Optics of the Human Eye

W. N. Charman

Introduction

Optically, the human eye is fairly typical of vertebrate eyes in general and is not distinguished by any remarkable characteristics. It lacks, for example, the exquisite resolution of the eyes of many raptors, the enormous range of focussing power of some diving ducks and cormorants or the subtle duplicated optical system of the four-eyed fish, anableps. Nevertheless its optical performance is well matched to the capabilities of the neural network which it serves. As Helmholtz remarked with characteristic acuteness over a century ago, ‘The eye has every possible defect that can be found in an optical instrument and even some which are peculiar to itself; but they are so counteracted, that the inexactness of the image which results from their presence very little exceeds, under ordinary conditions of illumination, the limits which are set to the delicacy of sensation by the dimensions of the retinal cones’ (Helmholtz, 1962).

Knowledge of the way in which light propagates through the eye is crucial to the understanding of the abilities of the whole visual system, since formation of an optical image on the retina is the first stage in the complex processes which lead to perception. In general the retinal image is not a simple, reduced-scale reproduction of the external world but differs from it in such factors as spatial form, spectral composition, polarization and light flux, due to the transmission and imaging characteristics of the ocular media.

In this review we shall consider first the optical characteristics of the individual components of the eye and then the way in which these combine to determine the overall optical performance. Related reviews which set these human characteristics in the wider context of the evolution of vertebrate and invertebrate eyes will be found in Volume 2 of this series (Gregory, 1991).

Optical Components of the Eye

The main optical features of the eye are illustrated in Fig. 1.1. Full details of these structures are given in numerous texts (e.g. Duke-Elder and Wybar, 1961; Records, 1979; Davson, 1980; Moses and Hart, 1987). The techniques used to determine the dimensions and optical characteristics of each component are discussed by Charman, Chapter 16 and Henson, Chapter 17.

Fig. 1.1 Schematic horizontal section of the human eye.

General Shape of the Eye

The globe of the adult eye can be approximated as a sphere with an average radius of ~ 12 mm. It is completed anteriorly by the transparent cornea, which forms a roughly spherical cap with a radius of curvature ~ 8 mm, the distance between the centres of the spheres being about 5 mm (e.g. Le Grand and El Hage, 1980). Most eyes are, in fact, somewhat flattened posteriorly and the larger sphere is slightly conical anteriorly. There is also often some asymmetry about the anterior-posterior axis (Deller et al., 1947;
Cornea

The vertical and horizontal diameters of the white cornea are 11.5 and 10.5 mm respectively. It is covered by the outer layer, cornea (Fig. 2), which is composed of six layers. Among other functions, this layer serves to maintain the transparency of the corneal surface. Undoubtedly, the transmissivity is the thickness of the components of this film. The corneal layer is composed of three to five layers of corneal epithelium, which progressively arise during the inner-bone period as a result of a complex interplay of factors (Kolb, 1959). These factors are important in the quality of the visual image but little attention is paid to these factors in the development of this for the refractive error are discussed by Young (Chapter 2).

Bird's eye

The cornea is relatively coarse structure made up of a series of cross-layer sections — the epithelium, Bowman's membrane, the stroma, Descemet's membrane and the endothelium, the stroma making by far the greatest contribution (99%) to the overall thickness of about 0.5 mm at the centre of the cornea and 0.7 mm at the periphery (Bender, 1954; Marmor and Baer, 1969; Hira and Lacroix, 1978; Aron and Taylor, 1969). The optical inhomogeneity contributed to the scattering of light from the cornea that allows this element to be seen in optical microscopes with the shortest wavelengths. Of particular importance is the way in which the corneal collagen fibrils, which 23-35 mm in diameter, are arranged in the cornea. Not only do its structure and arrangement lead to

Fig. 2. The corneal structure: (A) A schematic showing the anatomical parts in one individual cornea. The data are expressed in the form of the rectangular from which the height of the rectangular area, measured across the corneal surface, and the rectangular from which the thickness of the corneal surface is determined in the detailed plan view in degree of the corneal surface of the individual eye (after Dignment and Kyle, 1984). (B) A schematic showing the structure of the corneal superstructure parameters, P, is a sample of 70° (after Kars and Kyle, 1984). P, is represented in a cylindrical surface.

Pupil

This circular opening lies in the iris, approximately 6.2 mm in diameter, and is considerably smaller than the iris itself. The iris is a muscle that plays an important role in the formation of the optical system of the eye. It does not completely cover the corneal surface, allowing light to pass through to the corneal surfaces, but also affects the quality of that image through its influence on the dioptric aberration and the refractive surface of the eye. The depth of the anterior chamber is determined by the size of the pupil, allowing light to reduce the dioptric system and to prepare the eye for a return to darkness. A mobile pupil allows sub-

Lenses

The cornea and the pupil have different characteristics in different parts of the cornea. The corneal layers vary in thickness from 0.2 to 0.3 mm and are composed of highly complex and interrelated systems, making the cornea a complex structure. The corneal layers are composed of highly complex and interrelated systems, making the cornea a complex structure. The corneal layers are composed of highly complex and interrelated systems, making the cornea a complex structure. The corneal layers are composed of highly complex and interrelated systems, making the cornea a complex structure. The corneal layers are composed of highly complex and interrelated systems, making the cornea a complex structure. The corneal layers are composed of highly complex and interrelated systems, making the cornea a complex structure. The corneal layers are composed of highly complex and interrelated systems, making the cornea a complex structure.
since the venom tends to liquefy. The cornea normally increases in the lens towards the retina and from the centre towards the periphery (Le Grand and El Hage, 1988). Optically, the venom in the eye is almost clear and free of reflective irregularities, although these become more pronounced during age (Wein, 1962). The refractive index of the venom is about 1.336; Milhodes (1976) has suggested that this may increase slightly with age.

The Retinal Surface

Although an eye may produce a sharp image, it is necessary that the retinal surface be an accurate optical plate to accept this image. i.e. the retinal outer segments should be exposed to the retinal surface without any irregularities. On the other side the tissue that lines these outer segments is eroded by an enzyme system that can lead to make it, if not too hypertrophied (not visible). These effects have a counterplay at larger field angles. While the retinal surface appears to a sphere, this need not necessarily match the curvature of the image surface. Moreover, the retina sheath does not change too much with the axis of the eye, so that even if the outer components had perfect spherical symmetry, an image would occur between the optical image and the retinal surface at some parts of the field. Fortunately, the irregular surface is not too approximately smooth, often the flesh, which can be seen with adequate illumination, is significantly smooth. At the retinal surface illumination and absorption of light is in the retina outer segments is strongly affected by optical wavefront alteration, a phase that has been thoroughly reviewed (Chapter 12) and will not be considered further here.

Optic Asymmetries and the Optical Axis of the Eye

As has already been noted in the cases of the anterior cornea and retina, the optical surface of the eye may lack morphometric symmetry and their nominal centres of curvature may not lie on a common axis: additional changes in retinal curvature are evident in the lens of normal and in the lower, Chapter 18. The pupil may also be displaced. These effects are demonstrated by the observation of the Purkinje images (see Hansen, Chapter 17). Nevertheless, these various deformations, asymmetries and tilt are small. The anterior and retinal components, and the apparent cornea are therefore only adequate for objects with a refractive index between 1 and 2.7 and entrance pupil of between 1 and 5.5 mm. The lens image remains unaltered but can be used with care.

Potential models have been proposed by a variety of authors (e.g. Gullander, 1974; Emery, 1952; Ophl, 1968; Dukhin and Ophl, 1970; Le Grand and El Hage, 1988; Fitchett and Emery, 1964; Breger and Roberts, 1988), the models differing chiefly in their exact shape and their effects of accommodation and optical simplification involved. Examples are shown in Fig. 1.5 and the associated values of the parameters are listed in Table 1.1. In schematic eyes the corneas and lens are usually represented by a pair of surfaces: a single surface is used for the cornea and the simplified schematic eye. Since the two models and two principal planes are very close together in all the models, considerable simplification can be achieved by using a reduced eye model consisting of a single reflecting surface. A reduced eye model of this type is particularly adequate for many ocular applications (e.g. Bangerter and Klein, 1976).

Wide-Angle Models

With advantage in understanding of the form of the surfaces of the eye and the reflective index distribution in the lens, and in the application to computers of imitating to the models, there have been an increasing number of attempts to develop new-parabolic models which give useful predictions of performance away from the axis. The simplest approach is to introduce astigmatic or other retinal distortions while retaining homogeneous media (Lentwig, 1971; Drexler and Wolfhard, 1974; Drexler and Pannen, 1980; Kleinman, 1985; Nordheim, 1985). Such models can be validated by comparing their predictions of off-axis aberrations with that observed in real eyes. More realistic models may involve the use of inhomogeneous lenses. The introduction of lens inhomogeneity (whether in a paraxial or a wide-angle model) was Gullander (1952) who involved a high-deviation core and a lower index core, and the lens has been progressively extended to include thousands of types of refractive index (e.g. Gullander, 1952; Gullander, 1972; Parameswaran et al., 1972; Werblin, 1972; Riker, 1980). There is little doubt that, with progressive refinement in the light of best case in the model data, these models will make valuable contributions to understanding and application of the off-axis performance of the eye.

Ocular Aneropria

Real eyes are not modelled in their dimensions but, like the rest of the body, can be expected to show variation in its performance due to the presence of factors such as the radius of curvature of the corneas which are not just a matter of a factor which can be considered separately and a similar factor is found in other ocular dimensions (see below). It is reasonable to ask, then, whether any eye models can not indicate the magnitudes of change in any performance that is likely to lead to a clinically-applicable refractive error.

### Table 1.1: Parameters of some paraxial models of the human eye

<table>
<thead>
<tr>
<th>Model</th>
<th>Schematic eye (Drexler and Emery, 1970)</th>
<th>Simplified schematic eye (Drexler, 1962)</th>
<th>Reduced schematic eye (Drexler, 1962)</th>
</tr>
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<tbody>
<tr>
<td>Model</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Radius of</td>
<td>Anatomy</td>
<td>Anatomy</td>
<td>Anatomy</td>
</tr>
<tr>
<td>surface</td>
<td>Central cornea</td>
<td>Pupil</td>
<td>Central cornea</td>
</tr>
<tr>
<td>Central cornea</td>
<td>7.0</td>
<td>7.8</td>
<td>7.0</td>
</tr>
<tr>
<td>Pupil</td>
<td>6.0</td>
<td>10.0</td>
<td>6.0</td>
</tr>
<tr>
<td>Tissues</td>
<td>0.5</td>
<td>5.0</td>
<td>0.5</td>
</tr>
<tr>
<td>Anatomy</td>
<td>Anthropos</td>
<td>7.0</td>
<td>Anthropos</td>
</tr>
<tr>
<td>Pupil</td>
<td>7.0</td>
<td>12.0</td>
<td>7.0</td>
</tr>
<tr>
<td>Tissues</td>
<td>1.3</td>
<td>22.2</td>
<td>1.3</td>
</tr>
</tbody>
</table>

### References

Consider, for simplicity, Emnsey's reduced eye model (Fig. 1.5c). It is evident that a refractive error $K'$D can arise if the power of the dioptric elements $F_{O}=\frac{(w'-1)r}{r}$ (where $w'$ is the refractive index of the medium and $r$ is radius of curvature of the refracting surface) does not match the dioptric length of the eye $K=\frac{w'}{k'}$ (where $k'$ is the axial length of the eye), i.e.

$$K = K' - F_{O} = \frac{(w'-1)r}{r}$$  \hspace{1cm} (1.3)

To determine the change in $K$ which arises as a result of change in any one of the parameters we may write:

$$\frac{\partial K}{\partial x'} = \frac{\partial K}{\partial w'} + \frac{\partial K}{\partial r} \Delta w + \frac{\partial K}{\partial r} \Delta r$$

or

$$\Delta K = \frac{\partial K}{\partial w'} \Delta w' + \frac{\partial K}{\partial r} \Delta w + \frac{\partial K}{\partial r} \Delta r.$$

(1.4)

Substituting the standard values for $k'$, $w'$ and $r$ from Table 1.1 we find that the changes required to produce $1 D$ of myopia are approximately $\Delta w' = +0.37 \text{ mm}$, $\Delta w = 0.0074$, $\Delta r = -0.993 \text{ mm}$: the signs of these changes are reversed for $1 D$ of hypermetropia.

Obviously considerable approximation is involved in determining these values. A similar analysis could, of course, be extended to more sophisticated eye models but nevertheless the finding that changes of about 1,3 mm in axial length and 1/10 mm in corneal radius of curvature give refractive changes of about 1 D constitutes a useful approximate rule-of-thumb. Refractive index values vary very little from one eye to another (Le Grand and El Hage, 1980) except for the lens in some pathological conditions (see Howe, Chapter 3).

Distribution of Parameters in Real Eyes

Surface curvatures, component separations, and axial lengths show considerable variation. Various studies have shown that each follows an approximately normal distribution (e.g. Stenstrom, 1946; Sorsby et al., 1957, 1981) (Fig. 1.6(a) to (d)). The spread of values is such that, in the light of the previous section, a high prevalence of large refractive errors might naively be expected to occur in the general population if the overall refraction of the eye arose from random combinations of parameters having the distributions shown. In practice this is not the case.

![Image of diagrams showing distribution of some ocular parameters and of refractive error](image-url)

**Fig. 1.6 Distribution of some ocular parameters and of refractive error** (after Stenstrom, 1946). In each case, the dashed curve represents the corresponding normal distribution. Note that while the individual parameters are distributed approximately normally, the refractive errors are strongly peaked to near-emmetropia. (a) Corneal radius of curvature. (b) Anterior chamber depth. (c) Lens power. (d) Axial length. (e) Refractive error.

ars and Henry (1966) have made further measurements on whole eye and other preparations. Such measurements are difficult to make and the results are influenced by the proportion of scattered light included (see also Henson, Chapter 17). Nevertheless, the general form of the results is reasonably consistent, showing a rapid rise in transmittance at around 400 nm followed by high values through the visible and near infra-red: the transmittance.

![Image of graph showing transmittance of different wavelengths](image-url)

**Fig. 1.8 Transmittance of normal, human, crystalline lenses of different ages.** Although the measurements may not be entirely representative of in vivo performance, the relative transmittances are likely to be realistic (after Lerman, 1980).
due partly to the increasing pathlength through the progressively thicker cortex of the lens and partly to increased pigment deposition and, perhaps, scattering in the nucleus (Said and Weale, 1959; Mellerio, 1971, 1987). The energy of some of the short-wave radiation that is absorbed may appear as fluorescence at longer wavelengths (e.g. Lerman, 1972; Satoh et al., 1973; Spector et al., 1975; Bando et al., 1976; Lerman, 1980), although the effects of this light in reducing retinal contrast are believed to be small (Boytton and Clarke, 1964). Some investigators have suggested that the strong and increasing short-wave absorption of the lens is helpful in protecting the ageing retina from the 'blue light hazard' (e.g. Sliney and Wobbe, 1980; Marshall, 1985) and that, for this reason, intraocular implant lenses should have similar absorption characteristics (see Ridgway, Chapter 7).

It is worth noting that, because of the bi-convex form of the crystalline lens, lenticular absorption may have some influence on measurements of the Stiles-Crawford effect (Stiles and Crawford, 1933, see Enoch and Lakshminarayan, Chapter 12) at shorter wavelengths: the pathlength through the lens is substantially shorter for rays near the edge of the pupil, leading to a smaller absorption loss and hence a reduction in the measured Stiles-Crawford effect over that occurring at the receptor level (Weale, 1961; Vos and Van Os, 1975). As already noted, it is not strictly true to assume that the attenuation per unit path in the lens is position-independent, since regions of higher scattering and absorption obviously exist (e.g. Brown, 1973; Sasaki et al., 1980; Mellerio, 1987).

The light is further attenuated by the retina itself before it reaches the receptor outer segments. Not only is there some loss due to scattering and reflection, contributing some 30% of the total light scatter within the eye (Vos and Bouman, 1964) but there are further screening effects from the retinal blood vessels (Kishto, 1970). In the fovea region, the macular pigment, extending over the central few degrees of the retina (Stanworth and Naylor, 1955; Kilbride et al., 1989) and lying anterior to the receptor outer segments (Snodderly et al., 1984) absorbs heavily at short wavelengths (Fig. 1.7). It has been argued that this pigment plays a useful role in reducing the blurring effects of the longitudinal chromatic aberration of the eye, and hence improving acuity (e.g. Reading and Weale, 1974). However, the amount of pigment varies widely between individuals and may also be age-dependent (Bornstein, 1977); as yet there have been no investigations to explore the possibility of any correlation between the amount of pigment and the acuity achieved.

Since the cornea, lens and the oriented molecules of macular pigment all show birefringence, the polarization characteristics of light entering the eye are modified before the receptor outer segments are reached: likewise, the polarization of light reflected back out of the eye undergoes further modification. Bour discusses these effects in detail in Chapter 13.

**Ocular Radiometry and Retinal Illumination**

If we confine ourselves to uniform object fields subtending at least 1° at the eye so that blurring due to aberration or defocus has negligible effect, the retinal image would also be expected to be uniform across its area, except at the edges, provided that the field angles were moderate. Wyszecki and Stiles (1967) show that the retinal irradiance, or internal stimulus, in a wavelength interval \( \Delta \lambda \), corresponding to an external stimulus of spectral radiant energy \( E(\lambda, \theta, \phi) \) W per unit wavelength interval per cm² per unit
solid angle of emission, in a direction with respect to the eye given by the angular coordinates \((\theta, \phi)\) is then given by:

\[
\frac{L_x(\theta, \phi) \delta \lambda \rho(\theta, \phi) t(\theta, \phi, \lambda)}{m(\theta, \phi, \lambda)}
\]  \hspace{1cm} (1.5)

where \(\rho(\theta, \phi) \text{ cm}^2\) is the apparent area of the pupil as seen from the direction \((\theta, \phi)\); \(t(\theta, \phi, \lambda)\) is the fraction of the incident radiant flux which is transmitted through the eye; and \(m(\theta, \phi, \lambda)\) is an area magnification factor \((\text{cm}^2)\) relating the area of the retinal image to the angular subtense of the stimulus at the eye, which will vary somewhat with the parameters of the individual eye.

Use of this equation close to the axis of the eye is straightforward. In the peripheral field the situation becomes more complicated. The pupil then appears as an ellipse of increasing eccentricity and reduced area and, due to the retina lying on a spherical surface, the distance of the retina from the exit pupil of the eye and the retinal area corresponding to an object of constant angular subtense change markedly. Remarkably, theoretical calculations (Fitzke, 1981; Bedell and Katz, 1982; Charman, 1983, 1989; Kooijman, 1983; Pihl, 1983) show that these various factors combine so that an object field of constant luminance (i.e., a Ganzfeld) results in a retinal illuminance which is almost constant with peripheral angle (Fig. 1.9). This theoretical result has been broadly confirmed by practical measurements on both rabbit and human eyes (Kooijman and Witmer, 1986) showing that, from a photometric point of view, the design of the human eye as a wide-angle optical system is remarkably effective.

A full discussion of the photometric aspects of point and extended sources is given by Wright (1949).

Retinal Image Quality

The aberrations of the eye and their effects on retinal image quality have long been of interest and most of the major figures of optics and vision have contributed to the advancement of our knowledge of this topic, from Newton onwards. The retinal image is inevitably degraded by pupil-diameter and wavelength-dependent diffraction and the regular, monochromatic, Seidel aberrations that any system of centred, spherical surfaces is prey to, i.e., spherical aberration, coma, oblique astigmatism, field curvature and distortion. It also has the defects to be expected from a biological system with various tilts, decentrations and other asymmetries.

Specification of Image Quality

A variety of methods exist for specifying the quality of the image formed by any optical system. Perhaps the most obvious is in terms of the image that it forms of a point object, i.e., the point-spread function or PSF, \(P(x, y)\), where \(x, y\) are appropriate coordinates in the image surface. In general \(P(x, y)\), which varies with field position, wavelength and focus, lacks radial symmetry, making it difficult to describe simply. Moreover, the illuminance in the outer parts of the image will be very low, making it difficult to measure experimentally, even though an important fraction of the light flux is contained in this part of the image. From the measurement point of view, there are advantages in determining the orientation-dependent line-spread function or LSF, \(L(x)\), which, since a line is a series of points, is simply the line integral of the point-spread function, i.e.,

\[
L(x) = \int_{-\infty}^{+\infty} P(x, y) \, dy
\]  \hspace{1cm} (1.6)

It is assumed here that, as is normally the case with the eye, different points in the object plane are incoherently illuminated and that the aberrations can be considered as constant over the relevant areas of field. Although, like the PSF, the LSF gives a good intuitive indication of the likely acuity for objects of similar form, because much of the image flux is contained in the outer parts of the LSF it is often difficult to recognize the effects that this spread of light will have when extended objects are imaged. Fortunately, it is possible to move directly from the LSF to a description of imaging performance for extended objects in the form of cosinusoidal gratings of varying spatial frequency, \(R\). Any optical system images such an object as a similar grating but, usually, of reduced contrast or modulation (Selwyn, 1948). The images may also be shifted slightly perpendicular to the length of the grating bars, i.e., there may be a spatial phase shift. To move from the LSF to the optical transfer function (OTF), \(O(R)\), which describes these modulation and phase changes as a function of \(R\), we use the Fourier transform relationship:

\[
O(R) = \int_{-\infty}^{+\infty} L(x) e^{-2\pi i Rx} \, dx = T(R) e^{i\phi(R)}
\]  \hspace{1cm} (1.7)

where \(T(R)\) and \(\phi(R)\) are the modulation and phase transfer functions respectively (MTF and PTF). The PTF becomes zero if the corresponding LSF is symmetrical.

A further alternative description of the optical performance of the eye is in terms of the wavefront aberration. As is well known, the wavefronts in any system are surfaces which are orthogonal to the corresponding ray pencils. Hence, if in terms of geometrical optics an optical system forms a perfect point image, all the imaging rays intersect at that point or, alternatively, all the imaging wavefronts are spherical. If aberration is present there is no longer a point focus and hence the wavefronts are no longer spheri-
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(1.7)

The Aberration-Free Eye

If an eye is free of aberration, the wavefront aberration is always zero. The only factor contributing to the blur of the in-focus retinal image is the diffraction arising from the finite wavelength of light, $\lambda$, and the finite diameter, $D$, of the eye pupil: for this reason an aberration-free eye is often called a diffraction-limited eye. The point-spread function is then an Airy diffraction pattern and the LSF and MTF take similarly standard forms (the PTF will be zero since the PSF and LSF are symmetrical). Blur increases on either side of focus (Lommel, 1884; Linfoot and Wolf, 1956; Born and Wolf, 1975). For the in-focus case, angular resolution for two object points by the Rayleigh criterion is given by:

$$\theta_{\text{min}} = (1.22\lambda)/D \text{ rad}$$  \hspace{1cm} (1.8)

Fry (1955) has given a clear description of the way in which the PSF of an aberration-free eye changes as a function of focus: these results have important implications for the prediction required for the accommodation mechanism and during refractive procedures. The corresponding through-focus MTFs have been illustrated for various wavelengths and pupil diameters by several authors (e.g., Westheimer, 1964; 1965; Campbell and Green, 1965; Campbell and Gubisch, 1967; Charman and Tucker, 1977; Charman and Jennings, 1966; Charman and Heron, 1979; Charman, 1983). Much of this data is based on tables given by Levi (1974). Smith (1982) has given detailed consideration to the question as to the general applicability of physical and geometrical optical descriptions to imagery of the in and out-of-focus, diffraction-limited eye.

The Regular Monochromatic Aberrations of the Eye

As Guidoni (1972) has noted, the eye crudely approximates to a homogeneous system, since all the surfaces, including the retina, have centres of curvature lying near the centre of the aperture stop. In a truly homogeneous system, the chief ray, passing through the centre of the aperture stop, is always an optical axis, so that no off-axis aberrations occur. This is by no means exactly true for the eye but nevertheless, as Young (1801) noted many years ago, the retinal curvature does very closely match the curvatures of the eye's image surfaces, so that off-axis aberrations are quite well controlled.

In practical terms, we would expect that, if the eye were indeed a regular optical system, the only significant ocular aberration on the optical axis would be spherical aberration. The other regular aberrations would become increasingly important away from the optical axis, although it might be anticipated that distortion, a field-angle dependent magnification change, could potentially be corrected for by the higher visual centres. The latter is, indeed, almost certainly the case and it is of interest that similar compensation or adaptation can be observed to occur for the distortions associated with correcting spectacle lenses (Ogle, 1950).

Most investigators attempting to determine the nature of individual aberrations have, in fact, concentrated on spherical aberration and oblique astigmatism and have often assumed that it is adequate to consider that the optical and visual axes of the eye coincide (i.e. angle $\alpha$ is zero), so that any aberration measured for foveal vision should be pure spherical aberration. There is, of course, particular interest in determining the aberration associated with the foveal image in that it is in the fovea that the neural network makes the greatest demands on optical image quality.

Spherical Aberration

Earlier work on spherical aberration has been reviewed by several authors (Koome et al., 1949; Rosenblum and Christensen, 1976; Charman, 1983). As spherical aberration involves a regular, radially symmetric, change in power, most measurements have been made using apertures, often annular, to isolate different small regions of the entrance pupil and hence measure the associated power by appropriate subjective or objective techniques.

Results, as found by a variety of different investigators, are shown in Fig. 1.10; although the individual data vary, they suggest that spherical aberration is generally of the order of 1 D at the edge of a 4 mm diameter pupil. Also included in Fig. 1.10 is the spherical aberration for a schematic eye with spherical surfaces, together with the curve showing the amount of primary, positive, under-corrected
spherical aberration which Van Mee ten (1974) suggested was representative for real eyes. For the latter, the excess power of a zone of radius r is given by
\[ \Delta P = 4Ar^2 \]
and the wavefront aberration by
\[ W(r) = Ar^2 \]
van Mee ten's assumed value of A is \( 4 \times 10^4 \text{m}^{-3} \). Not surprisingly, the amount of aberration shows considerable variation between individual eyes and is accommodation-dependent, there apparently being minimal aberration when the eye is accommodating for an object at about 0.7 m from the eye (Ko omen et al., 1949; Ivanoff, 1947, 1953, 1956; Jenkins, 1963a; Berny, 1969), a distance which, intriguingly, corresponds to the equilibrium or ‘resting’ state of the accommodation system (see Giff reda, Chapter 11).

It is clear from Fig. 1.10 that the eye has less spherical aberration than would be expected from an eye with spherical surfaces and that the aberration is almost negligible for pupil diameters less than 2–3 mm. This is largely attributable to the asphericity of the eye’s surfaces, particularly the cornea, and to the index gradients in the lens. There is some disagreement as to whether the cornea and lens act in combination to minimize spherical aberration (El Hage and Berny, 1973) or whether they are each separately minimized (Millodot and Sivak, 1979).

Fry (1955) has computed some through-focus, retinal, point-spread functions, using the spherical aberration data of Ivanoff (1947). Berny (1969) has used wavefront aberration data to calculate the effect of spherical aberration on the ocular MTF and has demonstrated the loss of modulation transfer at intermediate spatial frequencies that can occur in comparison with a diffraction-limited eye. Similar MTF measurements and calculations have been presented by Charman and Jennings (1976a) and Charman et al. (1978).

As will be discussed further below in the context of the overall wavefront aberration, many of the above studies emphasize that, when an appropriate measurement technique is used, it is found that the power variation in the pupil of any individual eye rarely has true radial symmetry. Thus the concept of the eye displaying only pure spherical aberration near its axis has only limited validity. Even when eyes suffer from supposedly typical amounts of spherical aberration, the subjective refraction varies very little with pupil size (Ko omen et al., 1949, 1951; Charman et al., 1978). This is presumably due to irregular aberration, the Stiles-Crawford effect (which reduces the contribution of the outer zones of a dilated pupil under photopic conditions) and to the fact the spherical aberration has only a small effect on optical focus for periodic detail near the cut-off frequency for the eye (\( \sim 30 \text{ cdeg}^{-1} \)).

**Oblique Astigmatism**

In practice, measurements of ocular oblique astigmatism inevitably involve the determination of the positions of the astigmatic focal lines with respect to the retina (which may itself lack rotational symmetry about the axis), rather than the true oblique astigmatism of the dioptics. Most attention has been concentrated on the horizontal (nasal-temporal) meridian of the eye, using retinoscopy (skiascopy) or objective optometers (Ferre et al., 1931, 1932; Rempt et al., 1971; Hoogerheide et al., 1971; Millodot and Lamont, 1974; Millodot, 1981).

Representative data are shown in Fig. 1.11. The observed amount of oblique astigmatism is lower than that calculated for eye models with spherical surfaces: Dunne et al. (1987) have been able to achieve good agreement between the measured values and those for a model eye with aspheric surfaces, including that of the retina. It is of interest that the experimental data, plotted with respect to the visual axis, appear to be symmetrical about a nasally displaced point, presumably due to angle α. Variations in the relationship between the radial and tangential refractions and the central refractions for emmetropic, myopic and hypermetropic groups (Millodot, 1981) seem to be explicable in terms of variations in the axial lengths of the eyes concerned (Charman and Jennings, 1982). The amount of aberration measured increases slightly with the level of accommodation being exercised, presumably due to the shape changes in the crystalline lens (Smith et al., 1988).
Overall Monochromatic Wavefront Aberration

Determination of the overall wavefront aberration has the advantage that, since each individual Seidel aberration produces a characteristic form of wavefront distortion (e.g., Hopkins, 1950; Born and Wolf, 1975; Smith, 1978), in principle it is possible to deduce from the measured wavefront both the contributions of the individual aberrations and their combined effects.

Up to the present time, wavefront aberration has only been measured on the visual axis. The earliest study was that of Smirnov (1962), who used a very laborious coincidence technique in conjunction with a moveable 0.4 mm pupil to map the wavefront aberration in a square mesh across the full pupils of 10 eyes: a substantial period of data analysis was also required. Somewhat similar measurements of the local dioptric power of small regions of the pupil were made by Van den Brink (1962) and, very recently, Howland and Buettner (1989) have shown that these may also be used to deduce the wavefront aberration.

Objective methods were pioneered by Berny and Slansky (1969), who adapted the powerful Foucault knife edge method to secure the necessary information in two flash photographs, taken with two mutually perpendicular orientations for the knife edge. At that time, however, analysis of the photographs took several months, so that only a single eye was studied. Walsh et al. (1984) and Walsh and Charman (1985) modified the ingenious subjective aberroscope technique of Howland and Howland (1976, 1977) to allow objective aberroscope recording. The method involves viewing a point source through a grid which is sandwiched between two crossed cylinder lenses: each aberration produces a characteristic distortion in the retinal shadow image of the grid. Lastly, the wavefront aberration can be inferred from measurements of the retinal point-spread function (Artal et al., 1988a, 1988b).

Although there are differences in the form of aberration between individuals, which are not surprising in view of the known variation in such factors as corneal contour, and in the resolution in the detail of the wavefront which can be achieved by each method, all these studies agree in demonstrating that the wavefront aberration rarely displays the radial symmetry that would be expected if only spherical aberration was present. Some examples are shown in Fig. 1.12. In general, coma-like aberration often seems to be more important in the individual eye than spherical aberration. Nevertheless, if the wavefront errors of many eyes are averaged then the aberration shows much greater radial symmetry (Charman and Walsh, 1985) and, indeed, the radial change in power that can be deduced from this average wavefront aberration corresponds closely to the classically-measured amounts of under-
corrected spherical aberration that are shown in Fig. 1.10. The wavefront aberration of the individual eye is generally less than a quarter wavelength within the central 2–3 mm diameter of the pupil.

**Chromatic Aberration**

The longitudinal chromatic aberration of the eye has been a subject of study since the time of Newton (Charman, 1985). Typical results of modern subjective measurements are shown in Fig. 1.13. Objective studies produce broadly comparable data (Lau et al., 1955; Ronchi and Millodot, 1974; Charman and Jennings, 1976b). As can be seen, the aberration typically amounts to about 2 D across the full visible spectrum. It is at first sight surprising that correction of this aberration with a suitable achromatizing lens produces little effect upon acuity for white light (Hart ridge, 1947) but Campbell and Gubisch (1967) point...
Fig. 1.13 Average axial, or longitudinal chromatic aberration of the eye as measured by several authors. In each case, the mean data have been displaced so that the chromatic aberration is zero at 578 nm. ○ Wald and Griffin, 1947 (14 eyes); □ Ivanoff, 1953 (11 eyes); ● Bedford and Wyszecki, 1957 (12 eyes); △ Jenkins, 1963b, (32 eyes); ◆ Howarth and Bradley, 1986 (20 eyes). The dashed curve represents the overall range of individual observers, as found by Bedford and Wyszecki.

Itout that this is because the major effects of the aberration are to degrade modulation transfer at intermediate, rather than high, spatial frequencies. Some authors (Polack, 1923; Ivanoff, 1953; Le Grand, 1967; Millodot and Sivak, 1973; Bobier and Sivak, 1978; Sivak, 1982) have suggested that the accommodation system may make use of the range of focus conferred by longitudinal chromatic aberration to ‘spare the accommodation’, i.e. to minimize accommodative effort; on the other hand, there is little evidence for markedly different steady-state accommodation characteristics in white and monochromatic light (Charman and Tucker, 1978), nor is depth-of-focus as conventionally measured markedly greater in white light (von Bahr, 1952; Oshima, 1958; Ogle, 1960; Legge et al., 1987).

There have been suggestions in recent years that the longitudinal chromatic aberration may be age-dependent, possibly due to index changes in the various ocular media (Millodot, 1976; Millodot and Newton, 1976; Mordi and Adrian, 1985) but other recent studies (Ware, 1982; Howarth et al., 1988) deny this and as yet an age dependence cannot be regarded as being firmly established.

Transverse, or lateral chromatic aberration must also occur, i.e. the retinal images of a given object should be slightly different in size at differing wavelengths. Calculations (Van Meeteren, 1974; Howarth, 1984; Thibos, 1987) suggest that the aberration plays a significant role in reducing retinal image quality in white light. While the effects are of increasing significance in the periphery, they may also occur at the fovea, due to the misalignment between the visual and optical axes of the eye (angle \( \alpha \)). The effects are orientation dependent. The subjective measurements of Ogboso and Bedell (1987) appear to give values which are somewhat lower than the theoretical predictions, the transverse chromatic aberration between wavelengths of about 435 and 572 nm remaining less than 10° for field angles up to 40°. At the fovea, the measured transverse chromatic aberration is also less than would be expected for an angle \( \alpha \) of 5° (Simonet and Campbell, 1990; Thibos et al., 1990).

Intraocular Scatter and Related Effects

In all the foregoing discussion of aberrations, it has been assumed that the refractive indices of the media are either constant or smoothly varying and that the optical surfaces themselves are also smooth on the scale of the wavelength of light. In practice, a variety of regular and irregular small-scale inhomogeneities exist and these contribute to further light loss and a spread of light in the retinal image. The qualitative aspects of these effects exercised considerable fascination for earlier authors: the associated entoptic phenomena are described in Palmer (Chapter 15).

Quantitative measurements of the forward-scattered light were pioneered by Holladay (1926) and Stiles (1929), who used a technique based on the masking effect of a glare source. They expressed their results in terms of an equivalent veiling luminance, \( L_{eq} \) cd m\(^{-2}\), that would produce the same masking effect as a glare source giving an illuminance \( E \) at the eye, as a function of the angular distance, \( \alpha \) degrees, between the glare source and fixation. They found the approximate relationship:

\[
L_{eq} = \frac{10E}{\alpha^2} \quad (4^\circ < \alpha < 100^\circ) \tag{1.9}
\]

Later work, well summarized by Vos et al. (1976) led to the modification of this formula to take account of effects closer to fixation:

\[
L_{eq} = \frac{29E}{(\alpha + 0.13)^2} \quad (0.15^\circ < \alpha < 8^\circ) \tag{1.10}
\]

These equations apply to young adult eyes. The magnitude of the scattering undoubtedly increases throughout life, by a factor of at least 2–3 times, although the same angular dependence is retained (Allen and Vos, 1967; Hernenger, 1984). Roughly a quarter of the effective stray light comes from the cornea (Vos and Boogaard, 1963; Boynton and Clarke, 1964) and a further quarter from reflections off the retina (Vos, 1963; Vos and Bouman, 1964): the rest comes almost entirely from the lens, there being little contribution from the aqueous or vitreous. A theoretical analysis of the contribution of lens fibres to
intraocular scatter has been presented by Hemenger (1988). Attempts have recently been made to develop a clinical method for assessment of the glare effect caused by scattering, by measuring the impairment in the contrast sensitivity function in the presence of a glare source (Paulson and Sjostrand, 1980; Abrahamsson and Sjostrand, 1986): the method shows particular promise as an aid to following changes in cataractous eyes.

**Final Retinal Image Quality**

Estimates of the quality of the final retinal image can be made in three main ways: by calculation from the wave aberration; by a psychophysical method; and by direct measurement of the light distribution on the retina using a double-pass ophthalmoscopic technique.

Calculation from the Wavefront Aberration

Calculation of the optical transfer function (OTF) can be carried out by autocorrelation of the complex pupil function with its complex conjugate, using numerical methods originally devised by Hopkins (1962). The pupil function gives the variation in amplitude and phase across the exit pupil of the system. The local phase can be deduced directly from the wavefront aberration (each wavelength of aberration corresponds to 2π of phase) and it may either be assumed that the amplitude across the pupil is uniform or, if desired, pupil-weighting functions can be introduced in an attempt to take account of the effects of pupil-dependent lenticular absorption or the Stiles-Crawford effect (Stiles-Crawford apodization, see, e.g. Metcalf, 1965). The point-spread (PSF) and line-spread (LSF) functions may similarly be calculated from the wavefront aberration (e.g. Hopkins, 1962; Born and Wolf, 1975; Smith, 1978).

This approach was used by Berry (1969) to estimate ocular MTFs from the wavefront aberration as deduced from Foucault’s knife-edge measurements, and by Berry and Slansky (1969) to compare the retinal PSF with the ideal Airy disc: these latter authors concluded that the eye was essentially diffraction-limited for pupil diameters up to 2 mm. Van Meeteren (1974) took a more indirect approach, in that he estimated typical values for wavefront aberration from published measurements of the individual Seidel aberrations and other sources of image degradation. Interestingly, he found that making allowance for the Stiles-Crawford effect had little influence on the overall MTF for the natural pupil diameters (<5 mm) which occur under photopic conditions: in white light, chromatic aberration appeared to be the most important single aberration for typical photopic pupils.

The subjective aberroscope results of Howland and Howland (1974, 1977) are of particular interest in that a large sample (55) of eyes was studied. Hence it was possible to obtain some idea of the spread in performance between individual eyes. Fig. 1.14(a) shows the rank-ordered, calculated MTFs for monochromatic light at a wavelength of 555 nm and a 5 mm diameter pupil. Although Howland and Howland’s technique demanded that subjects sketch the image of the aberroscope grid that they saw, very similar results were obtained when using the objective variant of the method (Walsh et al., 1984, Walsh and Charman, 1985), as shown in Fig. 1.14(b). It will be noted that, for these 5 mm pupils, the performance of all eyes falls well below that set by the diffraction limit. The calculated phase transfer functions (PTFs) suggest that pupil-dependent optical phase shifts may have some role in limiting the visual system’s ability to discriminate spatial phase (Charman and Walsh, 1985).

---

**Fig. 1.14** Ocicular MTFs for an eye with a 5 mm pupil as calculated from wavefront data. (a) Rank-ordered MTFs for a group of 55 eyes and light of wavelength 555 nm. The 100% curve represents the best eye of the set (after Howland and Howland, 1977), the dashed curve being the MTF for a diffraction-limited eye. (b) MTFs for a sample of 10 eyes at a wavelength of 590 nm and a pupil diameter of 5 mm (after Walsh and Charman, 1985).
Calculations of retinal image quality from wavefront data suffer from the obvious disadvantage that no allowance can be made for the deleterious effects of light scatter in the media. Hence they may lead to too optimistic an estimate of retinal image quality. As already noted, it is possible to weight the pupil function for lenticular absorption or the Snell-Crawford effect, but such weighting necessarily rests on assumptions rather than direct measurement.

Psychophysical Method
The principle of this method is straightforward. If the subject views an external gratings of spatial frequency $R$ and modulation $M_o(R)$, the modulation in the retinal image must be $M_o T(R)$, where $T(R)$ is the modulation transfer of the ocular dioptrics at this spatial frequency. Suppose now we steadily reduce the modulation of the grating until it appears to the observer to be just at threshold. Then the threshold modulation on the retina, $M_o(R)$, will be given by:

$$M_o(R) = M_o(R) \cdot T(R)$$  \hspace{1cm} (1.11)

where $M_o(R)$ is the measured modulation of the external grating at threshold. The reciprocal of $M_o(R)$ is obviously the contrast sensitivity as conventionally defined, and measurement of $M_o(R)$ as a function of $R$ simply corresponds to the procedure used to establish the contrast sensitivity.

Clearly, $M_o(R)$ corresponds to the threshold for the retina/brain portion of the visual system and, if it can be established independently, then $T(R)$ can be deduced from $M_o(R)$ and $M_o(R)$. The internal threshold can, in fact, be determined by bypassing the dioptrics of the eye and forming a system of interference fringes directly on the retina (Le Grand, 1935, 1936; Byram, 1944; Westheimer, 1960; Arnulf and Dupuy, 1969; Campbell and Green, 1965; Berger-Leheureux, 1965; Campbell, 1968; Dupuy, 1968; Burton, 1973; Bour, 1980). Two mutually-coherent point sources are produced close to the nodal points of the eye and the two resultant divergent beams overlap to generate a system of Young's fringes on the retina. The fringe spacing, $\beta$ rad, is given by $\beta = \lambda/a$, where $\lambda$ is the wavelength and $a$ is the separation of the two coherent point sources, both measured in air. If the point sources have similar intensity, the fringes will be of unit contrast and it is necessary to have some means of varying the fringe contrast, either by varying the relative intensity of the sources or by adding a suitable background illumination to the retina. The threshold contrast for the retina/brain, $M_o(R)$, can then be measured as a function of $R$, so that we can deduce the MTF of the ocular dioptrics as:

$$T(R) = M_o(R) / M_o(R)$$  \hspace{1cm} (1.12)

Fig. 1.15 gives some typical results for in-focus, foveal MTFs as determined by this method. The data show that optimal MTF is achieved with a pupil diameter of around 2–3 mm. Bour (1980) has extended the method to explore through-focus changes in axial MTF and finds that irregular aberration may lead to more than one position of optimal focus. The method has also been applied to off-axis imagery; although Green (1970) and Enoch and Hope (1973) deduced that it was unlikely that optical factors contributed significantly to the well-known loss in acuity with increasing field angle, Frisén and Glacholm (1975) felt that their data suggested that optical degradation was of some significance. This discrepancy has yet to be fully resolved.

The major criticism of the psychophysical technique is that the assumption that the interference fringes are totally unaffected by the ocular media may not be justified. Ocular scattered light may well degrade the fringe contrast, particularly in older eyes. This would tend to lead to an over-estimate of the modulation transfer. It is also difficult to be sure that the subjects are consistent in their judgements of the internal and external thresholds, particularly in those studies where there are differences in the colour and field size of the two grating systems. Indeed, some studies using the technique have produced much less plausible results (Fraser and Morrison, 1987).

Ophthalmoscopic Methods
If the image of a suitable object is thrown onto the retina, a proportion of the flux in the retinal image will be reflected back out of the eye and, given an appropriate optical system, can allow an observer to view the relayed retinal image. This, of course, the principle of the ophthalmoscope (see Henson, Chapter 17). If, for example, the original object is a line, the relayed image will be a line-spread function. It will be noted that two stages of image degradation are involved in this process and it is necessary to assume that no coherence is preserved in the light reflected from the retina. Under these circumstances the
overall OTF is simply the product of the inward and outward OTFs. Although the scattering geometries involved might conceivably make these OTFs differ, it is usual to assume that they are the same, so that the double-pass OTF is simply the square of the desired single-pass OTF.

This type of measurement was pioneered by Flamant (1955) who used a photographic technique to record the double-pass line-spread function and went on to calculate its single-pass counterpart. Photographic techniques pose considerable problems of non-linearity and lack of sensitivity and all subsequent experimenters have used photoelectric techniques (e.g. Krauskopf, 1962, 1964; Röhler, 1962; Westheimer and Campbell, 1962; Campbell and Gubisch, 1966; Röhler et al., 1969; Jennings and Charman, 1978, 1981; Gorrand et al., 1978; Gorrand, 1979; Santamaria et al., 1987).

Most of the earlier authors measured the external line-spread function, took its Fourier transform to yield the double-pass OTF, square rooted this to give the single-pass OTF and, finally, took the inverse Fourier transform to give the single-pass line-spread function. In fact, in most instances the images were sufficiently symmetrical that phase terms could be ignored, so that only the M was considered. More recently, Santamaria et al. (1987) using a television camera and image analysis system (Fig. 1.16), have made direct measurements of the point-spread function: this has the advantage that it allows calculation of the LSF and OTF for any orientation.

In general, the results of this type of study agree with the findings of other methods. Fig. 1.17 shows some representative axial data. Ocular aberration is found to become increasingly significant as the pupil diameter exceeds 2–3 mm. Off-axis, image quality shows only a slight decline for field angles up to about 10°; thereafter the image progressively blurs and oblique astigmatism becomes more important. The oblique astigmatism determined by this type of measurement is similar in magnitude and form to that found by retinoscopic or optometer techniques (Jennings and Charman, 1978, 1981).

One major uncertainty in this double-pass ophthalmoscopic technique concerns the nature of the retinal reflection. It is assumed that all coherence is lost at the

![Diagram](attachment:image.png)

Fig. 1.16 Arrangement used by Santamaria et al. (1987) for recording the double-pass retinal point-spread function.
ntly symmetrical at only the MTF when astigmatism is lost at the retina and that the reflection itself does not introduce any degradation, i.e., it occurs at a single surface (see, e.g., Charman, 1983, for review). In practice some degradation must occur and the exact extent to which this affects the measured OTF remains somewhat uncertain. A further problem is that, when recording very faint reflected images, there may be a tendency to truncate the outer parts of the image where the illuminance is very low but which may still contain substantial amounts of light flux due to their considerable area: this can lead to a significant overestimate of modulation transfer (Simon and Denieul, 1973). Vos et al. (1976) have attempted to overcome this latter problem by combining ophthalmoscopic measurements of the retinal point-spread function (Campbell and Gubisch, 1966) with the estimates of other authors for the amount of wider-angle, entoptic stray light, to produce a realistic estimate of the light profiles in the foveal image of a white-light point source.

Future Developments

It seems likely that, with the further development and availability of improved low-light-level cameras, frame-grabbing, and image analysis techniques, rapid acquisition of data on retinal image quality will become much more routine. This will allow extended study of not only the naked eye but also the contact lens wearing eye, in which aberration as well as overall refraction is modified by lens wear. Clearly, too, there would be considerable interest in investigating image quality in eyes with intraocular implants or after refractive surgery: a full understanding of the image quality, both axial and peripheral, is that achieved should lead to improvements in lens design and surgical techniques.

Analytical approximations for the ocular MTF

Several authors have attempted to approximate the experimentally-determined ocular MTFs by analytic functions (see Charman, 1983, for review). Such functions have obvious merits in simplifying calculation and in allowing the comparison of different individual MTFs. Functions suggested include:

\[ T(R) = \exp\left[-R/R_c\right] \]

\[ T(R) = \exp\left[-(R/R_c)^2\right] \]

\[ T(R) = \exp\left[-(R/R_c)^n\right] \]

(1.13)

where \( R_c \) is some constant spatial frequency and \( n \) is a further constant. The last expression has been found to provide a reasonable fit to ocular MTFs at low and medium spatial frequencies and might, perhaps, be useful under some circumstances (Jennings and Charman, 1974; Drasdo and Cox, 1987; Thompson and Drasdo, 1989).

Ocular Depth-of-Focus

In considering the MTFs in the preceding section, it was tacitly assumed that the eye was optimally focused. There is, in fact, some ambiguity in defining optimal focus, since the focus at which modulation transfer reaches its highest value may be spatial-frequency dependent in the presence of aberration (e.g., Koornen et al., 1951; Green and Campbell, 1965; Charman and Jennings, 1976a; Charman et al., 1978). Thus the optimal focus may vary somewhat with the spatial frequency content of the object (i.e., its spatial form). In general, however, a shift away from the optimal focus produces an overall loss in modulation transfer, corresponding to an increase in image blur. In a geometrical optical approximation, the blur increases linearly with the pupil diameter and the dioptric defocus, although this approximation is poor near the region of focus. Fig. 1.18 plots the through-focus modulation transfer for a diffraction-limited eye, at a number of spatial frequencies.

We might expect, then, that the ability of the observer to detect defocus would depend upon the characteristics of the object under observation (form, spectral content, contrast, luminance), the pupil diameter and the visual characteristics at the retina/brain level. In particular, since only low spatial frequency information can be perceived at low luminances (Van Nes and Bouman, 1967), one might anticipate a corresponding increase in blur thresholds. For the same basic reason, it would be expected that low vision patients would show greater tolerance to blur, and hence greater depth-of-focus (Legge et al., 1987).

As the range, or depth, of focus over which blur has negligible effect is of considerable practical significance with respect to the need for refractive correction, the pre-
typical data as obtained under photopic conditions. That depth-of-focus decreases less rapidly with diameter than would be predicted from either geometric or physical optical considerations for an aberration-free eye. This may be due partly to the apodizing role of Stiles-Crawford effect and partly to the increasing aberration at the edge of dilated pupils.

Even if a constant technique is used, the measured depth-of-focus depends upon the criterion used to assess and it is striking that, in accommodation experiments, accommodation may be stimulated by very small changes (≤0.1 D) in the vergence (distance) of the target (Ludlam et al., 1968). The limited dioptric range within which a target can be moved without the detection of it implies, of course, the need for a focussing or accommodation system, so that the retinal image quality is usually slightly worse than would be obtained at optimal focus.

Matching Between Optical and Neural Quality

Helmholtz long ago suggested that, for resolution of grating, an unstimulated retinal element must be present between those elements which are stimulated by neighbouring bright bars of the grating (Helmholtz, 1924). The basic concept is now formalized within the framework of sampling theory. It is easy to show that if it is assumed that the retinal receptors are packed in a hexagonal array, with neighbouring receptors having centre-to-centre spacing: $D$, the highest sinusoidal spatial frequency that can unambiguously be resolved by the array is given by:

$$t = d\pi/180 \cdot D(3)^{1/2} \cdot \text{cdeg}^{-1}$$

$d$ is the posterior nodal distance (approximately 16.7 mm) (Snyder and Miller, 1977; Miller and Bernard, 1983). Gratings of higher frequency than this Nyquist limit, $t$, are undersampled and may appear as spurious gratings of lower frequency—the phenomenon known as 'aliasing.' Such aliasing can be observed under the very abnormal viewing conditions where interference fringes of high spatial frequency are generated on the retina, as in the psychophysical method for determining the ocular OTF. Several authors have used these aliasing effects to make deductions about the spatial arrangement of the cone mosaic in the retina (e.g. Williams, 1985; Coletta and Williams, 1987; Smith and Cass, 1987; Thibos et al., 1987; Williams, 1988).

In general, aliasing is likely to be unfavourable and ideally the cut-off frequency of the optics should be comparable to that of the receptor array. For incoherently-illuminated objects viewed in the normal way it would appear that this matching is at least approximately achieved in the foveal region. The attenuation provided by

![Diagram](image-url)
the modulation transfer of the eye's dioptrics substantially reduces the chances of aliasing being observed. It is possible that there would, in fact, be no advantage in maintaining the diffraction-limited performance of the eye for pupil sizes greater than 2-3 mm. The superior image quality available from a diffraction-limited eye with, say, a 6 mm pupil would mean that the effective optical cut-off frequency would substantially exceed that of the retina. In this sense, then, the axial aberration of the eye may not be disadvantageous. It would indeed appear reasonable that the optical quality should decline for large pupils, since the natural pupil only dilates when the light level is low and the retinal cut-off frequency is lowered. It is interesting to note that there is evidence that the degradation in image quality that occurs off-axis may serve to maintain the optical and neural matching into the peripheral regions, where the retinal ganglion cell intervals and receptive field sizes are larger (Jennings and Charman, 1978, 1981).

Factors other than the MTF of the eye's optics may, of course, also play a role in reducing the possibility of aliasing. Both disorder in the receptor array (Yellot, 1982; Hirsch and Miller, 1987) and averaging over the receptor aperture (Miller and Bernard, 1983) may be of importance. Recent measurements of human foveal cone spacing by Hirsch and Curcio (1989) lead them to suggest that within about 2° from the centre of the fovea conventional measurements of photopic visual acuity correlate quite well with those predicted from the cone spacing, implying that the optical performance of the eye can support its neural capabilities: only at the foveal centre is there a suggestion that optical performance may fall short of the ideal.

Much remains to be done to clarify certain aspects of the optics of the eye, particularly those relating to the refractive index distribution and shape of the lens as a function of age and accommodation, and to optical performance in the peripheral field. Nevertheless, it is unlikely that improved understanding of the eye will in any way diminish our respect for the way in which its optical performance closely matches the needs of the neural parts of the visual system.

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