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Specifying and controlling the optical image on the human retina

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Abstract

A review covering the trends that led to the current state of knowledge in the areas of:

- (a) schematic models of the eye, and the definition of the retinal image in terms of first-order optics;
- (b) the description of the actual image on the retina and methods for accessing and characterizing it;
- (c) available procedures for controlling the quality of the retinal image in defined situations; and
- (d) intra-receptor optical effects that cause differences between the light distribution on the retinal surface and at the level of interaction with photopigment molecules.

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A distinction can be made between outer and inner psychophysics, depending whether one considers the relation between the mind and the world outside or inside the body. The outside world is functionally related to the mind only *via* the operation of a mediating stage. (Fechner, 1860/1907)

The causes of the excitations of our senses are called stimuli. We see now that the word has two different meanings which must be clearly distinguished from each other: on the one hand the table in the geographical environment can be called a stimulus for our perception of a table; on the other hand the excitations to which the light rays coming from the table give rise are called the stimuli for our perception. Let us call the first the *distant* stimulus, the second the *proximal* stimuli. Then we can say that our question why things look as they do must find its answer not in terms of the distant, but the proximal, stimuli. By the neglect of this difference real problems may be overlooked and explanations proffered that are no explanations at all. (Koffka, 1935, p. 80)

1. Introduction

For vision, the first mediating stage between the outside and inside world, or between the distal and proximal stimuli, is the eye operating as an optical apparatus. It converts the physical object space, the distal stimulus, into its image on the retina, the proximal stimulus. To heed Koffka's warning that real problems may be overlooked and spurious explanations offered about the workings of the "inner" visual system, we need to ask at the outset how good a replica of the outside world the retinal image really is.

Early in the 19th century, Thomas Young and Jan Purkinje were among those who had realized that the explanation of some visual phenomena should be sought in the eye itself. Young looked for astigmatism and accommodative changes in the eye, Purkinje examined the reflection from the optical surfaces and the fundus and wondered about the entoptic origin of some percepts. During the rest of the 19th century, a firm understanding emerged of refractive errors and their optical basis, of procedures for their measurement and

of the technology of their correction. In this connection and in that of the eye's accommodative changes, the aim and end-point of measurement is the sharpest retinal image and maximum visual acuity. However, knowledge of the actual retinal image remained elusive. Only occasionally was it suggested that there might be a purely optical reason for a perceptual dissonance, e.g., that a dark square looks smaller than a bright one of equal size (Fig. 1).

Limitations in what the eye transmits to subsequent processing stages are predicated in part by the laws of physics that govern the propagation and imaging of light, and in part by the precision to which any biological structure can optimize performance within these physical limits. In vision research, this leads to the question of how accurately the optical image on the retina reconstructs the outside world.

It is convenient to make the distinction between geometrical optics, in which light propagation is described by rays obeying the rule of shortest path, and physical optics, where the subject is treated as a component of the more general study of electromagnetic waves and, more recently, of quantum phenomena.

Geometrical optics had been given a firm foundation by Gauss (1843). When its basic formula, Snell's law $n \sin I = n' \sin I'$ is expanded only to its first term, $nI = n'I'$, we have first-order geometrical optics, which is quite adequate for studying the relationship between the position and size of objects and their retinal images, and for straightforward descriptions of the eye's

Fig. 1. The white square on a dark background is exactly as large as the dark one on a white background. That the white one appears larger—an effect called irradiation—has been ascribed to light spread on the retina.

refraction and accommodation. In more demanding applications, e.g., when designing astronomical telescopes, microscopes and field glasses, geometrical optics needs to be extended to higher orders of expansion of the angles in Snell's law. In pursuing this program, Seidel (1856) was able to characterize image defects such as spherical aberration, coma, astigmatism of oblique incidence, distortion and curvature of field by collecting the third-order terms into five sums. When advances in technology, particularly the availability of glass in a range of refractive indices and dispersive powers, allowed the design and construction of sophisticated optical instruments, this benefited the measurements of biological constants of eyes which reached an excellent degree of accomplishment quite early (Abderhalden, 1920; Czapski and Eppenstein, 1924).

Physical optics had by the end of the 19th century progressed to a high level by Maxwell's completion of the electro-magnetic theory. The equations and knowledge of the parameters of wavelength and dielectric constants had made it possible to calculate the field strength in many situations, such as in the image plane of an instrument with a specific shape of aperture. Thus, all the principles of geometrical and physical optics that play a role in the generation of the retinal image in the eye were in place when the era under consideration opened. But, as will be seen, many subtle points that had been only implicit in the earlier formulations were made explicit and permitted the expression of the fundamental tenets of optics in forms that were both more elegant and better suited to technological advances. This review covers the salient trends in the development of the current knowledge of that part of the visual path that starts with targets in the outside world and that encompasses the stages culminating in photon interaction with a molecule of visual pigment in a retinal receptor. The significant advances now underway with wavefront measurement and modulation are only sketched in and remain subject for overview at a later time.

2. Defining the retinal image by first-order optics

2.1. Gaussian optics

The first approach to the representation of the outside world on the retina is the inquiry of how the eye's optical apparatus generates an optical image on the retina. After Gauss (1843) had set out the general theory for paraxial rays in coaxial optical systems consisting of several spherical surfaces, his student Listing applied it to the eye, using data on relative positions and radii of curvature of the surfaces and on refractive indices that were then available. It was one of the first uses of what is now called Gaussian optics, an elegant theory relating

points and lines in the object space to conjugate ones in the image space (Fig. 2). It allowed Listing to calculate and emphasize the importance of the *cardinal points*. These are:

The *first focal point*, from which rays have to originate to emerge parallel into the final image space.

The *second focal point*, to which parallel entering rays converge in the final image space.

The *first and second principal points* are conjugate planes of unit magnification in the object and image spaces of the whole system. That is, they are the particular pair of conjugate planes with the property that an incoming ray striking the first at a certain distance from the axis has its conjugate emerging ray emerge into the image space from the same distance.

The *first and second nodal points*, first identified by Listing, which are conjugate points on the axis in the object and image planes, of unit angular magnification.

Using this theory, Listing (1853) constructed a *schematic eye*, i.e., he assembled the cornea and the crystalline lens into an optical system, in which all surfaces were assumed spherical and had their centers of curvature on one line (Fig. 3). Once a serviceable model of the eye as a Gaussian optical device was in place, it proved adequate in the many practical situations encountered in ophthalmology, optometry and physiolo-

Fig. 2. Schematic of Gaussian optics. The tenets of the Gaussian theory of imagery for paraxial rays in a system of coaxial surfaces, with radii of curvature $r_1, r_2, \dots, r_l$, separated by distances $d_1, d_2, \dots, d_{l-1}$, where the media have refractive index $n_0, n_1, \dots, n_l$. Light travels from left to right; for each surface, its object space is to the left and image space to the right. Every line and point in the object space of the first surface has its conjugate in the image space of the last surface. In particular, the first focal point, F_1 is conjugate to infinity in the ultimate image space, and object-sided infinity (a parallel bundle of rays) is conjugate to the second focal point, F_2 .

Of particular interest are the principal planes, H_1 and H_2 . They are planes of unit magnification and represent the locations in the original object and ultimate image spaces, respectively, in which a hypothetical single surface would substitute for the whole optical system. Once the positions of the principal and focal points of the compound system have been calculated, all object-image calculations for the whole system can be performed as if this surface is placed in H_1 for the incoming light and in H_2 for the light emerging into the ultimate image space.

Fig. 3. Schematic and reduced eyes. The schematic eye (upper) assembled by Listing (1853) using then current values for the radii of curvature of the anterior surface of the cornea (r_1) and the anterior and posterior surfaces of the lens (r_2 and r_3). The refractive indexes of the aqueous and vitreous humors (n_1) were given the accepted value for water, and that of the lens (n_2) a value that was needed to provide the refractive power of the lens, given its shape and position within the eye. When Listing calculated the position of the principal points H_1 and H_2 , he found that they were only 0.3 mm apart. Having them coalesce enabled him to construct a *reduced eye* (middle) in which a single surface of radius 5.8 mm separating air (n_0) from water (n_1) would substitute for all optical components of the eye. It particularly clarifies the meaning of the single nodal point, now the center of curvature: any object-sided ray directed to it travels without deviation to the retina and permits quick evaluation of image position and size. Subsequently, Gullstrand (1909) constructed an "exact" schematic eye (lower) in which the cornea (refractive index n_1) has two surfaces and the lens consists of a cortex and a core.

ogy in which a first-order approximation suffices. These comprise the understanding of refractive errors, including astigmatism, the size of the image formed on the retina, blur caused by defocus, and the effect of changes in wavelength of light. Knowledge of the schematic eye also helped in the design of many ingenious clinical instruments that have been, and continue to be, invented for visualizing and measuring the optical components of the eye. The changes associated with accommodation were another area of concern in which a schematic eye led to newer methods of measuring the position and shape of the crystalline lens and of the refraction of the whole eye. Finally, the knowledge of the eye's optics could be utilized for research in understanding the anatomy and physiology of the inner eye and the apparatus for controlling the pupil and maintaining intra-ocular pressure.

A schematic eye has the virtue that the computation of the parameters of the whole system needs to be performed only once. Thereafter the laborious process of tracing the passage of light bundles through the surfaces one at a time for each situation can be short-circuited. Calculation of focusing and imaging for any

target can be carried out as if there is only one component. The bundle of rays from the object is traced to the first principal plane, and emerges into the image space from the second principal plane. When Listing had assembled his schematic model of the human eye's optical system, he found that, remarkably, the principal planes almost coincided. By making the further approximation of eliminating the 0.3 mm separation between them, he introduced his *reduced eye* (Fig. 3, middle). In this stripped-down model of optical imaging in the human eye, there is only a single (fictitious) surface separating the medium of the object space (air) from that of the image space (the vitreous). A further simplification is introduced by the fact that the position of the eye's nodal point, the reference for angular measures of objects and images, remains essential fixed at 7 mm behind the corneal surface, only marginally affected by differences in refractive state and accommodation.

Out of this approach arose a useful and now universally employed stratagem: the description of retinal image features not in terms of their actual physical size in, say, microns, but in terms of the angle that a target had to subtend at the eye for its image to cover the structure, expressed in, say, radians or degrees or minutes of arc. For example, the size of the fovea would now be given as $\sim 1^\circ$ of visual angle rather than 0.3 mm along the retina.

A succession of scientists, notably Helmholtz, Gullstrand and Tscherning, elaborated and refined Listing's model using more up-to-date values of the optical parameters. The posterior corneal surface, which Listing had left out, was now included. Listing understood the difficulty posed by the fact that the crystalline lens's refractive index is not uniform and presciently wrote about a curvilinear path of light through such a medium. The newer approaches lumped the whole of the refractive index gradient system either into a single homogeneous mass with just one value or into a compound of core and cortex, each with its own refractive index. It was only much later that good analytical approaches to this problem were developed (Campbell, 1984). Suffice it to say that by 1900 a very adequate scheme was in place that enabled the position and size of the retinal image to be computed within Gaussian terms.

Texts and handbooks of the period contain detailed theoretical presentation of schematic eyes (Rivers, 1900; Helmholtz, 1909; Tscherning, 1904) a trend that extended into the next generation of books (Southall, 1933; Duke-Elder, 1932; Emsley, 1939).

The topic of schematic and reduced eyes continues to allow fine-tuning as better values of the optical parameters of eyes emerge. Most writers were content with Gullstrand's model, given wide currency through its inclusion in the third edition of Helmholtz's treatise

and its English translation. Numerical simplification was achieved by Emsley when he gave the reduced eye a power of 60 D and the refractive index of 4/3 and, hence, a virtual single surface of 5.55 mm radius of curvature. These values were amended by Bennett and Rabbetts (1989) to a refractive index of 1.336 and radius of 5.63. A much more complex schematic eye, with a gradient refractive index crystalline lens and an aspherical cornea was proposed by Pomerantzeff et al. (1984).

2.2. Pupil

The limitations on the width of the entering light beam are important in an optical system because they have an impact on the intensity of light reaching the image plane and on the sharpness of the image. In the eye, the pupil, i.e., the aperture of the iris, is the responsible structure. For practical purposes, one uses the entrance pupil, which is the image of the real pupil as seen through the cornea. Fortunately, it is located very close to the real pupil and only a few percent larger. Calculations of geometrical image size and shape, regardless of the state of focus, use as reference the “chief ray”, i.e., the ray from the object point to the center of the entrance pupil. It identifies in the retinal plane the image of a point object, or, if the eye is out of focus, the center of the corresponding blur patch (Fig. 4).

From purely geometrical considerations, the quantity of light from any object reaching the retina is proportional to the area of the pupil. To ensure that this is factored in explicitly when specifying light intensity,

Fig. 4. Although the width of the beam of light entering the eye is actually limited by the pupil, an outside observer sees the “entrance pupil”, i.e., the image of the real pupil formed by the cornea. The beam entering the vitreous appears to originate from the exit pupil, the image-sided conjugate. The ray from a point object to the center of the entrance pupil, termed “chief ray”, gains its importance from the fact that its image-sided conjugate intercepts the retina in the center of the blur patch if there is defocus. Hence, it defines retinal image location, regardless whether the eye is in focus or not. In a typical schematic eye, the entrance pupil lies 3.2 mm behind the corneal apex and the angular magnification of object- to image-sided chief rays is 0.82. Thus, an incoming ray that makes an angle θ with the optic axis at the center of the entrance pupil emerges into the image space from the center of the exit pupil at an angle 0.82θ .

Troland (1917) proposed a new unit, to which his name is now attached. A troland is the retinal illuminance which results when a surface of luminance 1 cd m^{-2} is viewed with an entrance pupil of 1 mm^2 . It was fortunate that the Optical Society of America took on the task of defining and standardizing units of light and luminance (Optical Society of America, 1953).

2.3. Axes and angles between them

It was recognized quite early that, although in most eyes the centers of curvature of the major refracting surfaces lie on a single line, the eye’s optical axis, this line passes neither through the fovea nor the center of the pupil (Fig. 5). The fovea is usually situated 1–2 mm temporalward from the intersection of the optic axis with the retina. Thus, in connection with the schematic eye, several other lines or axes were defined and names given to the angles between them. Gaussian theory deals with rays close to the optical axis. If this does not apply to foveal vision, questions of aberrations due to oblique incidence, which of course always arise for images on the peripheral retina, would have to be confronted at the outset. However, the angle involved is small enough, typically about 5° , that this question can be neglected. The problem has, however, clinical implications, in the measurement of the angle of strabismus and eccentric fixation. At various times angles were described, and given greek-letter names, involving a variety of lines: optic axis (line joining center of curvature); pupillary axis (line joining center of pupil and center of curvature of anterior corneal surface); primary line of sight (joining fixation point and center of entrance pupil); visual axis (line joining fixation point and nodal point). The confusion of nomenclature, which had beset the problem for decades, had abated by the time the pre World War II (WWII) standard textbooks of ophthalmology (Duke-Elder, 1932) and optometry (Emsley’s first edition, 1936) had appeared and there is now no disagreement on definitions (Schapero et al., 1960; Carpenter, 1977).

Fig. 5. In a typical eye, the fovea does not lie on the optical axis of the eye, but a little temporalward. The chief ray to the fovea (which in the object space passes through the center of the pupil) typically makes an angle of 5° with the pupillary axis, i.e., the line normal to the cornea and also passing through the center of the pupil. There is a simple operational procedure for measuring the angle in a given eye. Other axes and the angles between them have been defined, but they cannot be identified operationally in a given eye. The diagram shows the top view of the right eye.

2.4. Chromatic aberration

The retinal image is formed by bundles of rays passing through the vitreous, whose refractive properties are essentially those of water. One consequence is that the focal length will differ with the wavelength of light (Fig. 6 top, upper panel). This chromatic difference in focus can still be described in terms of first-order optics once the eye's refracting power for different wavelengths is known. Measurement of chromatic aberration, performed over the period, including those by Ames and Proctor (1921), Wald and Griffin (1947), Bedford and Wyszecki (1957) and Howarth and Bradley (1986), confirmed and refined the consensus, existing since Fraunhofer's days, that a reduced eye consisting of water adequately describes the focus differences across the visible spectrum (Fig. 6, middle).

Chromatic aberration, besides causing a defocus, can also introduce a position shift. When light rays from a target point that does not lie on the eye's optical axis are refracted, the angle their path takes in the image space depends on the effective refractive index and hence on the wavelength. Red and blue rays originating from the

same object will, therefore, impinge on the retina in different locations (Fig. 6 top, lower panel), i.e., there is a chromatic difference in magnification. The curious phenomenon of *chromostereopsis* has its origin in this effect (Fig. 6, bottom). When there is a mirror-symmetrical displacement of the pupil in the two eyes, the displacement of red and blue rays from the same target will be in opposite directions in the two eyes. This occurs in a typical eye because the principal line of sight intersects the retina somewhat temporal to the optic axis, more so for red rays than blue. Hence, a red object is imaged with a crossed disparity relative to a blue originating in the same object plane and will appear nearer. The effect is distinct from chromatic difference in focus, the principal line of sight defining object retinal location for all states of focus.

2.5. The moving eye

In normal situations, the eye in the orbit moves, to a high degree of approximation, as if it were a ball and socket joint, i.e., a single point in the eye remains stationary in the orbit. This center of rotation is located near the center of curvature of the globe, about 12 mm behind the corneal apex. If the center of the entrance pupil coincided with the center of rotation, there would never be a dissonance between the retinal location of an eccentric target and the angle through which the eye would have to rotate to bring the eccentric target onto the fovea. Because the center of the entrance pupil is about 10 mm forward of the center of rotation, the eye rotation associated with bringing a target imaged in a given eccentric retinal location to the fovea depends on the target distance (Fig. 7). Hence, retinal local signs cannot be rigidly tied to eye rotations, as has been postulated by, e.g., Wundt.

3. Describing the actual retinal image

3.1. Indirect estimates

Specifying the parameters of the retinal image from principles of first-order geometrical optics, important as it is in enabling comparison with the measured size of retinal structures, is, however, only a beginning step. Any real retinal image differs from this schematic one in several ways. In some simple cases, they can still be encompassed by first-order geometrical optics. For example, the diffusion of light caused by defocus, the so-called blur circles, depends on the pupil size and when there is regular astigmatism the shape of the blur patch—ellipses, lines, a circular disk—depends on where the retina intercepts the image beam.

But as soon as one leaves the confines of first-order object-image calculations, in which the human eye is

Fig. 6. Chromatic aberration. (Top) The nature of the focusing errors and image position differences for light from the blue and red ends of the spectrum are shown in the upper and lower panels, respectively. (Middle) The refractive power of the eye varies with wavelength of light, essentially as if the eye were composed of water. Average axial chromatic aberration of 12 eyes. Data from Bedford and Wyszecki (1957). (Bottom) Chromostereopsis. A target P, not on the optic axis of either eye, emitting red and blue rays, has its retinal image dispersed in the manner shown, because the eye's refractive index is higher for blue than red. Compared to the location of the actual target, the blue rays will be imaged with uncrossed disparity and hence appear to be originate at P', relatively behind those in the red end of the spectrum, which appear to originate at P''.

Fig. 7. Relationship between retinal location of a peripheral target (A) and the eye rotation needed to image it on the fovea (F'). (Left) Eye initially is directed to a fixation point F at infinity, which is imaged on the fovea (F'). A target A, also at infinity, is imaged in retinal location A', which is defined in the eye's object space by the angle FEA at the center of the entrance pupil. To bring the image of A to the fovea, the eye has to rotate through the angle FCA at the eye's center of rotation, located about 10 mm behind E. When F and A are at infinity, angles FEA and FCA are equal. (Right) The same situation except that both F and A are close to the eye. Angles FEA and FCA are now no longer equal.

analyzed by paraxial rays passing through a series of spherical refracting surfaces with a single optical axis, major difficulties are encountered. Following Seidel's (1856) thinking one can start computing the aberrations under his several rubrics, e.g., spherical aberration, coma, curvature of field, etc., and deduce their influence on the quality of the retinal image. But sensible limits must be placed on this course. For example, off-axis calculations of aberrations need to take account of the fact that in the periphery the retina is a curved, not a plane, surface and the anatomical grain is coarser there. On the other hand, for central vision, spherical aberration would be more relevant. Many of the earlier treatises feature elaborate drawing of the caustics, that is patterns of envelopes of light rays entering through different pupil zones. But once it is understood that the eye's optical surfaces are not spherical, and that their exact shape differs from eye to eye, it is realized that such approaches, though instructive to visualize as examples, lack generality.

From the days of Fraunhofer, the wave interpretation of light allowed the calculation of the diffraction that make actual images of a point source differ from the point image postulated by first-order geometrical optics. Wavelength and aperture diameters are the parameters. The exact shape of the image distribution depends on the shape of the aperture, and its width varies directly with wavelength and reciprocally with aperture. The eye is usually taken to have a round pupil a few millimeters in diameter, and the wavelength used in the calculation is the one with the highest luminous efficiency, 555 nm. The diffraction pattern, called Airy disk, then has the shape shown in Fig. 8 and width at half-height (WHH) of the order of 1 arcmin, about the distance between foveal cones, thus giving a satisfactory understanding of visual acuity.

The universal presence of diffraction and chromatic and spherical aberrations leads to an inevitable spreading of light in the retinal image of a sharp object, such as a white-black border. Diagrams that sketched such a gradual fall-off of light in the image of a sharp edge were shown in textbooks from Helmholtz's time (Fig. 9, left). Explaining to his 1895 readers how such a distribution might arise, Lehmann (1895) revealed a good understanding of what nowadays is called convolution. His apparently complex diagram (Fig. 9, right) is meant to illustrate that the final edge-image distribution OGMF is made up of the sum of the assumed point-spread function (drawn as ORPK for the ray at point AE) for all points in the object distribution OAEF. It is notable that in these, as in all similar examples of the time, the axis of abscissae, referring to distance along the retina, lacked a specific scale. Two approaches were followed to remedy this deficiency.

The first involved calculations based on diffraction and chromatic aberration, both requiring prior specifi-

Fig. 8. Airy disk, the image of a point source as spread out by diffraction for an optical system like the eyes with a round pupil. The width is normalized. The scale factor is directly proportional to the wavelength of light and inversely proportional to the pupil diameter. In an eye with a 3 mm diameter pupil and light of 555 nm wavelength, the distance between the first zeroes on either side of the central peak is about 1.5 arcmin.

Fig. 9. (Left) Realizing that chromatic aberration (Fig. 6), spherical aberration and diffraction (Fig. 8) cause inevitably image smearing, Helmholtz drew this diagram to depict what he thought would be the retinal image distribution of a sharp edge (ABC). While it is common to draw such figures with normalized ordinate values, showing proportionate rather than absolute light intensity, note however the absence of a scale along the abscissa representing distance along the retina. (Right) An early attempt by Lehmann (1895) to explain the concept of convoluting the eye's point-spread function with the object distribution: the spread functions ORPK for each point in the object distribution OAEF add up to yield the retinal image OGMF of an edge.

cation of pupil size and the wavelength of light. At this stage, and when the pupil is kept small, the higher aberrations could be neglected. Hartridge (1918), with this kind of background information, made an estimate of a line-spread function, and for the first time drew a figure for the distribution of light at a black-to-white edge that showed an explicit scale of retinal distance and hence could be used for comparison with cone diameters and visual acuity (Fig. 10). This kind of analysis allowed Shlaer (1937) to calculate the modulation of the retinal image of a 50 cycles/degree square-wave grating, arriving at an estimate of a Michelson contrast of 0.21. Because such a grating could just be resolved, Shlaer was able to draw conclusion about the limits of the retinal detection apparatus for intensity discrimination of adjoining peaks and troughs. Shlaer had,

Fig. 10. Hartridge (1918, 1922) was the first to estimate the light distribution in the retinal image of a sharp black/white edge, which was known to have a sigmoidal shape, with a scale along the axis of abscissae that enabled the comparison with retinal structures. In this figure, based on Hartridge's data, the width of a foveal cone would be 0.39 arcmin.

therefore, achieved precisely what is being sought by the conceptual decoupling of optical image from later neural processing: prior knowledge of optical factors provides the critical description of the proximal stimulus that is needed to probe the neural function of the retina. A little later, in a thorough examination of the situation at that stage of knowledge, Byram (1944b) drew the Airy disk for 2.4 mm pupil as representing the, to him, confirmed retinal point-spread function.

The approach followed by, e.g., Hartridge and Shlaer, that of trying to dissociate optical from retinal processing of spatial visual stimuli, must be contrasted with that of the many other contemporary researchers who followed Plateau's lead in arriving at their estimates of the actual retinal light spread. Plateau had noted in the 1830s that brighter stars looked larger and he initiated the strategy of using psychophysical measurements for the purpose of gauging the spread of light by the eye. Irradiation is the word used for the phenomenon, best illustrated by the fact that when viewing two patches of equal size but opposite contrast polarity, the brighter one looks larger (Fig. 1). The cause was thought to lie in the fact that light invaded the darker areas. To measure this, an experiment was performed which in modern terminology would be called a vernier task with edges of opposite contrast polarity (Fig. 11). The null position, when such edges appear aligned, shows that an observer assigns edge location somewhere beyond the inflection point of the actual light distribution. Distances involved were of the order of a minute of arc or two. However, already Plateau had noticed that this effect increased with light level, whereas light spread was always accepted to be a passive process. Moreover, to the adherent of Hering's teaching—that the sensation of

Fig. 11. Plateau's arrangement to measure irradiation by finding positions in which edges of opposite contrast polarity appear aligned (from Hofman, 1920). Such measurements of apparent spread conflate optical and neural factors that are involved in the assignment of border location.

blackness was just as much an active process as that of brightness—it was not obvious why the apparent shift should be toward the darker side.

The discussion on irradiation continued on for many decades. However, Helmholtz had already quite early on expressed his reservation about the need to separate out neural processing when determining the mean location of a sharp bright-to-dark edge as a tool for estimating optical image spread, but his warnings were not widely heeded. One author who was able to make this distinction was Tschermak (1903), who, in one diagram (Fig. 12), showed a thoroughly modern view of the relationship between physical object, retinal light spread, spatial distribution of retinal excitation, spatial neural interaction and ultimately percept. Careful study of the diagram for an extended object reveals a place even for Mach bands in the scheme.

Fry and Cobb (1935) used a more complex approach to estimate light spread by means of psychophysics. They posited at the outset that the line-spread function has a Gaussian shape, and conjectured that it had standard deviation of $44''$. From this they derived by calculation the distribution for bars of various widths (Fig. 13, upper) and found that they reached their maximum height with bars width of about 4 arcmin. They then plotted foveal increment thresholds for such bars. Threshold dropped in a manner that almost exactly parallels the reciprocal of the maximum height of the bar-spread functions (Fig. 13, lower). Because they had assumed that increment thresholds for long bars depend entirely on the light intensity of the center of their retinal light distribution, they felt they had validated their estimate of the line-spread function being Gaussian with $44''$ standard deviation. This value is,

Fig. 12. Tschermak's (1903) schematic diagrams depicted optical, receptor, retinal and higher neural stages in the processing of a single bright spot of light (upper) and a wider bar (lower). Tschermak, well in advance of his time, distinguished between the physical stimulus, the light spread on the retinal surface, the excitation pattern in an array of receptors, lateral interaction between adjoining zones and the emergence of a spatial perceptual pattern which includes Mach bands.

however, wider by a factor of about 2 than later estimates. The discrepancy has its origin in the fact that the psychophysical procedure folds in unknown factors of retinal summation; thresholds depend not just on the peak but on the total light within a summation zone. Although it had unknown components of retinal summation and the recently discovered eye tremor (Adler and Fliegelman, 1934), the $44''$ Gaussian shape was widely accepted as a measure of image spread and integrated into sophisticated theories of visual acuity (Marshall and Talbot, 1942; Bartley, 1941).

On the other hand, in the work emanating from Hecht's biophysics laboratory at Columbia University

Fig. 13. Fry and Cobb's (1935) concept and experiment. It was postulated at the outset that the line-spread function had a Gaussian profile with standard deviation 44". Convolution with target bars of increasing widths would then yield the retinal light distributions illustrated on the upper panel. Increment detection threshold for such targets (lower) decreased precisely as would be predicted if the threshold depended only on the central height of the distributions. Because the procedure conflates optical and retinal factors, the estimate of light spread was too large by a factor of about two.

before WWII it was fully accepted and clearly articulated that in the stream of visual processing, optical light spread has to be treated separately from and prior to the photochemical stages with which that laboratory had been predominantly identified. In two studies, in particular, the optical image played a significant role in the argument. As mentioned above, Shlaer (1937) in an exemplary way attempted to tease out the extent to which optical light spread, receptor spacing and light difference detection were limiting factors in visual acuity, using Hartridge's estimates of the optical spread.

A little later, Hecht and Mintz (1939) used light-spread calculations in a pivotal paper on the detection of extremely thin lines. A very thin dark line seen against a uniform bright background produces a retinal light distribution that is a shallow dimple with the shape of an inverted line-spread function. When the line width is much less than the width of the line-spread function, the shape of the image distribution remains essential unchanged with increasing width, but the depth of the dimple increases. By this means they demonstrated that there was nothing mysterious about the normal observer's ability to detect the presence of a dark line when it subtends even less than an arcsec at the eye. The width threshold, although measured by the angle subtended at the eye, is really converted into a decrement threshold for a retinal light distribution of fixed shape but increasing modulation (Fig. 14). Hecht and Mintz, in line with the results emanating from Grahams' laboratory (Graham et al., 1939), recognized that the physical variable responsible for the detection threshold is not the height in the middle, but the light deficit integrated over the retinal summation zone, which extends for several minutes of arc in the fovea. The conceptual separation of optical spread and retinal summation in analyzing visual processing became paradigmatic for future research in this area.

Besides the neural factors that had often not been disambiguated from optical spread, there are other discrepancies between what was calculated and what

Fig. 14. Hecht and Mintz (1939) estimated that the light spread in the retinal image of very thin lines were dimples of identical shape but depth increasing with line width. The figure depicts the calculated retinal image spread, based on the optics of a diffraction-limited eye with a 3 mm pupil. On the top of the figure, distances are marked out in measures of cone diameters in the fovea. Ordinates represent normalized retinal illuminance. The widths of the line objects, scaled appropriately, are shown as horizontal lines. Hecht and Mintz regarded the integrated light deficit over the retinal summation zone as the physical aspect of the stimulus that determined the visual thresholds.

observers reported they saw when shown a star or other point source. Many are usefully included under the general rubric of entoptic phenomena, i.e., distortions of imagery that originate from structures within the eye, such as the lamellae of the crystalline lens. At one time there was great preoccupation with the changes in appearance of targets caused by entoptic phenomena, e.g., stria and spokes in star images, and it was properly directed to their intra-ocular source. The topic was important in astronomy and was relegated to vision when photography had become the gold standard in astronomy and it had become possible to separate, e.g., the actual shape of comets or the canals on Mars from entoptic phenomena caused by the ocular media when they are viewed by the human eye.

3.2. Post-WWII

Although the fundamentals of optical imaging—geometrical optics, the chromatic and monochromatic aberrations, diffraction—needed little extension as the 20th century progressed, a change in point of view occurred. It was predicated on a set of attitudes and technological developments that took form during WWII and that began to permeate science in the immediate post-war period. Concepts involving information theory, the systems' approach and cybernetics gripped the scientific community. In optics, the most influential was a slim paperback, in French, “L'intégral Fourier et ses applications à l'optique”, which heralded a radical turn in the approach taken to optical systems and imagery (Duffieux, 1946). And on the practical side, light sources and photocells became available that permitted, for the first time, an experimental approach to the image formed by the eye.

The importance of Duffieux's monograph lay not so much in any fundamental novelty as in the clarity of exposition. Abbe, who developed the theory of microscopic imagery in the 1870s (see Abbe, 1910), had written about spectra formed when transilluminated grating objects are viewed through objectives. If Rayleigh (1896) had been asked in the 1890s whether diffraction equations could not be seen as Fourier transforms, he would have said “Of course!” and pointed to several sentences in his 1896 paper on the image-forming properties of microscopes where he wrote about expansion in Fourier series. So did Born (1933) when reviewing Abbe's theory.

Duffieux's treatment had the virtue that he hammered in the notions (a) that optical imaging is linear, (b) that Fourier decomposition gives a complete description, (c) that sinusoidal objects were always imaged as sinusoids, albeit with possible changes in modulation and phase, and (d) that the cumbersome procedure of convolution which, as we have seen, is essential in dealing with retinal imagery, becomes the much simpler one of

multiplication when performed in the Fourier domain. When lasers came on the scene to provide a ready source of coherent light, all that was needed was to conduct these transactions in the realm of amplitudes of the electro-magnetic disturbances before transferring back to the intensity domain.

In coherent imagery, all beams, where they are superimposed, can interfere constructively and destructively and therefore the phase of the vibrations, which depends on path length, is of consequence in the summing process that determines the amplitude of the disturbance. In the ultimate interaction with matter, however, the relevant parameter is intensity, basically obtained by squaring the amplitude and discarding the phase. When the source is incandescent, interaction occurs separately for light from each element of the source; in the image plane there is summation of light intensity (phase having already been discarded) originating from each of the elements of the source.

A significant turn taken at that time was the replacement of the point- or line-spread functions, which up to that time had been the norm, with the sine-wave grating as the basis for investigating and describing image formation. The foundations for this change were solid:

- (a) The two formulations are formally equivalent and complete.
- (b) The transfer between them is easily accomplished by standard mathematical expressions and computer algorithms.
- (c) The Fourier domain is actually more appropriate in capturing the physical nature of the imaging process, viz., the wavefront in the pupil plane and the distribution of electro-magnetic disturbances in the image plane.

Moreover, the sinusoidal pattern had just become a universal basis for information transmission in the time domain, so engineers pioneering the electro-optical technology of television found it a natural language. Its conquest of visual science was inevitable.

Not that the use of a grating target to test the quality of optical images or the visual process was anything novel. Gratings had been used as test pattern for resolution since they were introduced in 1754 by Mayer (1754) and, by Duffieux's time, had already gained full recognition in the image evaluation sphere (e.g., Selwyn, 1954). Once their sinusoidal form was adapted as the basis of all imagery and it was understood that any object could be expressed in their terms, the preferred method of specifying the performance of optical systems became the contrast transfer function, which describes the demodulation and phase shift experienced by the sinusoids in the imaging process as a function of spatial frequency.

3.3. Direct measurements

The enormous advances in instrumentation that ushered in the electronic age soon transformed the study of the optical image formed by the eye. Although the actual image was not accessible in the human eye, measurements of an indirect kind could be carried out. A beginning was made in animal eyes. After peeling off the sclera, the ocular image of a bright light was scanned by a small photocell. Needless to say the spread observed was more extensive than might reasonably be expected in the intact human eye (DeMott, 1959, p. 578). In spite of some protestations ("How is it that, if the retinal image is so poor, we see so well?"), experiments in excised ox and sheep eyes could not really be accepted as paradigmatic for the normal human eye.

In a procedure that yielded much more acceptable results and proved to be a turning point in the development of the subject, Flamant (1955) imaged a bright slit on the retina and studied the light distribution in the ophthalmoscopic image that results from reflection at the fundus. Even though Flamant measured light intensity by a rather cumbersome photographic procedure, her data were surprisingly close to what later emerged as the consensus values. The crucial element of Flamant's study, however, was her pioneering application of the Fourier theory of optics, to which she had been exposed in her studies at the Institute d'Optique in Paris. The light from the slit target imaged on the retina and, after reflection, in turn imaged on the photographic plate, is subjected twice in succession to the spreading action of the eye's optics: the convolution of the slit with the eye's line-spread function (the retinal image) and the latter with itself on the return path (Fig. 15). A deconvolution is needed to extract the line-spread function for a single traverse of the eye's optics from the observed double convolution and this is easily performed in the Fourier domain, where convolution becomes multiplication. Thus, a full characterization of the image spread can be obtained by Fourier transformation of the external image distribution and, in order to undo the one of the two successive convolutions, extracting the square root. From the schema in Fig. 16 this is the eye's contrast transfer function and on reverse Fourier transformation will reveal the line-spread function.

Flamant's results, because they were obtained by a rather insensitive method involving photographic film and because they were so obviously different from the animal data of DeMott, needed confirmation with state-of-the-art photoelectronic measurements, and this was promptly supplied by Westheimer and Campbell (1962). Even more extensive and painstaking replication by Gubisch (1967) in Campbell's Cambridge laboratory achieved line-spread functions so narrow and so well

Fig. 15. Method introduced by Flamant (1955) for measurement of the line-spread function in the living human eye. A slit source, normal to the plane of the paper, is imaged on the retina. The distribution of light reflected from the fundus is measured in a plane conjugate to the retina. It has suffered image spread both in the incoming and reflected path. The single-path spread is calculated by deconvolution in the Fourier domain. Diagram from Westheimer and Campbell's (1962) implementation of the procedure by scanning with photomultiplier. (Right) Estimated line-spread function for three normal eyes under normal viewing conditions.

matched to parallel studies by the best procedures of interference-fringe psychophysical tests (Campbell and Green, 1967, see below) that they became for a long time

Fig. 16. Schema from Fourier optics, relating the pupil transmission function, the contrast transfer function and the electro-magnetic amplitude and intensity distributions in the image plane.

the accepted measure of focal light spread on the retina. The results showed clearly that in a normal eye, pupil diameter matters and that the 2.5–4 mm range, previously recognized as optimal, retains validity.

Subsequently, the Flamant procedure was subjected to more searching critical analysis because, after all, it is still an indirect approach to retinal imagery, depending as it does on reflection of light from the fundus. Theoretically, it was pointed out by Artal et al. (1995) that the double-pass process will not reveal possible asymmetries in the spread functions, such as would be generated by coma. Moreover, scatter within the retina (Gorrand, 1989) is decidedly a factor, degrading the quality of the reflected image and throwing further doubt on whether this kind of methodology will ever yield the ultimate experimental measurement of retinal image spread. In spite of these reservations, reflected light from the fundus of a living eye has been important in advancing knowledge about the photochemical process, about the presence and distribution of macular pigment, and has remained of overwhelming significance in the clinical examination of the eye.

3.4. Scatter

The sharpness of the central peak of the point-spread function and, equivalently, the high-frequency end of the contrast transfer function are the relevant desiderata for visual acuity and sharpness of edges. In the contrast transfer function, the cut-off spatial frequency is usually difficult to identify though there is always an absolute

limit defined by the prevalent pupil diameter and the wavelength of the light. The WHH of the spread function is a number somewhat easier to agree on. However, if there is pronounced scatter, the point-spread function will have a long tail. This proves to be a matter of considerable interest in connection with glare, and several attempts were made over the decades to define how far out the scatter from a single bright light source reaches. In the research into the scatter functions, psychophysical approaches had become acceptable, because, unlike in the irradiation controversy discussed above, the retinal distances are large and the light gradients shallow. The veiling glare produced by a bright source many degrees away can be simulated by large dim uniform fields with little danger of neural interaction entering the measurement. This “equivalent background” procedure (Holladay, 1927; Stiles and Crawford, 1937; Fry and Alpern, 1953; Vos, 1962) usually leads to an expression of the form

$$I = AE/\theta^n,$$

where I is the retinal illuminance at a distance θ from a glare source of illuminance E , A is a constant and the exponent n has a value, dependent on the study, of about 2. To give a numerical example, the “veiling glare” in the center of a 1° dark circle embedded in a large uniform field is of the order of 1%.

The quantity of light from a glare source that falls on a retinal region many degrees away is small, though it can act to reduce sensitivity. Yet when integrated over annular zones, quite substantial fractions of the total flux from the source are involved. While the point-spread function might sink to 1% of its maximum within a few minutes of arc, the annular zone beyond 2° can contain 10% or even more of the total flux from the source.

3.5. Strehl ratio

A concept of the Strehl ratio then gains significance. The gold standard of all optical instrumentation is the light distribution in the focal plane when diffraction is the only limitation. Under all other conditions, the spread will be wider and hence, in general, the height at its highest point less. The Strehl ratio is defined as the ratio of the maximum height in the point-spread function in any given condition compared to that in the purely diffraction-limited case. Using beginning results on the point-spread function in normal eyes in good focus with a 3–4 mm pupil (yielding optimum acuity) Gubisch (1967) calculated Strehl ratios of about 0.2, but when the light in outlying zones is taken into account, the values drop to near 0.1 and, in older eyes with a lot of scatter, as low as 0.02 (Westheimer and Liang, 1995). The possible influence of this on target detectability is obvious, but final conclusions cannot be

drawn from the Strehl ratio alone, because it merely points to the height of the central peak in the image of a point target, whereas detection involves areal summation properties of the subsequent neural stages. The retinal illuminance of extended sources is given by the integral under the point-spread function and hence is substantially unaffected by its shape in the middle.

3.6. Transmission by media

In addition to the lowering in the peak of the point-spread function caused by optical factors and expressed by the Strehl ratio, there is attenuation of light in its passage through the eye media by absorption. Exact measurements in the living human eye are difficult and depend very much on age, because the crystalline lens increasingly absorbs light of short wavelengths with age. The original data of Ludvig and McCarthy (1938), which suggested a transmission of only 50% at 550 nm, have over the years been revised upward (Alpern et al., 1965; Norren and Vos, 1974). Still, only about 50% of the incident light at 450 nm reaches the retina, rising to about 80% or better at 650 nm.

By the beginning of the 20th century it had been established that the yellow pigment, which gave the name *macula lutea* (yellow spot) to the structure, was not a post-mortem artifact (Polyak, 1941). The macular pigment has a strong absorption band between 400 and 510 nm, peaking near 460 nm. This was initially measured by comparing luminosity curves in the central and peripheral retinas (Wald, 1949), a method complicated by the deficiency of short-wavelength sensitive receptors in the fovea (Stiles, 1949) but there is a good match with the absorption spectrum of the carotenoid that can be extracted from the retina (Wald, 1945; Brown and Wald, 1963; Rudock, 1972). The widely quoted curve of Wyszecki and Stiles (1982) shows a peak absorbance of 70%, but this value includes a normalization factor; whereas Brown and Wald (1963) base their density estimate of 0.4 (absorption of 60%) on actual measurements in the human macula. Direct comparison between absorption by the involved pigments in their natural environment and the transmission defects estimated psychophysically have confirmed that pigment density is of this order (Bone et al., 1992; Davies and Morland, 2004).

There are wide individual variations in the spatial distribution of (Maxwell's (1856) spot, an entoptic phenomenon, often taken to be a visualization of macular pigment (Hering, 1893; Walls and Mathews, 1952), on the other hand, vehemently espoused the view that Maxwell's spot represents the receptor-type distribution pattern (RDP). The dispute between those who proposed that macular pigment accounts for Maxwell's spot and for the foveal short-wavelength luminosity curve deficit, and those who advanced the competing

theory of blue-receptor paucity, at various times involved all major figures in color vision in the first half of the 20th century, and illustrates the crucial role of a firm knowledge of the properties of the retinal image.

3.7. Polarization

With one exception, mammalian vision does not depend on the state of polarization of the incident light. The exception is an entoptic phenomenon known as Haidinger's brushes, where an observer sees, centered on the fixation point, an hour-glass pattern, especially in blue light, rotating with the plane of polarization of a piece of polaroid. The phenomenon has its origin in the dichroic properties of the pigment molecules (Bone and Landrum, 1984) impregnating nerve fibers that form a pattern radiating outward from the fovea (Misson, 1993).

3.8. Wavefront reconstruction

Technological advances have made available to visual optics the highly sophisticated technique of wavefront sensing (Liang et al., 1994). In the electro-magnetic theory, one works with the proposition that the basic descriptor of the action of an optical system is the way it changes the shape of a flat incoming wavefront, i.e., a parallel sheaf of rays. For example, in a perfect, i.e., purely diffraction-limited, system, a plane incoming wavefront is changed to a spherical one, centered on the second focal point. By means of diffraction theory one then calculates how the amplitudes of the disturbances emanating from each point on the spherical wavefront, integrated over the whole aperture, combine at each point in the image plane to produce the resultant disturbance at that point. Because at this stage one still remains in the domain of amplitudes, the phase of the arriving elements of disturbance matters. Seen from that point of view, defocus and aberrations are deviations of the wavefront from this focus-centered sphericity, and whenever the wavefront deviations are known exactly, the light distribution in the image can also be calculated exactly. Because, as we have seen, the diffraction equations are in effect Fourier transformation, the approach can lead, equivalently, to the contrast transfer function, which will, of course, in general be a complex function, including amplitude and phase terms.

Liang et al. were able to implement the Hartman–Shack methodology, in which the shape of the wavefront is sampled at discrete points in the pupil and the measurements are utilized to calculate the expected image spread in the plane of the retina. Good concordance was found with results obtained by the improved Flamant double-pass technique and also with the calculated image spread estimated by psychophysical

means (Liang and Williams, 1997). This approach has found an important role in the description of asymmetrical image distributions, opaque to the double-pass technique, and has been increasingly useful in a variety of clinical settings.

3.9. Retinal location

The deviations from sphericity of the entering wavefront and the resultant image defects including defocus are usually derived for the region of the retina in the vicinity of the intersection of the optical axis. Data are applicable to regions up to an eccentricity of 5–10° (Ferree and Rand, 1932; Jennings and Charman, 1981). Beyond that, the visual resolution has declined sufficiently to make optical defects less relevant.

4. Controlling the retinal image

4.1. Modifying the entering beam

With growing insight into theory and technology of image formation, the ability increased not only to describe the retinal image but also to control it. Once it was understood that at best the retinal image for an eye with a round pupil would be that given by Airy's disk, and that for small pupils aberrations are negligible, it became popular to use artificial pupils. Often the diameter was chosen to be 2.33 mm, because then the point image would match the foveal retinal mosaic. If, in addition, monochromatic light was used, the resulting retinal light distribution, at least in the vicinity of the focal image, is known to a good approximation and could be factored in where assurance was needed that a visual finding or phenomenon should be assigned to neural stages and not to passive optical image spread.

Chromatic aberration, however, then still remains an issue. It had been measured over the years and always constituted a barrier to sharp images for light with wide representation in the wavelength spectrum. One solution to this problem was the design of achromatizing lenses, which have no refractive power themselves, but neutralize the eye's chromatic aberration (Bedford and Wyszecki, 1957; Howarth and Bradley, 1986). They were on occasion utilized in color vision and other experiments, but did not eliminate the chromatic difference in magnification, which could still generate colored fringes at edges.

The role played by the external and internal oculomotor apparatus has to be recognized. Because the retina is not uniform across its surface, the rotational stance of the eye matters. With normal observers it usually suffices to provide a fixation point and give the instruction to keep looking at it. That this produces, by and large, the desired relation between the

target and retinal structures is attested to by its widespread utilization in the clinical testing of visual field defects. However, precise stability of the order of the dimension of individual receptors is difficult to attain because of small involuntary eye movements (Adler and Fliegelman, 1934; Riggs et al., 1954). For a while, this was regarded as affecting some visual functions and indeed, when the microneystagmus is abolished by clever optical arrangements, vision fades (Yarbus, 1967). On the other hand, there was an opposing view in which these small movements were assigned a special role in resolution by transferring the task from the space into the time and space domains (Marshall and Talbot, 1942). This proposition is thrown in doubt by the finding that low-velocity target movements across the retina are not detrimental to resolution or even stereoacuity (Westheimer and McKee, 1978).

Instability of focus can also affect the retinal image. As soon as the retina is no longer conjugate to the target, the point-spread function widens and the modulation transfer function suffers, in direct proportion to the diameter of the pupil. Just instructing an observer to keep the target in focus does not usually suffice, because there are often a steady-state accommodative error (Morgan, 1944) as well as microfluctuations of accommodation (Campbell et al., 1959; Arnulf and Dupuy, 1960). For these reasons, pharmacologically induced cycloplegia is occasionally resorted to in some experiments. It is usually accompanied by mydriasis, thus eliminating any unwanted effects of the intraocular musculature. The optics of eyes with paralyzed ciliary muscles and fully dilated pupils, may, of course, differ considerably from those in their normal state.

4.2. Maxwellian view

The pupil also acts to change the total light flux entering the eye. To duplicate retinal illuminance from experiment to experiment, artificial pupils were widely employed, ensuring both constant light flux and defined retinal image quality (Riggs, 1965). To counteract the resultant decrease in available light, a trick was employed, first invented by Maxwell, who used a lens to image the exit slit of a spectroscope in the pupil. The observer then sees the lens filled with monochromatic light of high intensity. When this procedure, now called the Maxwellian view, is translated to vision research there is, however, an unintended consequence. As seen in Fig. 17, a single light beam now fulfills a dual role. One is to image the small, high intensity source in the pupil, and the other is to image a defined target on the retina. The procedure is equivalent to the microscopy of translucent targets, needing the special consideration given to this in Abbe's theory (Rayleigh, 1896; Abbe, 1910). The Maxwellian view was given a detailed theoretical treatment by Westheimer (1966).

Fig. 17. Principles of Maxwellian view. A small bright light source is situated at the first focal point of lens L_1 and is then imaged by lens L_2 in the plane of the eye's pupil. A target T is placed in the beam so as to be imaged sharply on the retina by lens L_2 and the eye's optics. The process involves the generation of a diffraction pattern in the plane of the pupil. For full fidelity imagery, all parts of this diffraction pattern, even those containing little energy, need to be transmitted into the eye. The smaller T , the more spatially distributed the diffraction pattern, exceeding the geometrical image on S in P . Hence, in principle, even in Maxwellian view, pupil diameter remains a factor in the quality of the retinal image.

The essentials of the procedures are illustrated in Fig. 17. A point source of monochromatic light is imaged in the pupil, and the target is placed in the beam so that it is conjugate to the retina. The target is now limiting the beam and will produce a diffraction image in the plane of the pupil. From the theory developed in Section 2, the retinal image will be synthesized from a wavefront in the pupil plane that has the amplitude and phase of the electro-magnetic disturbance arising from diffraction due to this aperture. If the target is a circular aperture, its diffraction image is an Airy's disk with diameter proportional to the wavelength and inversely proportional to the aperture diameter and thus may extend well beyond the confines of the eye's pupil. An artificial pupil when using Maxwellian viewing is thus not an immaterial issue.

Shlaer (1937) realized that when the target is a square-wave grating, the diffraction pattern in the plane of the pupil will have the form of its spatial-frequency spectrum, with discrete beams for each spatial frequency entering the pupil in different locations. When converged by the eye's optic on the retina, they will combine, but only to the extent that the higher-order spatial frequencies are in fact admitted into the eye. Specifically, when only the first-order beam makes it into the eye, the retinal image will be a sinusoid. Shlaer applied what was later called spatial frequency filtering to produces a sinusoidal grating image on the retina.

4.3. Interference fringes

A more straightforward procedure for the same purpose is to physically limit the beam entering the pupil in the manner of the Young's double-slit interference-fringe experiment. Although Byram (1944a) described such an experiment, it is doubtful,

from what he writes, that he had actually succeeded in implementing it, because 0.1 mm slits in front of the pupil would give an extremely low retinal illuminance and the result he claims (resolution limit of 150 cycles/degree) is many times finer than seen by anyone else. On the other hand, Le Grand (1935) who pioneered this approach, found no difference in the acuity between ordinary fringes and interference fringes.

In the first modern experiment of this kind informed by the post-war emphasis on Fourier decomposition of optical images and the realization that it could be manipulated to bypass the eye's imaging apparatus, Westheimer (1960) implemented the idea by focusing two coherent beams in the pupil and creating interference fringes in the region where the beams overlap in the eye's image space. Such fringes are unaffected by focusing defects and have periods that depend on the wavelength of light and inversely on the separation of the entry points in the pupil. By controlling this separation, which governs the spatial frequency of the fringes, and the modulation depth, the modulation threshold curve of the retinal and neural stages of vision could be measured and compared with the optical contrast transfer function. There was a remarkable concordance between the two at higher spatial frequencies. The interference-fringe procedure for generating a defined retinal image pattern, which played some role in the then-developing Fourier theory of vision, was most effectively utilized by means of laser light a few years later by Campbell and Green (1965), who used it to estimate the optical transfer function.

4.4. Conditioning the wavefront entering the eye's image space

Advancing optical technology and a better grasp of the theory of optical imaging have recently enabled the development of much more sophisticated and powerful ways of controlling the retinal image. Basic to their consideration is the understanding that the light distribution on the retina is determined by the wavefront entering the vitreous. In the ideal situation it is spherical, centered on the retina, and limited only by the pupil aperture. The simplest deviation from this case is defocus, when the wavefront is still spherical but centered on a point in front of or behind the plane of the retina. It is easily seen that there will then be an increasing separation between the two spherical shells. (A purely spherical spectacle lens suffices to bring the two back into coincidence.) The separation, or the deviation of the actual wavefront from the ideal, is usually measured in terms of wavelengths of light, because that is the relevant variable taken into account in estimating the summed electro-magnetic disturbance at all image points that defines the quantity of light impinging on it.

By artificial means external to the eye it is now feasible to condition the wavefront by changing either its shape or its amplitude, or both, in more elaborate ways than by merely providing an appropriately shaped spectacle or contact lens.

4.4.1. Changing the shape of the wavefront by adaptive optics

The most revolutionary development in the history of controlling the optical image on the retina after the invention of the spectacle is surely the use of adaptive optics. Once the wavefront deviations from sphericity have been characterized in a given eye, the beam entering the eye is shaped by technologically advanced devices (e.g., deformable mirrors) to give it exactly the opposite deviation. This neutralizing process is capable of generating a perfectly spherical wavefront for any available pupil aperture and for any kind of aberration, not just spherical and cylindrical refractive errors. In its full implementation, it allows retinal images to be generated (and retinal structures visualized) with arbitrary precision within the limits set by the eye's pupil diameter and the wavelength of light (Liang et al., 1997). Enthusiastic application of this technique is resulting in a voluminous literature whose summary and review is outside the confines of this report.

4.4.2. Changing the amplitude of the wavefront

A more demanding and technically challenging task is to modify not just the shape but also the amplitude across the surface of the wavefront. We have seen in Fig. 16 that the complex amplitude distribution in the plane of the eye's entrance pupil determines the amplitude distribution of the electro-magnetic disturbance in the image. They are related by Fourier transformation. The phase of reference is the sphere centered on the point of intersection of the line of light and the retinal image plane. It follows that, given a desired image distribution, it is a simple matter to identify the needed aperture function. At the outset it is convenient to consider monochromatic coherent light and this is not a drawback since it can be provided by lasers at will.

The Young's interference method described above can serve as an example. If the pupil aperture function is restricted to just two points, the image distribution becomes sinusoidal, its frequency depending directly on the wavelength and reciprocally on the separation of the points. The situation emphasizes that the wider the pupil aperture, the higher the spatial frequencies that are admitted and hence the fidelity of the optical image.

A more elaborate example of shaping the pupil amplitude function in the service of a desired retinal image pattern is Liang and Westheimer's (1993) procedure to produce a two-humped light distributions on the retina (Fig. 18). Analogous to the interference-fringe method, it enabled the measurement of two-point

resolution at the retina by a procedure largely detached from focus and aberration defects in the eye (which in any case could be neutralized if the method were coupled to an adaptive optics device). But as compared with the ordinary two-line resolution experiments of, e.g., Hartridge (1922), it permitted for the first time to explicitly decouple and separately control separation of the peaks and the contrast, in this case the depth of the intervening trough. This is the kind of procedure that is needed for the disambiguation of the retinal and central visual components in localized visual resolution thresholds.

5. Intra-receptor optics

5.1. Photon interaction with photopigment molecules

If quantum theory taught nothing else it was the realization that light location and intensity are not determined until photon interaction takes place. Although the characterization of the eye's point-spread function or, equivalently, contrast transfer function, was a major advance, it omits an important subsequent step in the optical information passage from object through the eye to the next stage, viz., the light uptake by the photochemical transducers in the photoreceptors. As laid out so far, the point-spread function was arrived at by measurement of light reflected from the fundus. Even if the influence on the retinal structure (absorption by macular pigments, modification of the polarization and phase properties of the light, difference in focal plane of the reflection and receptor layers) were fully known, one would still be dealing with the free-field electro-magnetic disturbance in the image plane. However, the strength of the electro-magnetic disturbance utilized in the reception process depends also on the properties of the latter. Two of these properties are the possible influence of the shape of the receptor cells, where funneling and waveguide effects may operate, and the energy exchange (absorption) by the photopigment molecules.

The photopigment molecules, in both rod and cone receptors, are located in the outer segments; for light to reach them it has to traverse not only all the other layers of the retina but also most of the length of the receptors. The receptor molecules are anchored in disk membranes which are more or less normal to the long axis of the receptors; the molecules point along the long axis of the receptor and are capable of rotation around that axis. The probability of a photopigment molecule undergoing photoisomerization depends on the quantum efficiency at the particular wavelength, and the direction of incidence and angle of polarization of the light beam. The wavelength distribution (absorption spectrum) of photopigments is well understood, though it is important to make the distinction between absorption,

Fig. 18. Example of a method of conditioning the wavefront from a source of coherent light to control the retinal image light distribution. The amplitude/phase pattern of the wavefront as it enters the image space of the eye and the amplitude/phase pattern of the retinal image distribution are Fourier transforms. In this experiment (Liang and Westheimer, 1993), the wavefront was such that its Fourier transform has two peaks, whose separation and contrast could be varied to measure two-point resolution on the retina.

extinction, action and difference spectra (Rushton, 1959). However, dichroic properties have been demonstrated. When a beam of light is directed sideways at a receptor, light polarized in the longitudinal direction (i.e., along the axis of the receptor cell) is better absorbed than that orthogonally (Harosi and Malerba, 1975). But there is no such dichroism for head-on incidence. It seems that the directional properties of the receptor molecules and their anchoring in the disks enhance the acceptance of light impinging in its normal passage from the pupil to the retina. This is both more efficient and helps to screen out obliquely scattered light. Light reaching the receptor molecule obliquely would have its efficiency reduced as a function of the square of the cosine of the angle of incidence multiplied by the dichroic ratio.

Even if the total number of pigment molecules within a receptor and the quantal absorption at the wavelength are known, this does not lead immediately to the information of the total number of photoisomerizations. In addition to the direction of incidence, it depends on the effective pigment density in the region within the receptor. From a comparison of real and effective pigment density (Rushton, 1963), it seems that the incident beam has become more concentrated when it reaches the outer segment, although there are differences in opinion about the exact factor (Brown and Wald, 1964). There is the further aspect of self-screening (Brindley, 1960) where the shape of the absorption spectrum changes with pigment concentration.

The physical shape of photoreceptors cells facilitates the funneling of electro-magnetic flux in its passage into and through them to the site of photochemical interaction in the outer segments.

5.2. The Stiles–Crawford effect

One of the most remarkable discoveries of visual optics of the 20th century highlights the active role of retinal receptors in the acceptance of energy by the phototransductive process. Trying to estimate the size of an observer's pupil indirectly by measuring the apparent brightness of a light target for various pupil diameter, Stiles and Crawford (1933) found that large pupils were not nearly as effective in raising the brightness of a constant-luminance target as might have been expected if there is passive summation of energy from all zones of the pupil. Employing more sophisticated procedures of channeling narrow beams of light to the retina through different locations of the pupil, they found that peripheral zones of the pupil were less efficient in eliciting visual excitation than the pupil's center. It is as if there were a progressive darkening of the pupillary aperture toward its edge. Unfortunately, this simple explanations did not suffice, because the Stiles–Crawford effect, as it has come to be called, is substantial in

cone and present only to a minor degree in rod vision (Flamant and Stiles, 1948; van Loo and Enoch, 1975) and cannot therefore have its cause in simple shading properties of the ocular media (Fig. 19). A search for an understanding of the underlying mechanism must also take the differential color effect with oblique pupillary entry, the so-called Stiles–Crawford effect of the second kind (Stiles, 1937) into account.

Most researchers view the Stiles–Crawford effect as caused by a guiding of light into the receptors. Theoretically, this can be treated in the first instance by geometrical optics (Snyder, 1975; Winston and Enoch, 1971): light arriving in the inner segment of a receptor is funneled into the outer segment by a series of total internal reflections at the interface of the receptor cell and the extracellular space, where the difference in refractive index (~ 1.04) is sufficient to sustain the process. The consequence would be a reduction of the uptake efficiency of rays arriving obliquely at the entering plane, which is thought to be the mouth of the tapered section of the inner segment, the ellipsoid. In a more sophisticated theoretical framework, the wave

Fig. 19. Relative luminous efficiencies of narrow beams entering the eye at various positions in the pupil along the horizontal meridian, in scotopic vision (upper) and photopic vision (lower). The Stiles–Crawford effect is prominent only for cones. From van Loo and Enoch (1975).

nature of light and the electro-magnetic properties of the cell membranes are taken into account and the receptor is viewed as a waveguide. Modal patterns, characteristic of wave guides (Huxley, 1947), have been demonstrated empirically (Enoch, 1961). (Modes are patterns of non-uniformity in the energy distribution within a structure that arise through the geometrical property of a structure when it is of the dimension of the wavelength of radiation.) In spite of the mathematical sophistication brought to the analysis of receptors as waveguides (Horowitz, 1981; Snyder, 1975), there remain some major issues. The theories postulate smooth surfaces with idealized geometrical properties, no irregularities of refractive index as light passes through intra-cellular structures, such as mitochondria, and acceptance of light in only one transverse retinal plane. Moreover, they do not grapple with the differences of shape between rods and cones, and among cones in different locations of the retina.

5.3. Apodization

Directional selectivity, or acceptance lobe, of receptors is relevant in the overall understanding of retinal image distributions and their application in vision research. The proximal image, i.e., the information handed on by the eye as an optical apparatus to the photochemical stage of vision, is in effect the spatial distribution of photon absorption in the receptors. Assuming that each receptor acts as a single spatial unit, the excitation level will in the first instance depend on the number of absorbed photons. This in turn depends on the quantum efficiency of the photopigment for the wavelength distribution of the incoming light, and on the magnitude of the electro-magnetic disturbance integrated over the wavefront passing through the pupil as conditioned by the receptor's acceptance lobe. Hence, the spatial distribution of excitement of receptors will differ depending on their Stiles–Crawford effect. The change in the point-spread function produced by a gradual shading of the aperture toward its edge had been described as an apodization (Dossier, 1954), because it reduces the height of the surrounding rings in the Airy disk. The question whether the Stiles–Crawford effect ought to be integrated into the calculation of retinal diffraction images, in the manner of an apodization effect, depends whether the cause is a pure funneling of the electro-magnetic disturbance into the receptor through a single entering aperture. If it is, the answer is in the affirmative and then the amplitude of the wavefront at each pupil location would have to be multiplied by the square root of the Stiles–Crawford effect at that pupil location [square root because the S–C effect has been measured for intensity and not amplitude], prior to the transformation leading to the retinal image light distribution. This would result in changes in

the modulation transfer function (Carroll, 1980) and point-spread function (Artal, 1989). When applied to a real eye, rather than a theoretical diffraction-limited one, the implication emerges: outer zones of the pupil, where the wavefront is more aberrated, now have their influence reduced and hence the performance of the eye with a wide pupil improves. Because the Stiles–Crawford effect changes with retinal location and differs between rod and cone vision, it follows that spatial retinal light distributions for identical targets and optical states of the eye would differ depending on the receptor population that is activated under particular circumstances (Fig. 20).

It would be premature, however, to regard the matter as settled and to proceed as if the measured relative directional efficiency of light entering through different parts of the pupil were unquestionably equivalent to an attenuation of the wavefront for purposes of computing image light distributions in diffraction theory. There is, e.g., a dissenting view, though not widely subscribed to, viz., that the measured Stiles–Crawford effect is the result of a statistical distribution of cone-orientations each with an even more restricted acceptance lobe (Safir and Hyams, 1969). If this were the case, the wavefront amplitude distribution in the pupillary plane, on which the diffraction-image calculation is based, would lead to a stronger apodization effect and a wider effective intra-receptor point-spread function than if the calculations were based on the overall Stiles–Crawford measurements. More serious are the reservations about assigning all directional efficiency changes to light guided into the receptors seen as optical fibers with a single accepting aperture. Light obliquely incident on the retina will surely, at least to some degree, enter also along the length of the receptors and reach the photopigment molecules in directions other than along the long axis of the receptor cells. The superposition of the electro-magnetic vibrations, which is the basis for the diffraction calculations, may then have a more complex character. Specifically, such an alternative explanation would interpret the directional sensitivity of cones not as a reduction in number of photoisomerizations of the whole population of photopigments in each receptor, but a reduction of the available population of photopigments when incidence is oblique. Evidence for such a view is seen in a whole series of experiments, starting with Makous (1968) and enumerated by Enoch and Bedell (1981) in which transient visual changes are found on sudden displacement of the entering beam in the pupil, as if a fresh supply of photopigment molecules were being accessed. Because the collapse of the wavefunction associated with the absorption of a photon occurs individually for each photopigment molecule, it would then be inappropriate to factor in the raw Stiles–Crawford curve in the diffraction calculations leading to the retinal image specifications.

Fig. 20. Influence of the Stiles–Crawford effect on the quality of the retinal image, assuming that it acts to progressively reduce the amplitude of the wavefront in the outer pupillary zones which suffer increasingly from aberrations. Contrast transfer functions have been normalized, and the axis of abscissae is in cycles/degree. Three conditions have been applied to the average wavefronts for 10 normal eyes with, respectively, no, moderate and strong Stiles–Crawford effect ($\rho = 0, 0.05$ and 0.1). The improvement in quality of cone vision is most apparent when the pupil is large (figure kindly provided by Dr. J. Liang).

Regardless of the ultimate resolution of these questions, intra-retinal light processing cannot be excluded as an element when tracing the optical stimulus from the

external visual object to the source of the excitation which entrains the photochemical and then the neural stages of vision.

6. Summary, conclusions and future directions

For many practical purposes, the basic characteristics of the optical image and its relationship to the retinal structure can be developed using the tools of geometrical optics and diffraction, based on established anatomical data. Once a schematic eye is in place, the effect of refractive errors including astigmatism, pupil diameter and chromatic aberration can be easily calculated.

However, the actual image differs from the theoretical one because a typical eye does not usually conform to the ideal surfaces and uniform and transparent media of the models. This gap can be closed only by empirical means.

Adequate knowledge of the quality of the optical image in a given human eye had to wait till the second half of the 20th century, for two reasons:

- The failure of many early researchers to make the conceptual distinction between optical factors in the eye that contribute to the spread of light, and properties of the neural retinal apparatus which accept and process the incoming light.
- The lack of the sophisticated optical and electro-optical tools necessary for the non-invasive capture of light reflected from the fundus.

When these obstacles were removed, point-spread and contrast transfer functions were established for normal eyes, and could be utilized for the definition of the optical stimulus in vision experiments. However, exact data for long-distance spread of light (stray light) and of the Strehl ratio (height in center of light spread compared to ideal image) still remain elusive.

In view of these factors, procedures were devised to control the retinal image in specific situations. They included the use of artificial pupils, elaborate several-stage optical viewing devices (Maxwellian view), and procedures to circumvent the usual optical path in the eye by interference phenomena, utilizing coherent light sources.

Beginning with the 1990s, optical technology has made available the important new tool of measuring and conditioning the wavefront of the light at the pupil. It affords a more complete description of image quality than lumping deviations from a Gaussian point image into categories of defocus and individual aberrations, such as spherical, aberration, coma, etc. Progress has been rapid in the measurement of the shape of the wavefront to characterize the optics of an individual eye, in particular in the aid of refractive surgery. Deformable

mirrors are employed to neutralize refractive errors and aberrations, making the eye diffraction limited even for large pupils and therefore making visible retinal structures not ordinarily accessible for observation and, conversely, producing high-resolution retinal image pattern. The more challenging tasks of conditioning not only the shape but also the amplitude of the wavefront is still in its infancy.

The stimulus for vision is, however, not the light impinging on the retinal surface but that absorbed by the photopigment molecules in the outer segments of receptors, where photoisomerization entrains the subsequent chemical and the neural events. Hence, it is necessary to enquire about the extent to which their structure influences the passage of light inside the receptor cells, especially because this phenomenon is prominent only in cones. Though Stiles and Crawford described the reduced efficiency of obliquely incidents rays in 1933, it has still not been fully elucidated how this affects the image quality of a beam filling a large pupil. Funneling of light entering the inner segment, light incident along the length of the receptor cells, waveguide properties, and molecular acceptance lobes all merit consideration. Such distinctions can lead to differences in how light arriving at a given retinal location along various directions is integrated in the strength of the electro-magnetic vibrations for the quantal interaction with the photopigment molecule.

The review has highlighted the transition from a geometrical approach to the optical image in the eye to the current more nuanced viewpoint in which neural retinal factors are strictly segregated from purely optical ones, richer descriptions of imaging, such as contrast transfer functions and wavefront characteristics are employed, and the fundamental role of intra-receptor optics is realized.

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