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VISUAL ACUITY AND RETINAL ORGANIZATION. (U)
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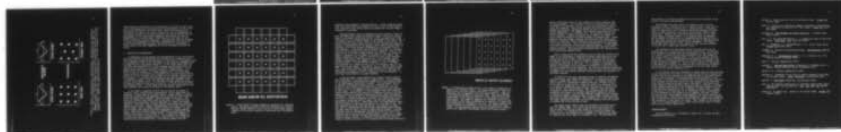
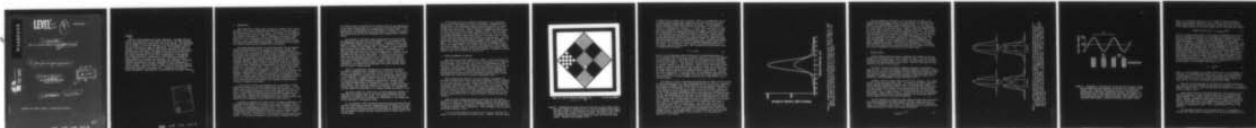
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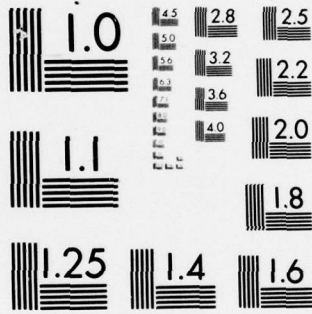
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9 FINAL REPORT

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6 VISUAL ACUITY AND RETINAL ORGANIZATION

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ABSTRACT

Visual acuity depends upon three components: the image upon the retina, the dissection of this image by the retina, and the processing of the signals from the receptors by the visual system. The limitations upon the image on the retina imposed by the optical system of the eye and the wave nature of light are summarized. The receptor mosaic is related to the retinal image by point spread functions for both monochromatic and white light. The image on the retina and receptor mosaic are reviewed as the accepted ultimate limitations on visual acuity. The neural organization of the retina as epitomized in the ganglion cell receptive field is introduced as a mechanism for extending the limits imposed by the optics and receptors. Two types of retinal organization--point-to-point and converging--are developed. The point-to-point representation is shown inadequate from the standpoint of retinal anatomy. The performance of eagle and hawk eyes with ganglion cell-to-receptor ratios of 1:4 and 1:10 are used to illustrate possible mechanisms operating in the human fovea. Suggestions are made for future experimental investigations to choose between alternative models.

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1. INTRODUCTION

Most theories of visual acuity ascribe the ultimate visual acuity attained to the retinal image size as related to the size and shape of the photoreceptors in the retinal mosaic. The details of the image on the retina are such that the wave properties of light itself determine the intensity distribution. That is, something so distant in visual space that it is a point source from the standpoint of geometrical optics. A star, for example, is focused on the retina not as a point but rather as a diffraction-limited image. The details of the diffraction limited image are then dissected by the receptors.

The most important aspects of the retinal mosaic are the minimum center-to-center spacing of the receptors, their size, shape, and refractive index, all of which determine their waveguide properties. The majority of the analyses of visual acuity in relation to the retinal mosaic have been concerned with how the retinal anatomy is matched to the image on the retina as calculated and measured with point spread functions and modulation transfer coefficients derived from a spatial frequency analysis. Models based on such analyses contain an implicit assumption that information transfer through the visual system presents a point-to-point topographical representation of the retinal receptor mosaic up to the cortical level. Thus, as an end result, each retinal receptor is represented in the cortex by a single cell or group of cells. In these models the responses of the cortical cell contain coded messages representing the intensity of the light on the appropriate receptor. However, the details now available of the anatomical structures in the human visual system and the functions as presently known of any of the cells within the visual system are not compatible with a strict point-to-point representation for information transfer about location of images on the retina.

In much of the retina, each ganglion cell is connected to large numbers of receptors to produce overlapping receptive fields. In the foveal region (the center of the retina) where the visual acuity is the best, the histological analysis of the retina suggests that there is nearly a one-to-one relationship between receptors and ganglion cells with, however, slightly fewer ganglion cells than receptors. This agreement with a point-to-point representation may be more apparent than real as will be discussed in more detail in a later section.

Although the standard for visual acuity is usually considered to be a minimum visual angle of one minute of arc, this performance can be bettered to 0.5 minutes of arc by many individuals, presumably with the same type of retinal makeup (LeGrand, 1967). Also, within the visual system there are neural mechanisms which could act to increase contrast by amplifying small differences in intensity (Ratliff, 1965). This process could aid in the detection of the borders which determine visual acuity. It has been the purpose of this project to examine the basis

for visual acuity, and especially to consider what role the organization of the neural system (that is, its anatomy and coding functions as now known) plays in determining the ultimate limit of visual acuity. It is possible that the distortion of the information by receptor to ganglion cell connections may form the fundamental and ultimate limit of visual acuity.

In any model of the human visual system which has point-to-point representation there must be as many ganglion cells as receptors and the connections between them must be simple. A suggestion that a high degree of visual acuity can be attained without this sort of organization can be found in some animal eyes. For example, in hawk and eagle eyes the optics and visual acuity are as good as in humans, if not better (Shlaer, 1972; Miller, 1976; Fox *et al.*, 1976). However, in the eagle and hawk foveas, the receptor to ganglion cell ratio is quite different from that in the human fovea. In both birds there are at least three and possibly 10 receptors to one ganglion cell (Miller, 1976; Fite and Rosenfield-Wessels, 1972). This indicates that good visual acuity does not require as many ganglion cells as receptors. Furthermore, in these visual systems, at least, point-to-point representation of the receptor stage throughout the visual pathway cannot form the basis of visual acuity.

There is an additional consideration in computing the ratio of receptors to ganglion cells: ganglion cells are not all the same. They are not equivalent to each other in their function. On the basis of these differences in function they can be grouped into several distinct categories. As some categories may not be involved with visual acuity, the ratio of ganglion cells to receptors may be far less than is calculated from simple anatomical examinations. Ganglion cells carry many different types of information in a sort of time sharing relationship. They carry the intensity information required for border contrast along with information about color contrast, for information can only leave the retina when it is funneled through the ganglion cells.

The whole problem of visual acuity is best understood, perhaps, by describing the various parts of the visual system beginning with the formation of an image on the retina. An examination of the receptor anatomy and location will be followed by a discussion of the connections of the receptors to the ganglion cells.

H. von Helmholtz (1924) introduced the notion that the brain did not perceive visual space as exactly corresponding to the image on the retina. This idea can be restated to the present discussion. The visual system does not reproduce the distribution of light upon the retina in the brain, but calculates or guesses the most probable source in visual space of the retinal image.

As the first step in the detailed discussion of the information flow in the visual system it is best to introduce a standard test for visual acuity. The information about this pattern can then be traced through each stage of the visual system with an emphasis on any distortions that are present. Figure 1 shows a checkerboard pattern which is often used to test visual acuity (Goldmann, 1943). When the angle at the eye subtended by the black square or white square is less than the minimum resolvable visual angle (that is, below the limit of visual acuity) then the whole pattern is perceived as a uniform grey. When the size of the visual angle subtended by a single square is increased, the checkerboard pattern finally becomes apparent at the minimum visual angle. It is this minimum visual angle that will be examined in relation to the image formed on the retina, the dissection of this image by the visual receptors, and the further processing of the receptor information by the various neurons in the visual pathway, although the retinal ganglion cells will be given the largest role.

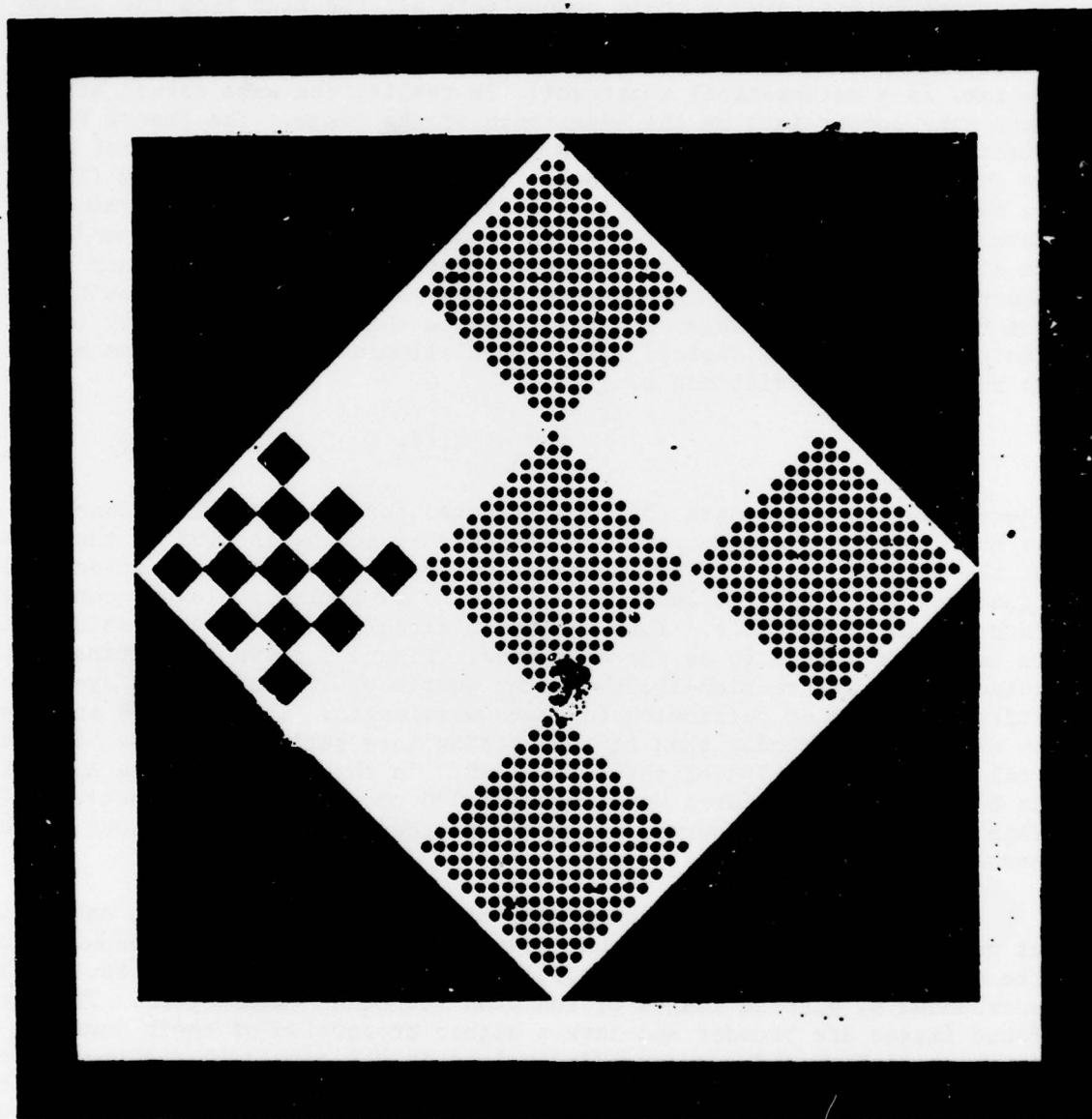
2. OPTICAL PROPERTIES OF THE EYE

The human eye is often compared to a camera: the cornea being the analogue of the camera lens with the pupil corresponding to the camera's iris diaphragm; the crystalline lens of the eye corresponding to the bellows of the camera (as both compensate for changes in the distance of the object from the image plane); and the final inverted image on the camera film corresponding to the inverted image on the photosensitive portion of the retina. A television camera is a better comparison as the photosensitive surface and its associated electronics more closely approximate the retina than the passive photographic film.

When comparing the optics of the eye to those of the camera one must keep in mind another remark once made by Helmholtz (1924), partially in jest, that the eye is a poor optical instrument and would be rejected by any self-respecting optician. Indeed, the eye is not a good optical instrument; even an old box camera could do as well if not better. The cornea often departs from a spherical or radially symmetrical lens. The pupil is usually so small as to create severe diffraction difficulties and when it is large enough to avoid diffraction difficulties, the poor optical characteristics of the various refractive surfaces become more apparent.

There are four refracting surfaces in the eye, but only three of them have an index of refraction sufficiently different from the adjacent medium to be effective. The optical characteristics of the biological lenses do not allow good corrections for either chromatic (LeGrand, 1967) or spherical (Bernay, 1964) aberrations. Thus the image on the retina has appreciable amounts of both.

If the eye were geometrically perfect at the ocular surfaces, the image of a point would also be a perfect point. However, the wave nature



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Figure 1. Checkerboard pattern which is often used to test visual acuity. The whole figure is reduced in size to test the minimum visual angle. The dots in four of the diamonds (the center and three of the corners) are always small enough to be seen as grey. The fifth corner is a checkerboard which can be seen distinctly above the limit of visual acuity. Adapted from Goldmann (1943)

of light does not permit such a solution. That is, by geometrical optics a perfect optical system could concentrate all the flux from the source in the smallest possible point image on the retina. The illumination would be maximum at this point and zero at all others. This notion, of course, is a mathematical construct. In reality the wave nature of light puts many constraints on the appearance of the image. The theory for the exact distribution of illumination within the image area was first given by the astronomer Airy and has been fitted to the eye by LeGrand (1967). In this approach the distribution of flux on the retina is determined by interference between the wave fronts passing through the center and those passing through the sides of the aperture (or iris). Interference between those wave fronts forms the pattern of maximum and minimum intensities on the retina. In the image of a point source the maximum intensity is in the center along the optical axis. This illumination then decreases until it becomes nil at distance r .

$$r = \lambda_1 x_1 / d_1 \quad (1)$$

where λ is the wavelength (560 nm) selected for minimum aberrations, x_1 is the distance from the pupil to the source, and d_1 is 0.92 of the diameter of the entrance pupil. The substitution of these values into associated equations shows that at least 82% of the total luminous flux is contained in a circle of radius r . This defines a circular area on the retina which is usually referred to as the Airy disk. Figure 2 shows the retinal illumination for a diffraction-limited point source of 560 nm, as the eye has a different index of refraction for each wavelength. This disk is surrounded by rings, each broader than the succeeding more peripheral ones. The central zone contains 70% of the total flux. In the human eye, the Airy disk is 6 μm in diameter for a wavelength of 580 nm and a pupil diameter of 4 mm. This calculation, of course, assumes that there are no aberrations in the cornea or lens.

The image of a source containing many wavelengths of light can be in focus at only one wavelength; all other wavelengths must be out of focus. Therefore, the diffraction image of the central Airy disk at the selected wavelength is surrounded by blurred images of the disk for other wavelengths. The out-of-focus images are broader and have a higher proportion of their luminous flux in the periphery and correspondingly less in the Airy disk (LeGrand, 1967). In Fig. 2 the intensity distribution for a white light source is shown focused for the same wavelength as the one shown for a monochromatic source (580 nm). Although in the monochromatic case only a little light appears to be outside of the central disk, the peripheral flux must be integrated over a very large area. However, the important thing is that the signal-to-noise ratio in this image is the peak-to-surround ratio. For white light the ratio is less than one-half that for monochromatic light when both sources are at the same absolute intensity. On the basis of this analysis the minimum visual angle in the white light should be approximately twice that in monochromatic light. As all measurements of function show much less difference between white and monochromatic tests than this, it is interesting to speculate on the course.

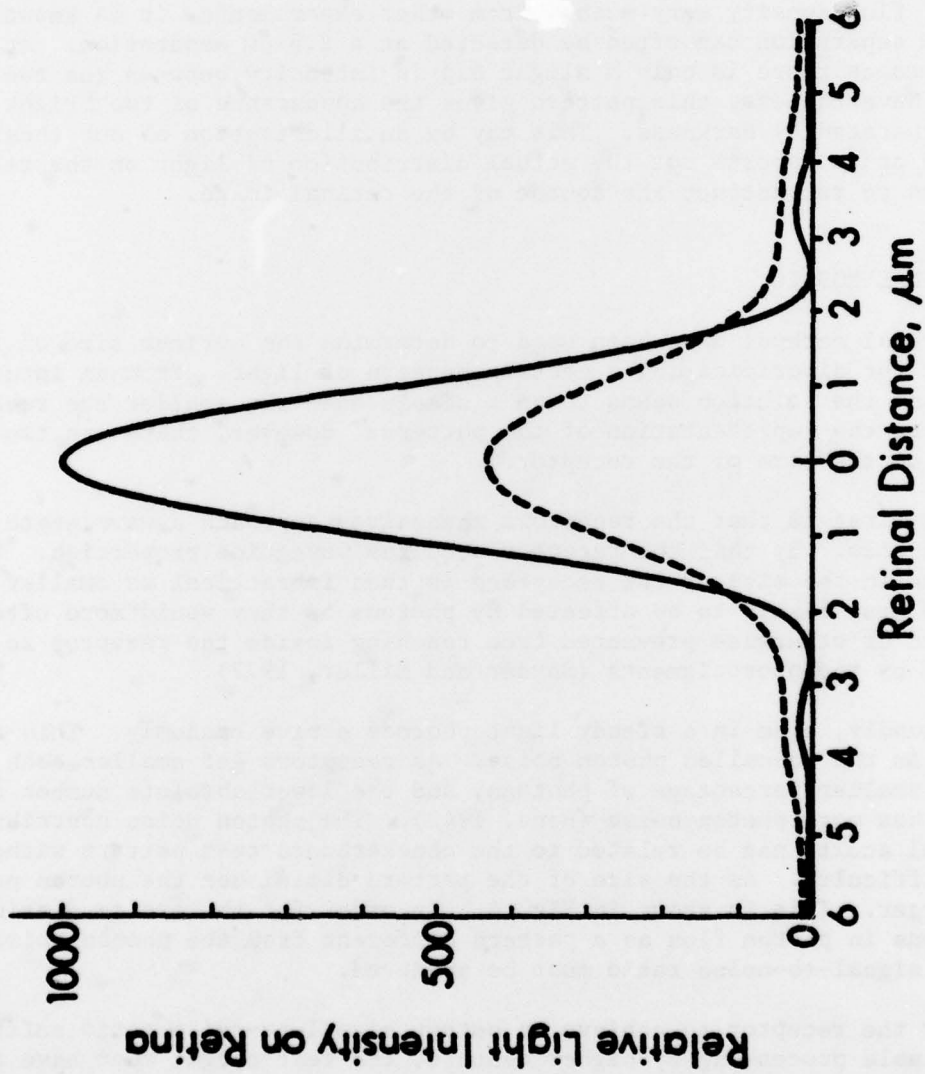


Figure 2. Intensity distribution of the diffraction pattern in the retinal image of a point source. The solid line shows the Airy disk for a monochromatic source at 560 nm. The dashed line shows the intensity distribution for a point source of white light at the same intensity in focus at 560 nm. Adapted from Le Grand (1967)

The next problem to consider is the distribution of light in two diffraction-limited images equivalent to the image of two adjacent white squares in the checkerboard pattern presented in Fig. 1. For this purpose an area near the light corners is selected where they are separated by a small portion of the dark square. Figure 3 shows the algebraic sum as the two light squares of the pattern approach each other. The luminous flux only begins to add up as the two become very close. As the two are from different sources, interference phenomena do not affect the calculations of flux density very much. From other experiments, it is known that the separation can often be detected at a 2.5 μm separation. At this distance there is only a slight dip in intensity between the two peaks. Nevertheless, this pattern gives the appearance of two bright areas separated by darkness. This may be an illustration of our thesis that the brain reports not the actual distribution of light on the retina but tries to reconstruct the course of the retinal image.

3. RETINAL MOSAIC

Several methods have been used to determine the optimum size of the receptor for discriminating a certain pattern of light. From an intuitive standpoint the solution seems to be a simple one--the smaller the receptor the better the representation of the pattern. However, there are two limitations on the size of the receptor.

The first is that the receptors themselves approach a wavelength of light in size. By this the receptor acquires waveguide properties. Further reduction in the size of the receptors is then impractical as smaller receptors are less likely to be affected by photons as they would more often be scattered or otherwise prevented from reaching inside the receptor to be absorbed by the photopigments (Snyder and Miller, 1977).

Secondly, even in a steady light photons arrive randomly. This random process is the so-called photon noise. As receptors get smaller each captures a smaller percentage of photons, and the lower absolute number of photons has more photon noise (Rose, 1942). The photon noise contribution to visual acuity can be related to the checkerboard test pattern without great difficulty. As the size of the pattern diminishes the photon noise gets larger. This is shown in Fig. 4. In order for the eye to distinguish variations in photon flux as a pattern different from the photon noise, a certain signal-to-noise ratio must be achieved.

For the receptor to achieve an output signal-to-noise ratio sufficient for reliable processing by higher centers, the test target must have at least a 1% modulation. This can also be expressed in terms of the photon noise at the optimal receptor layer. The noise photons in a pattern on the retina fluctuate by the root mean square relationship.

$$\sigma_{\text{(noise)}} = n^{1/2} \quad (2)$$

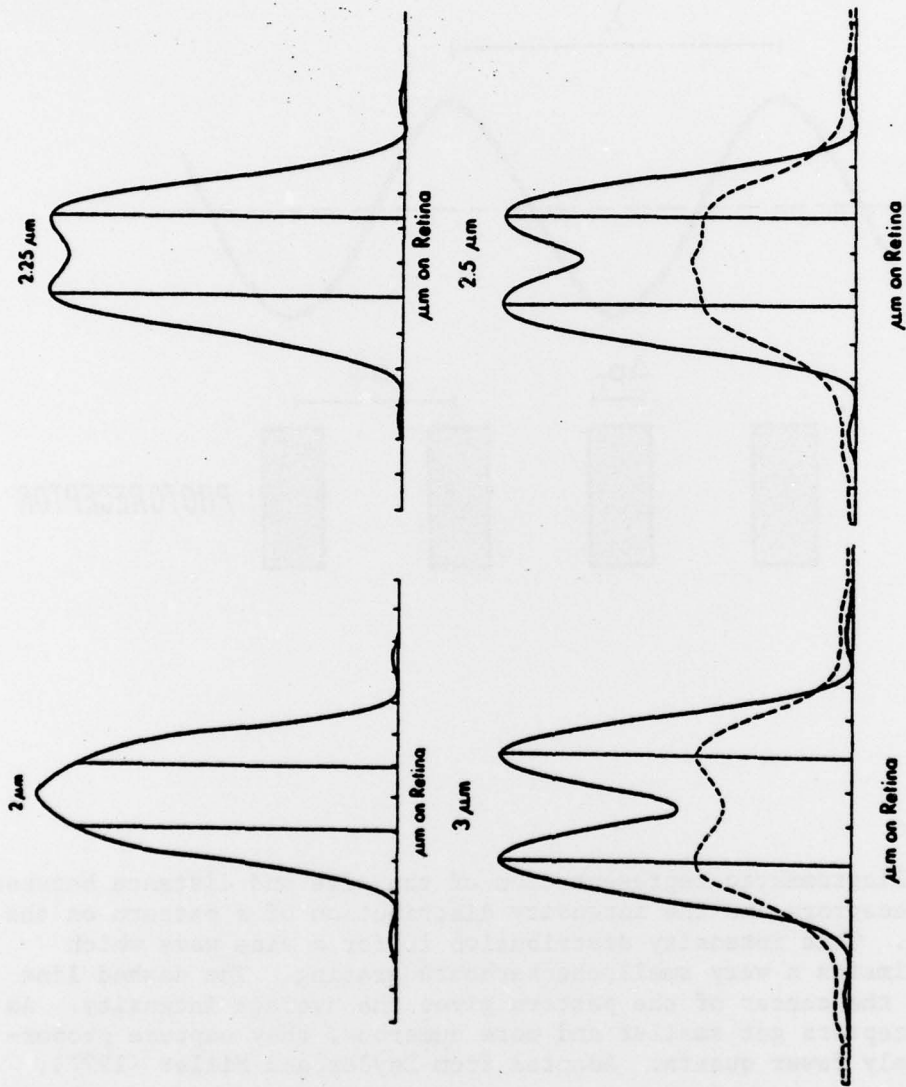


Figure 3. Intensity distribution on the retina of the image from two adjacent point sources of light. The solid lines show the algebraic sum of two monochromatic point sources which individually have the same retinal image of the point sources as shown in Fig. 2. The dashed lines are for white light. A separation of $2.5 \mu\text{m}$ gives the image corresponding to a visual acuity of $3/6$ ($10/20$). At this separation there is a very small dip in the central intensity distribution of monochromatic light. For white light sources there is no dip.

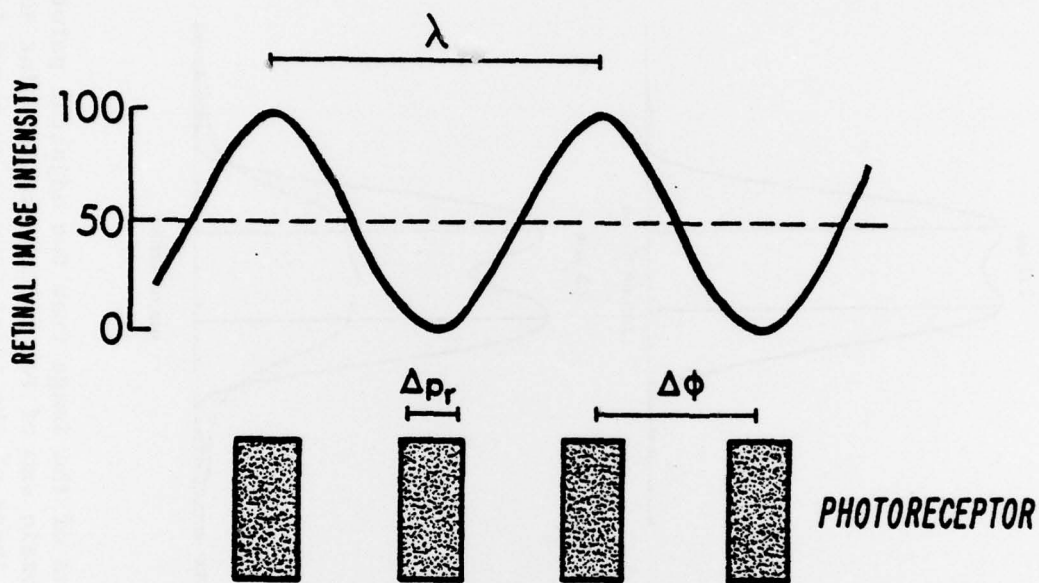


Figure 4. Diagrammatic representation of the size and distance between photoreceptors and the intensity distribution of a pattern on the retina. This intensity distribution is for a sine wave which approximates a very small checkerboard grating. The dashed line across the center of the pattern gives the average intensity. As the receptors get smaller and more numerous, they capture proportionately fewer quanta. Adapted from Snyder and Miller (1977).

where σ is the photon noise and n is the number of photons absorbed during the integration time of the eye. An analysis of this relationship by Barlow (1965) and Snyder and Miller (1977) shows that the ratio of the signal photons to the noise photons has the following relationship:

$$\text{signal-to-noise ratio} = m \sigma_{(\text{noise})} M_1 M_r \quad (3)$$

where m is light-to-dark ratio in the original checkerboard test pattern, M_1 is the diffraction properties of the pupil size in relation to the optical refraction of the eye, M_r is the modulation transfer function for the photoreceptors. In general below the wavelength of the incident light, the smaller the diameter of the photoreceptor the smaller M_r . Thus when all other functions are held constant reducing the size of the photoreceptor below some optimum value near the wavelength of light there is a marked diminution in visual acuity. The best solution is a compromise between decreasing the receptor size to give better image dissection, and increasing receptor size to minimize photon noise. It is best to have the receptors so large that they touch (to increase photon capture) and small enough to be able to handle the highest spatial frequency by the diffraction-limited optics. Snyder and Miller (1977) derive the relation of the minimum center-to-center spacing (in a hexagonal array) of the photoreceptors to the minimum visual angle ϕ as:

$$\phi = \lambda/d\sqrt{3} \quad (4)$$

where λ is the wavelength of the light (555 nm) and d is the diameter of the pupil in the diffraction-limited case (2.4 mm). This corresponds to a visual angle of 27.4 arc sec. This visual angle when related to the focal length of the eye (2.15 μm) gives a center-to-center spacing for cones of 2.0 to 2.3 μm in the central region of the fovea.

With the calculations based on the detection of spatial frequencies (bar pattern) and with different assumptions than used for Fig. 4, similar spacing is shown in Fig. 4 but this can easily be extended to two-dimensional cases as shown in Fig. 5.

Other models using the waveguide properties of the receptors lead to similar conclusions. There is one difficulty with all those analyses. The performance of the visual system is modeled on monochromatic light input. However, although the same target in white light has a much more blurred retinal image due to the large amount of chromatic aberration in the eye, the overall visual performance is remarkably similar to that achieved by monochromatic light. This is not predicted by any of the analyses.

The preceding discussions have indicated that it is reasonable to suppose that visual acuity, as measured by the overall performance of the

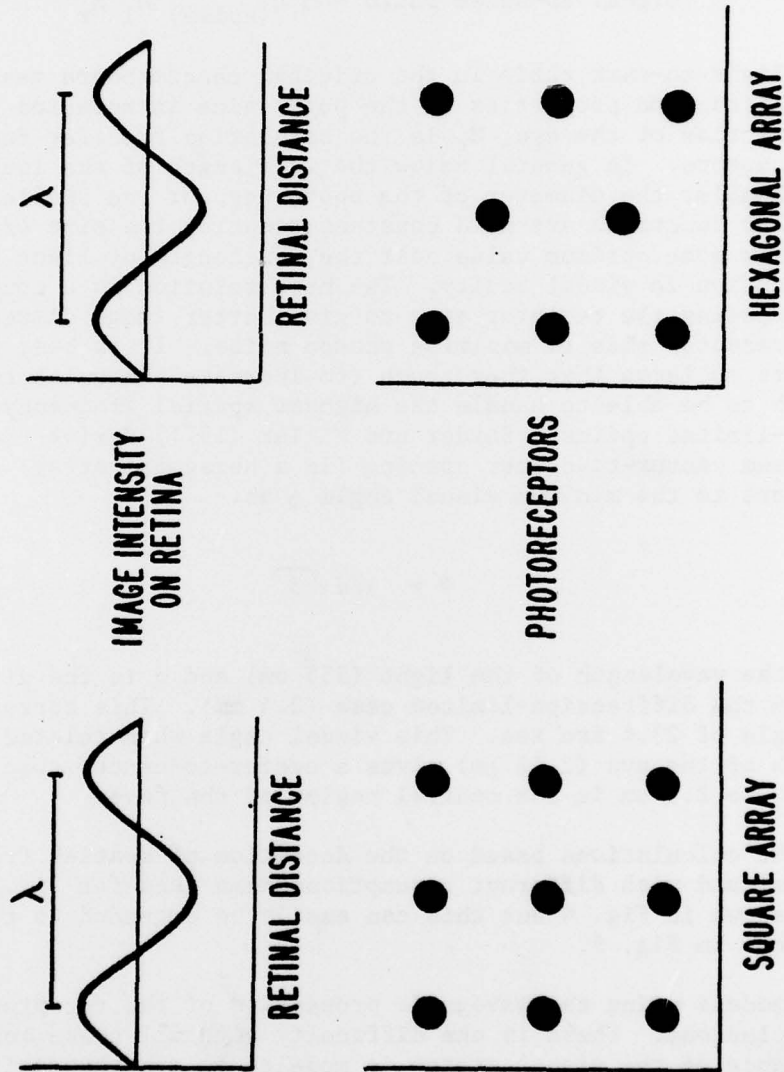


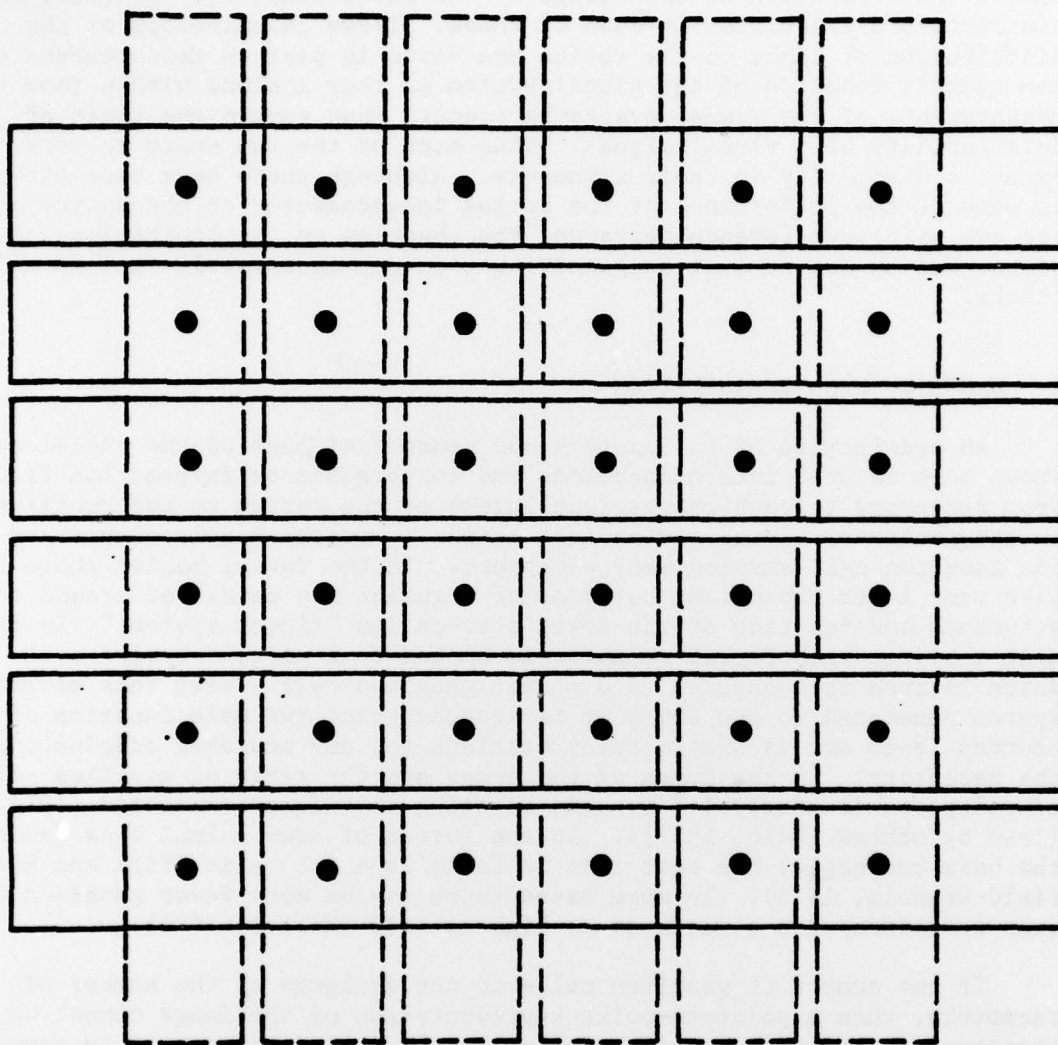
Figure 5. Relation of photoreceptors to retinal patterns. This figure is the expansion of Fig. 4 into a two-dimensional array with the receptors arranged with both square and hexagonal spacing. The angle between receptors for a given visual acuity has the value $1/2$ the spatial frequency for a square array while it is $1/\sqrt{3}$ for the hexagonal case. Adapted from Snyder and Miller (1977).

visual system, is predicted by the limitations of the image on the retina, and of the dissection of this image by the photoreceptors. However, there are certain difficulties in each of these. These calculations of the distribution of light on the retina are based in part on measurements of the overall function of the visual system as they include within them the measurements of the visual system parameters that govern the limit of detectability of a visual signal. Thus each of the two share to some extent a similarity in their arguments. Although there have been attempts to measure the performance of the retina independently of the optics of the eye with interference patterns, the theories on the limitations of visual acuity are at best suggestive but do not necessarily exclude all others.

4. GANGLION CELL ORGANIZATION

An examination of the anatomy and neurophysiology of the visual system shows both lateral interconnections and convergence as information flows from receptors through the various layers of the retina to the ganglion cells. In the periphery of the retina information is most severely compressed with one ganglion cell serving many receptors. In the foveal region there are also many interconnections but a major argument has developed around the structure and function of the fovea's so-called "midget system." In the midget system each foveal receptor is hooked to a midget bipolar cell which in turn is connected to a midget ganglion cell. With this midget system connected to the fovea it is supposed that the sole function of all neurons is to act as simple relay stations for any messages originating in the receptors. In the fovea of the human eye the ratio of ganglion cells to receptors is nearly 1:1 by some counting techniques (Missotén, 1974) (less by others [Kolb, 1977]). In the foveas of some animal eyes (such as the hawk and eagle) the best that is found is a 1:3 ratio (Fite and Rosenfield-Wessels, 1975). In some cases there may be many fewer ganglion cells than receptors with a ratio of as high as 1:10 (Miller, 1976).

If the number of ganglion cells is not as large as the number of receptors, then a point-to-point representation of the image cannot be preserved in every stage of the visual system. Indeed, merely to connect sufficient receptors to each ganglion cell to satisfy the ratio would not solve the visual acuity problem. This would make it much worse. The blocks of receptors that result would be the basis of a point-to-point representation system which would be equivalent to a model with larger receptors. This would have a coarser retinal grain which would obviously degrade visual acuity. However, paradoxically, even larger visual fields will be better; that is, larger receptive fields with overlap. In this type of model, each receptor will have connections to several ganglion cells. This type of hook-up gives the possibility of achieving as good minimal visual acuity as is actually found. A simplified schematic of this type of system is shown in Fig. 6. The receptors are arranged in a square array while the ganglion cell receptive fields are oblong and form vertical and horizontal slits. The combined signals from the



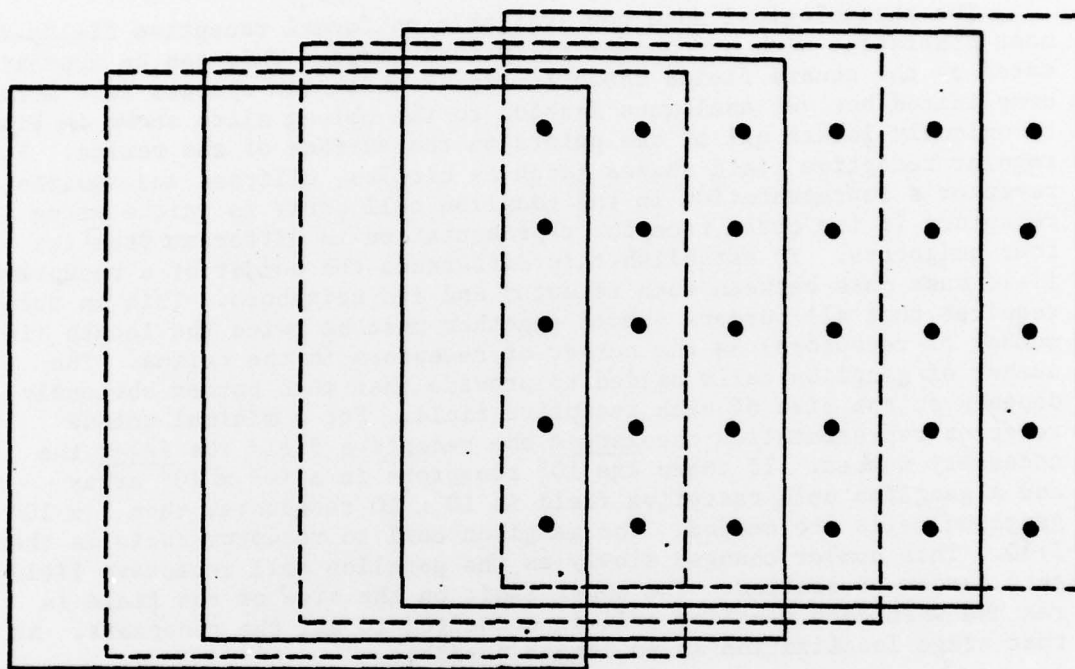
OBLONG GANGLION CELL RECEPTION FIELDS

Figure 6. Localization of retinal stimulus by ganglion cell receptive fields. The oblong receptive fields have horizontal and vertical (row and column) overlap in such a way as to allow unique identification of all retinal receptors by specifying only two ganglion cells.

ganglion cells designates a "unique location." Actual receptive fields with these oblong spatial characteristics are not seen in the ganglion cells connected to the foveal region in primates and a further stage of refinement is necessary.

The physiological data now available on foveal receptive fields is most consistent with a round or elliptical shape. This can be approximated by the square fields shown in Fig. 7 which can operate in a more complicated but yet analogous fashion to the oblong slits shown in Fig. 6 to uniquely locate all of the points on the surface of the retina. For regular receptive field shapes (such as circles, ellipses and squares) a receptor's representation in the ganglion cell array is unique among all receptors if its total receptor representation is different from its four neighbors. To establish this difference the border of a receptive field must pass between each receptor and its neighbors. This in turn requires that all borders summed together must be twice the length (in number of receptors) as the number of receptors in the retina. The number of ganglion cells needed to provide that much border obviously depends on the size of each receptive field. For a minimal unique receptor representation the larger the receptive field the fewer the necessary number. If there are 10^6 receptors in a $10^3 \times 10^3$ array and a ganglion cell receptive field is 10×10 receptors, then 5×10^4 ganglion cells are needed. The ganglion cell to receptor ratio is then 1:20. This number changes slowly as the ganglion cell receptive field gets larger or smaller. The upper limit on the size of the field is reached when each ganglion cell is connected to all the receptors. At that stage localization is no longer possible.

In the mid-range, larger ganglion cell receptive fields produce more sensitivity for the detection of single points. This performance can be improved by introducing other parameters of the receptors based on the physiological data known at present. One requirement would be to consider varying sensitivities within a receptive field. If the pattern of each receptive field sensitivity is different, then the possibility that a few ganglion cells can identify the visual stimulus is very large. As an example, if three ganglion cells have receptive fields covering exactly the same set of receptors and each of the three ganglion cells has a different sensitivity profile, good localization is possible. The particular set of sensitivity profiles that will work very well is to have one ganglion cell with a flat sensitivity profile, one linearly decreasing from the center, and the third exponentially decreasing from the center. These three cells can simultaneously determine the position of the light and whether it is one spot or two. The flat sensitivity profile will describe the total quantity of light. This taken in combination with the linearly decreasing profile defines the exact radius at which a point of light would be located. A further comparison with the exponentially decreasing sensitivity profile will determine whether the previously defined radius is proper for a single stimulus point or whether the light distribution would be better represented by several sources. An estimate of the maximum size of such receptive fields can be made if it is assumed that a noticeable difference



GANGLION CELL RECEPTIVE FIELD BORDERS

Figure 7. Localization of single points on the retina by interaction of ganglion cell receptive fields. The square fields shown here overlap in such a way that unique localization is possible. There are additional sets of ganglion cells (not shown) which are displaced in the vertical direction in successive rows. This gives the same localization in the vertical plane as is illustrated in the horizontal plane. The number of ganglion cell receptive fields of this type needed to give unique localization in relation to a given number of receptors is discussed in the text. The square ganglion cell receptive fields are equivalent to the circular fields in a real retina. The same analysis applies when the ganglion cell receptive fields have comparable displacement within the receptor matrix.

along a radius will result if each receptor is 2% less sensitive than its inside neighbor. For the linear receptive field the radius would be limited to 50 receptors, and for a 2 log unit logarithmic receptive field, 200 receptors. This latter disparity would allow interaction between non-concentric overlapping fields and lead to a much more complex retinal organization. For example, the receptive field need not have uniform sensitivity over its entire area. An inhibitory surround can also be assumed. A simple calculation can be made of the number of unique points specified by any given assembly of ganglion cells. Twenty ganglion cells are enough to specify the location of any single point within 10 receptors, while 40 ganglion cells would allow the specification of any two points. This is a reduced system and is not equivalent to the whole retina with a multi-point stimulus pattern. In the present form only a few points can be located simultaneously; many more would produce confusion. Thus additional information about the external world could require more ganglion cells.

Even if there are as many ganglion cells as there are receptors this number is not sufficient to allow point-to-point representation at each stage of the visual system. Ganglion cells must carry other kinds of information and can be sorted into different categories on this basis. For example, there are at least two kinds of receptors with different spectral sensitivities in the fovea. It is necessary to segregate and compare the information from each group of receptors in such a way that the color sensitivity can be preserved. The color and intensity categories of ganglion cells are further subdivided into on-center and off-center types. Presumably each type carries different information about the character of the border contrast.

In addition to the color information there is intensity information (the grey scale), even though discrimination of a visual acuity target appears to depend very little on a grey scale. For example, where the acuity target is a checkerboard compared with grey, as shown in Fig. 1 at the limit of visual acuity, it does not appear as a dark grey check on a light grey background, which would be the case for a variable contrast system. Only the extremes are seen, either a solid gray object or pattern of black checks on white. This indicates that the system responsible for contrast is nonlinear and inserts additional contrast in certain situations. All of these different categories tend to lessen the effective number of ganglion cells to carry border contrast information about any particular target. This suggests that in the human fovea, for normal computation purposes, the ratio of ganglion cells per receptor is probably one to four and may be less.

The higher visual centers treat the information from both eyes as part of a single image. For a given visual acuity this divides the restrictions upon both the retinal image and the retinal grain by a factor of two. If information can be closely correlated between the two eyes and the two retinas kept in alignment (or register) the number of receptors per visual angle is increased by two. The psychophysical

data supports a functional increase as the tests show binocular visual acuity to be better than monocular.

Eye movements are often cited as an important part of vision (Ditchburn, 1973), although they do not appear to play a large part in achieving the limits of visual acuity. Approximations of the normal limit of visual acuity can be achieved without eye movement with short pulses of light presented to the eye by an electronic flash or some such source. However, the integrating characteristics of the visual system cannot be ignored either. It is possible that eye movements act to degrade the image while the integrating effects make up for it. The high visual acuity from long exposures can then be achieved because the integrating properties nullify the eye movements. This balance allows high visual acuity at lower levels of light than are necessary for vision with a single high intensity flash.

The problem of the limitations imposed on visual acuity by the various parts of the visual system is by no means solved. As more and more information is gained about the various parts of the visual system it is easier to match the functional performance with that assumed by the various models to determine which, if any, of the present theories are correct. A better understanding of the detailed functioning of the visual system will perhaps indicate which factors act to increase visual acuity and which to degrade it. Thus it will be possible in the future to manipulate the features of a target in such a way that its visibility can be increased or decreased by a knowledge of how the visual system will act on the various components of it.

At the present time more information is needed about the fine structure of the receptive field in order to indicate exactly how many receptors and of which type may be connected to the ganglion cells in the foveal region. There is also a paucity of information about the effectiveness of the connections; for example, is the sensitivity of the ganglion cell receptive field constant over its whole area or do the receptors at the edge have a lower effective sensitivity than those in the center. More data on the actual makeup of foveal receptive fields will make it possible to formulate a more soundly-based theory of the information-carrying capability of the retina and what limitations if any it imposes on visual acuity. Indeed, a description of any distortion of the information which is necessitated by the convergence of the receptors on the ganglion cell will in itself pave the way for a more complete understanding of the overall activity of the visual system. This review of the mechanisms of visual acuity suggests that in some way the visual system looks beyond the image on the retina and that perception to some extent is a guess. Thus, gestalt of the probable cause of the retinal image may be a rather more accurate report of visual space than the retinal image itself.

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