination of the sensitivity profile of human photoreceptors at the level of the cornea (Stiles-Crawford effect, review: Enoch and Bedell 1981).

Direct methods use the response of the photoreceptor cells, either their membrane potential (e.g., Washizu et al. 1964) or their pupillary response (Beersma 1979; Bernard and Wehner 1980). Angular sensitivities are usually obtained from responses to flashes of constant intensity at different positions in the receptive field of the cell. Afterward a correction is then necessary for the (usually nonlinear) stimulus-response curve of the cell. Methods not needing this correction are counting responses to single photons, and clamping of the response to a constant level by feedback to the intensity of the stimulus (Franceschini 1979; Smakman and Pijpker 1983). Finally, angular sensitivities can also be inferred from the response of the visual sense cells to sinusoidal gratings of varying spatial frequency, by Fourier transforming the so-obtained optical transfer function (Dubs 1982; see Goodman 1968 for an explanation of the method).

2.2.2 Optical Methods

Optical methods for studying physiological optics are defined here as those methods that aim at determining directly optical properties of the investigated systems. One approach is to determine structure and properties, e.g., refractive indices, of the optical components through anatomy and interference microscopy. An early example of this is Exner's work on *Limulus* cones (Exner 1891). Recent examples are the work of Seitz (1968) on the fly optical system (see also Stavenga 1974), of Varela and Wiitanen (1970) on the honeybee optical system, and of Nilsson and Odselius (1981), Nilsson et al. (1983), and Nilsson (1983) on crustaceans, combining anatomy, interference microscopy, and ray tracing. A limit to this approach is the wavelength of light: it is next to impossible to obtain reliable refractive indices about structures varying at the scale of wavelengths. Unfortunately, this is also a range where theorizing is difficult and where interesting properties are likely.

It is also possible to directly obtain optical properties of the whole system, like its angular sensitivity. This approach can be subdivided into orthodromic and antidromic methods. An example of an orthodromic method is the technique using eye slices, where the light transmitted through the waveguides is monitored at their cut end, with the remaining optics intact (Kuiper 1966; Eheim and Wehner 1972). This method works well if only LP_{01} is present. If more modes are propagated, however, it can give erroneous results, because the modes are absorbed independently (see Sect. 2.1.4). This absorption will be different for each mode, thus the weighting of the various modes will not be the same for the light transmitted by the waveguide (used in this method) and the light absorbed by the waveguide (determining the angular sensitivity of the photoreceptor cell).

Antidromic methods have the same problem (discussed in van Hateren 1984, 1985, and van Hateren and Nilsson 1987), but can be highly accurate at longer wavelengths, where the waveguide is monomodal. This approach has been mainly used on two insect species, flies (Kirschfeld and Franceschini 1968; Franceschini 1975; van Hateren 1984) and butterflies (Land 1984; Nilsson et al. 1984, 1988). Although the latter studies use orthodromic light to begin with, they use in fact antidromic light reflected back from the tapeta as their main diagnostic tool.

3 Results

3.1 Observations of Modes

Observations of mode patterns are interesting, because they prove that photoreceptors behave as dielectric waveguides. Various mode patterns were observed by Enoch (1963). These observations were done in relatively wide photoreceptors, often leading to quite complicated patterns. More recently, observations in fly (far field: Franceschini and Kirschfeld 1971; Pick 1977; van Hateren 1984; cornea: van Hateren 1985) and butterfly (cornea: Nilsson et al. 1984, far field: Nilsson et al. 1988) showed clear LP_{01} and LP_{11} patterns. Examples are shown in Fig. 4; in Fig. 4a the far field radiation pattern from a single ommatidium of the fly at several

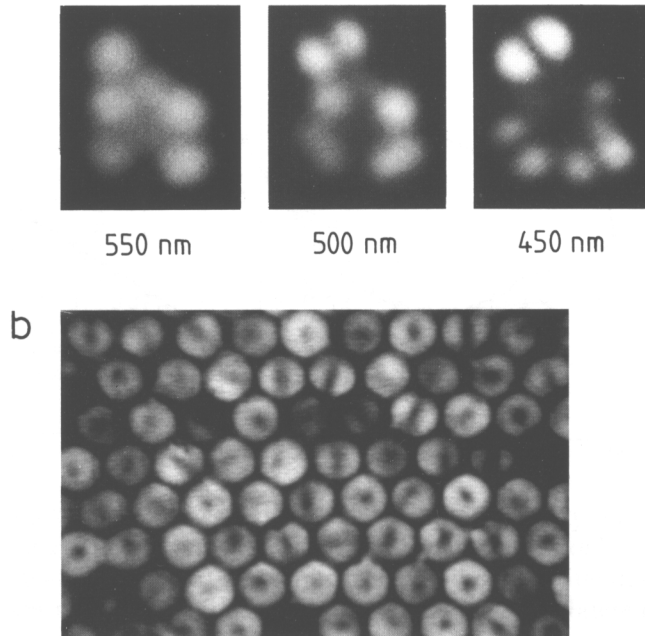


Fig. 4.a Modes seen in the far field radiation pattern of a single ommatidium of the fly, containing seven waveguides. With a wavelength of 550 nm, only LP_{01} is observed, whereas LP_{11} is present at 500 nm, and strongly so at 450 nm. *b* Cornea of a butterfly using a technique with polarized light introduced by Nilsson et al. (1984). Mainly LP_{11} is observed (*b* courtesy of Dr. D.G. Stavenga and Mr. H.L. Leertouwer)

wavelengths (550 nm, yielding only LP_{01} ; 500 nm, yielding also some LP_{11} ; and 450 nm, yielding predominantly LP_{11}), and in Fig. 4b patterns seen at the cornea of a butterfly, mainly showing LP_{11} .

3.2 Angular Sensitivities

Angular sensitivities have been measured in visual sense cells by many investigators (e.g., Washizu et al. 1964; Järvilehto and Zettler 1973; Laughlin 1974; Hardie 1979). Explaining the measurements with models derived from photoreceptor optics also has a long history. One model (Kuiper 1966; Horridge et al. 1976) assumed diffraction at the lens, and subsequent convolution of the intensity of the diffraction pattern with a rectangular acceptance function for the waveguide. This procedure is accurate when the waveguide behaves according to geometrical optics (approximately correct if four or more modes are supported, thus for $V > 3.8$), but gives erroneous results if only one or two modes are supported. Smakman et al. (1984) performed accurate measurements of angular sensitivities of fly photoreceptors by a feedback method, and succeeded in interpreting these data with a model using a complete wave-optical analysis. An example of these measurements and theoretical fits is shown in Fig. 5. In this study it was found that

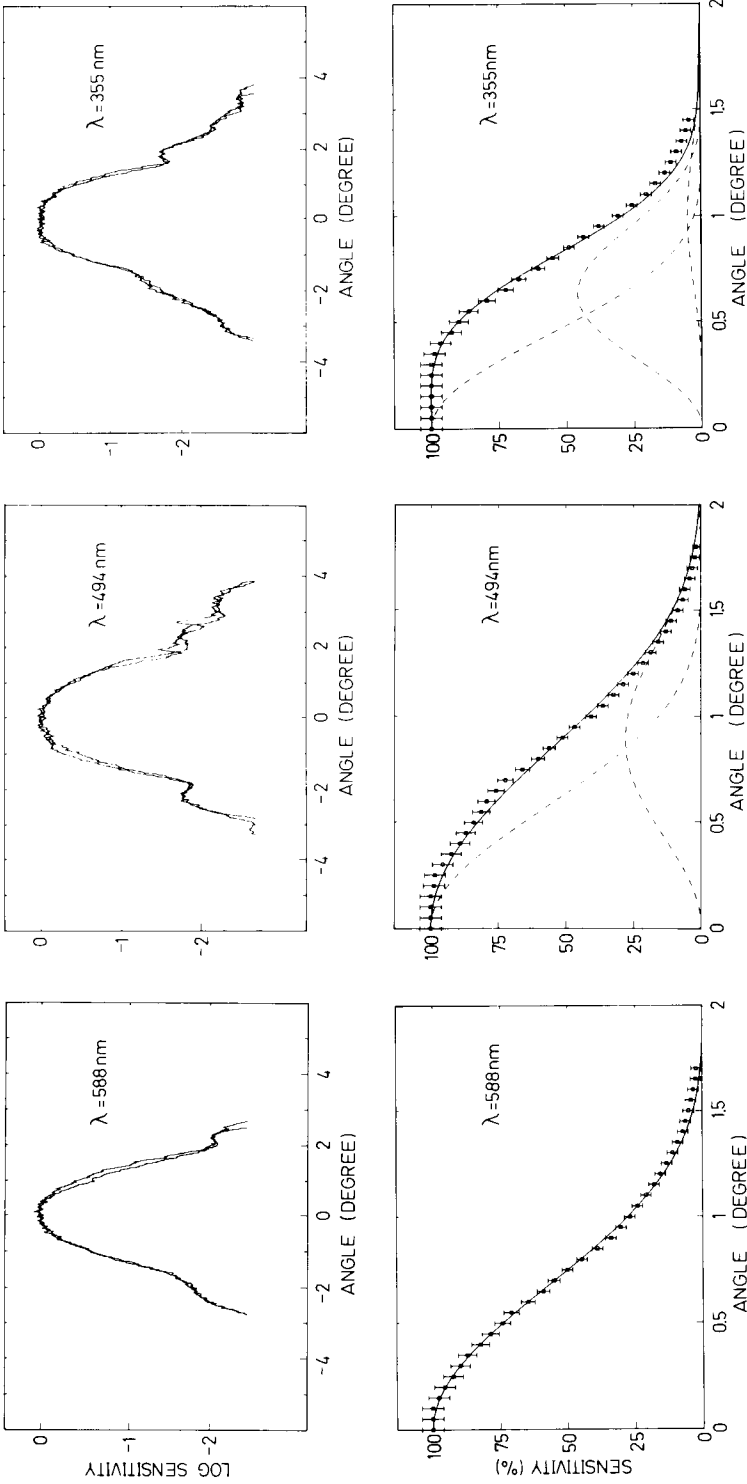


Fig. 5. Angular sensitivities in a fly photoreceptor (R1-6). The upper figures show raw data, to which theoretical fits using waveguide theory were made (lower figures). The continuous line at $\lambda = 588$ nm corresponds to $LP_{-0,1}$ and $LP_{1,1}$ (494 nm), and $LP_{0,1}$, $LP_{1,1}$, and $LP_{-1,1}$ (355 nm). (Smakman et al. 1984)

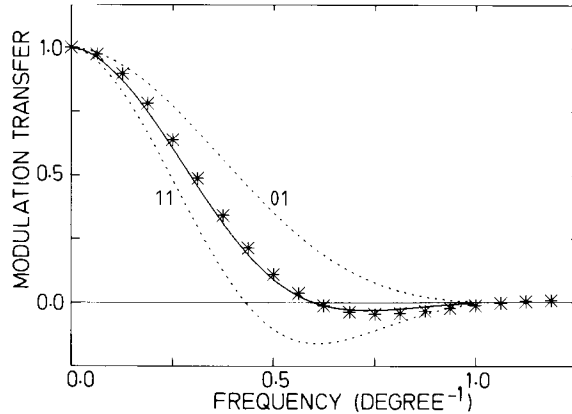


Fig. 6. Optical transfer function of a fly photoreceptor (R1-6). Asterisks Fourier transform of a measured angular sensitivity ($\lambda = 450$ nm); solid line theoretical fit, consisting of OTFs from LP_{01} and LP_{11} (broken lines). The fit was obtained by adjusting the relative weighting of the modes. All other parameters, including the lens diameter ($27 \mu\text{m}$), were known or measured

closure of the longitudinal pupil narrows the angular sensitivity slightly, presumably because the pupil absorbs more light from higher-order modes like LP_{11} than from the more narrow LP_{01} . Optical measurements of angular sensitivities were performed by Eheim and Wehner (1972), Land (1984), and van Hateren (1984).

Optical transfer functions (OTF's) were measured by Dubs (1982). Fourier transforming the OTF's yields the angular sensitivity (see, e.g., Goodman 1968). On the other hand, the transfer function may be obtained from the angular sensitivity by Fourier transforming it. Figure 6 shows an example of the latter procedure of an angular sensitivity at $\lambda = 450$ nm in the fly, thus involving LP_{11} as well as LP_{01} . We see that both theory and experiment yield a transfer function with a negative part, caused by LP_{11} . In this spatial frequency range the cell gives a maximum response while in reality looking at a minimum in the stimulus (a sinusoidal grating). This contrast reversal is also known from defocused lenses (Goodman 1968), and may lead the experimenter astray: he should be aware of the possibility of contrast reversal, and check the phase of the response as well as the modulation transfer.

3.3 Corneal, Spectral, and Polarization Sensitivities

Corneal sensitivities, i.e., the directional sensitivity of the photoreceptors measured at the level of the cornea, were investigated electrophysiologically and optically in the fly (van Hateren 1985) and optically in the butterfly (Nilsson et al. 1984, 1988). Most work has been done on this subject, however, in the vertebrate lens eye, where it is called the Stiles-Crawford effect (Stiles and Crawford 1933).

Although the spectral sensitivity is in principle influenced by the optics, e.g., through the wavelength-dependent emergence of waveguide modes, the influence seems to be small in practice. An important point to note is the fact that in fly photoreceptors the angular sensitivity has approximately the same half-width over the entire wavelength range: the emergence of higher order modes at shorter wavelengths compensates for the narrowing of the diffraction pattern at these

wavelengths (see Fig. 5). In effect, the influence of waveguide effects on spectral sensitivity is only slight (Smakman and Stavenga 1986). Much more important for the spectral sensitivity are effects caused by absorption by the visual pigment, such as self-screening (Snyder and Pask 1973; Hardie 1985), lateral filtering (Snyder et al. 1973), and the spectral properties of the longitudinal pupil (Hardie 1979; Vogt et al. 1982).

Polarization sensitivity in visual systems is mainly determined by the way the visual pigment is packed in the rhabdoms. A discussion of polarization sensitivity is beyond the scope of this review, but can be found in the review of Hardie (1985) on the fly retina.

4 Discussion

4.1 How Accurately Must a Lens-Waveguide System be Built?

An important question, particularly for the owner, is how accurately a lens-waveguide system must be built in order to function properly. We will discuss in the following the effects of skewness of the waveguide, and of defocusing and aberrations of the lens.

Ideally, the waveguide must be pointing to the center of the lens. If it is not, it does not trap as much light as it could, and the angular sensitivity is broadened. Both effects can be understood intuitively by realizing that the acceptance profile of the waveguide must match the lens aperture. A mismatch leads to a smaller effective lens aperture, reducing the light capture and leading to stronger diffraction. Wave-optical calculations show that for fly photoreceptors a 2.5° misalignment leads to a 10% reduction in sensitivity (van Hateren 1985).

Similar effects occur when the waveguide is not in the focal plane of the lens: this also causes a mismatch (see McIntyre and Kirschfeld 1982). Finally, lens aberrations also cause these problems, because they lead to phase mismatches: a lens with aberrations converts a plane wave into a wave front which is not perfectly spherical. This means that the match with the waveguide acceptance profile becomes worse, or, equivalently, that the phase of the resulting diffraction pattern is less well matched to the (plane) phase front of the mode. Lenses in compound eyes, however, seem to be effectively aberration-free (Stavenga et al. in prep.), thus lens aberrations are not really a limiting factor.

4.2 The Future of Photoreceptor Optics

Although the paradigmatic lens-waveguide system is now reasonably well understood, photoreceptor optics is far from being a finished subject. Many optical structures in eyes need a more detailed study, e.g., oil droplets just in front of photoreceptors of birds, and other specializations found in front of the photoreceptors elsewhere. Furthermore, the shape of many visual waveguides is far from circular, but rather elliptical, rectangular, or even more complicated. We do not at

all understand the consequences of this for vision. Moreover, many eyes deviate from the simple lens-waveguide scheme. Often, eyes seem to use their cone as well as their facet lenses to funnel the light into the waveguide, and more complicated designs using mirrors or optical superposition may yield surprising results when studied in great (optical) detail (see Nilsson, this Vol.).

A potentially very powerful method not yet applied to waveguides in eyes is the use of sinusoidal gratings consisting of coherent light (instead of incoherent as for determining the OTF). With this method the role of the various modes can be studied directly, because the modes show different phase shifts for coherent light. Also, transfer functions for coherent light easily yield many other interesting properties of the system. The potential of Fourier methods in physiological optics is still vast.

Photoreceptor optics may also be expected to play an important role in the addressing of ecological and evolutionary problems (see Land and Nilsson this Vol.). Furthermore, it provides a solid basis for understanding higher-order processing, including problems like hyperacuity and problems related to sampling and flow fields. Last but not least, the thorough understanding of the optics we now have in several insects allows the investigator of higher order neurons to make use of the acquired techniques, e.g., for methods of stimulating individual photoreceptors very precisely (Franceschini 1975 and this Vol.; Riehle and Franceschini 1984; Lenting 1985; van Hateren 1986, 1987).

References

- Barlow H (1952) The size of ommatidia in apposition eyes. *J Exp Biol* 29:667–674
- Beersma DGM (1979) Spatial characteristics of the visual fields of flies. PhD Thesis, Univ Groningen, NL
- Beersma DGM, Hoenders BJ, Huizer AMJ, Toorn P van (1982) Refractive index of the fly rhabdomere. *J Opt Soc Am* 72:583–588
- Bernard GD (1975) Physiological optics of the fused rhabdom. In: Snyder AW, Menzel R (eds) *Photoreceptor optics*. Springer, Berlin Heidelberg New York, pp 78–97
- Bernard GD, Wehner R (1980) Intracellular optical physiology of the bee's eye. I. Spectral sensitivity. *J Comp Physiol A* 137:193–203
- Born M, Wolf E (1965) *Principles of optics*. Pergamon, Oxford New York
- Buchner E (1976) Elementary movement detectors in an insect visual system. *Biol Cybernet* 24:85–101
- de Vries HL (1956) Physical aspects of the sense organs. *Prog Biophys* 6:208–264
- Dubs A (1982) The spatial integration of signals in the retina and lamina of the fly compound eye under different conditions of luminance. *J Comp Physiol A* 146:321–343
- Eheim WP, Wehner R (1972) Die Sehfelder der zentralen Ommatidien in den Appositionsaugen von *Apis mellifica* and *Cataglyphis bicolor* (Apidae, Formicidae; Hymenoptera). *Kybernetik* 10:168–179
- Enoch JM (1961) Nature of transmission of energy in the retinal receptors. *J Opt Soc Am* 51:1122–1126
- Enoch JM (1963) Optical properties of retinal photoreceptors. *J Opt Soc Am* 53:71–85
- Enoch JM, Bedell HE (1981) The Stiles-Crawford effects. In: Enoch JM, Tobey FL, Jr. (eds) *Vertebrate photoreceptor optics*. Springer, Berlin Heidelberg New York, pp 83–126
- Exner S (1891) *Die Physiologie der facettierten Augen von Krebsen und Insecten*. Deuticke, Leipzig
- Franceschini N (1975) Sampling of the visual environment by the compound eye of the fly: fundamentals and applications. In: Snyder AW, Menzel R (eds) *Photoreceptor optics*. Springer, Berlin Heidelberg New York, pp 98–125

- Franceschini N (1979) Voltage clamp by light: rapid measurement of the spectral and polarization sensitivity of receptor cells. *Invest Ophthalmol Vis Sci Suppl* Apr:5
- Franceschini N, Kirschfeld K (1971) Etude optique in vivo des éléments photorécepteurs dans l'oeil composé de *Drosophila*. *Kybernetik* 8:1–13
- Goodman JW (1968) Introduction to Fourier optics. McGraw-Hill, New York
- Götz KG (1965) Die optischen Übertragungseigenschaften der Komplexaugen von *Drosophila*. *Kybernetik* 2:215–221
- Hardie RC (1979) Electrophysiological analysis of the fly retina. I. Comparative properties of R1–6 and R7 and R8. *J Comp Physiol A* 129:19–33
- Hardie RC (1985) Functional organization of the fly retina. In: Ottoson D (ed) Progress in sensory physiology, vol 5. Springer Berlin Heidelberg New York, pp 1–79
- Hateren JH van (1984) Waveguide theory applied to optically measured angular sensitivities of fly photoreceptors. *J Comp Physiol A* 154:761–771
- Hateren JH van (1985) The Stiles–Crawford effect in the eye of the blowfly, *Calliphora erythrocephala*. *Vision Res* 25:1305–1315
- Hateren JH van (1986) Electrical coupling of neuro-ommatidial photoreceptor cells in the blowfly. *J Comp Physiol A* 158:795–811
- Hateren JH van (1987) Neural superposition and oscillations in the eye of the blowfly. *J Comp Physiol A* 161:849–856
- Hateren JH van, Nilsson D-E (1987) Butterfly optics exceed the theoretical limits of conventional apposition eyes. *Biol Cybernet* 57:159–168
- Horowitz BR (1981) Theoretical considerations of the retinal receptor as a waveguide. In: Enoch JM, Tobey FL, Jr. (eds) Vertebrate photoreceptor optics. Springer, Berlin Heidelberg New York, pp 219–300
- Horrige GA, Mimura K, Hardie RC (1976) Fly photoreceptors. III. Angular sensitivity as a function of wavelength and the limits of resolution. *Proc R Soc London Ser B* 194:151–177
- Järvilehto M, Zettler F (1973) Electrophysiological-histological studies on some functional properties of visual cells and second order neurons of an insect retina. *Z Zellforsch* 136:291–306
- Kirschfeld K, Franceschini N (1968) Die optischen Eigenschaften der Ommatidien im Komplexauge von *Musca*. *Kybernetik* 5:47–52
- Kirschfeld K, Franceschini N (1969) Ein Mechanismus zur Steuerung des Lichtflusses in den Rhabdomeren des Komplexauges von *Musca*. *Kybernetik* 6:13–22
- Kirschfeld K, Snyder AW (1976) Measurements of a photoreceptor's characteristic waveguide parameter. *Vision Res* 16:775–778
- Kuiper JW (1966) On the image formation in a single ommatidium of the compound eye in Diptera. In: Bernhard CG (ed) The functional organization of the compound eye. Pergamon, Oxford New York, pp 35–50
- Land MF (1984) The resolving power of diurnal superposition eyes measured with an ophthalmoscope. *J Comp Physiol A* 154:515–533
- Laughlin SB (1974) Neural integration in the first optic neuropile of dragonflies. III. The transfer of angular information. *J Comp Physiol A* 92:377–396
- Lenting BPM (1985) Functional characteristics of a wide-field movement processing neuron in the blowfly visual system. Thesis, Univ Groningen, NL
- Mallock A (1922) Divided composite eyes. *Nature (London)* 110:770–771
- Marcuse D (1974) Theory of dielectric optical waveguides. Academic Press, New York London
- McIntyre P, Kirschfeld K (1982) Chromatic aberration of a dipteran corneal lens. *J Comp Physiol* 146:493–500
- Nilsson D-E (1983) Evolutionary links between apposition and superposition optics in crustacean eyes. *Nature (London)* 302:818–821
- Nilsson D-E, Odselius R (1981) A new mechanism for light-dark adaptation in the *Artemia* compound eye (Anostraca, Crustacea). *J Comp Physiol A* 143:389–399
- Nilsson D-E, Odselius R, Elofsson R (1983) The compound eye of *Leptodora kindtii* (Cladocera). *Cell Tissue Res* 230:401–410
- Nilsson D-E, Land MF, Howard J (1984) Afocal apposition optics in butterfly eyes. *Nature (London)* 312:561–563
- Nilsson D-E, Land MF, Howard J (1988) Optics of the butterfly eye. *J Comp Physiol A* 162:341–366

- Pick B (1977) Specific misalignments of rhabdomere visual axes in the neural superposition eyes of dipteran flies. *Biol Cybernet* 26:215–224
- Riehle A, Franceschini N (1984) Motion detection in flies: parametric control over on-off pathways. *Exp Brain Res* 54:390–394
- Seitz G (1968) Der Strahlengang im Appositionsaug von *Calliphora erythrocephala* (Meig). *Z Vergl Physiol* 62:61–74
- Smakman JGJ, Pijpker BA (1983) An analog-digital feedback system for measuring photoreceptor properties with an equal response method. *J Neurosci Meth* 8:365–373
- Smakman JGJ, Stavenga DG (1986) Spectral sensitivity of blowfly photoreceptors: dependence on waveguide effects and pigment concentration. *Vision Res* 26:1019–1025
- Smakman JGJ, Hateren JH van, Stavenga DG (1984) Angular sensitivity of blowfly photoreceptors: intracellular measurements and wave-optical predictions. *J Comp Physiol A* 155:239–247
- Snitzer E, Osterberg H (1961) Observed dielectric waveguide modes in the visible spectrum. *J Opt Soc Am* 51:499–505
- Snyder AW (1969a) Asymptotic expressions for eigenfunctions and eigenvalues of a dielectric or optical waveguide. *IEEE Trans Microwave Theor Tech* 17:1130–1138
- Snyder AW (1969b) Excitation and scattering of modes on a dielectric or optical fiber. *IEEE Trans Microwave Theor Tech* 17:1138–1144
- Snyder AW (1975) Photoreceptor optics – theoretical principles. In: Snyder AW, Menzel R (eds) *Photoreceptor optics*. Springer, Berlin Heidelberg New York, pp 38–55
- Snyder AW (1979) Physics of vision in compound eyes. In: Autrum H (ed) *Handbook of sensory physiology*, vol VII/6A. Springer, Berlin Heidelberg New York, pp 225–313
- Snyder AW, Love DJ (1983) *Optical waveguide theory*. Chapman & Hall, London New York
- Snyder AW, Menzel R (eds) (1975a) *Photoreceptor optics*. Springer, Berlin Heidelberg New York
- Snyder AW, Menzel R (eds) (1975b) Introduction to photoreceptor optics – an overview. In: *Photoreceptor optics*. Springer, Berlin Heidelberg New York, pp 1–13
- Snyder AW, Pask C (1973) Spectral sensitivity of dipteran retinula cells. *J Comp Physiol A* 84:59–76
- Snyder AW, Menzel R, Laughlin SB (1973) Structure and function of the fused rhabdom. *J Comp Physiol* 87:99–135
- Stavenga DG (1974) Refractive index of fly rhabdomeres. *J Comp Physiol A* 91:417–426
- Stavenga DG (1975) Optical qualities of the fly eye – an approach from the side of geometrical, physical and waveguide optics. In: Snyder AW, Menzel R (eds) *Photoreceptor optics*. Springer, Berlin Heidelberg New York, pp 126–144
- Stiles WS, Crawford BH (1933) The luminous efficiency of rays entering the eye pupil at different points. *Proc R Soc London Ser B* 112:428–450
- Toraldo di Francia G (1949) Retinal cones as dielectric antennas. *J Opt Soc Am* 39:324
- Varela FG, Wiitanen W (1970) The optics of the compound eye of the honeybee (*Apis mellifera*). *J Gen Physiol* 55:336–358
- Vogt K, Kirschfeld K, Stavenga DG (1982) Spectral effects of the pupil in fly photoreceptors. *J Comp Physiol A* 146:145–152
- Washizu Y, Burkhardt D, Streck P (1964) Visual field of single retinula cells and interommatidial inclination in the compound eye of the blowfly *Calliphora erythrocephala*. *Z Vergl Physiol* 48:413–428