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DEPENDENCE OF FOVEAL VISUAL ACUITY ON THE SIZE OF THE RECEPTIVE--ETC(U)
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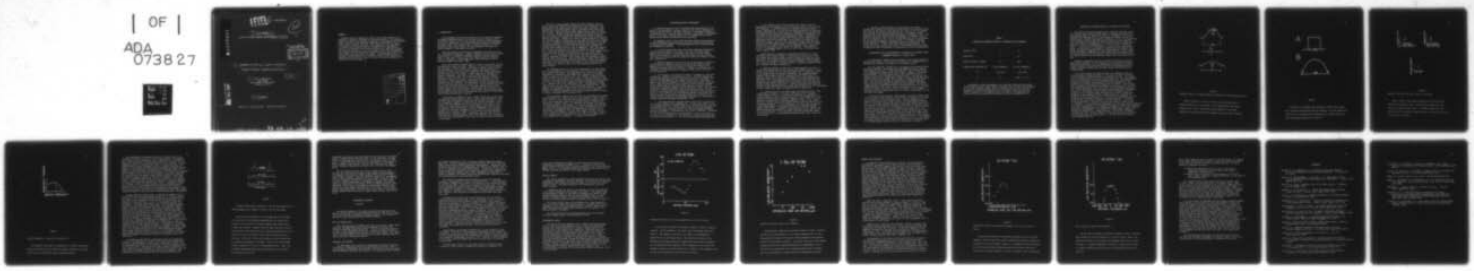

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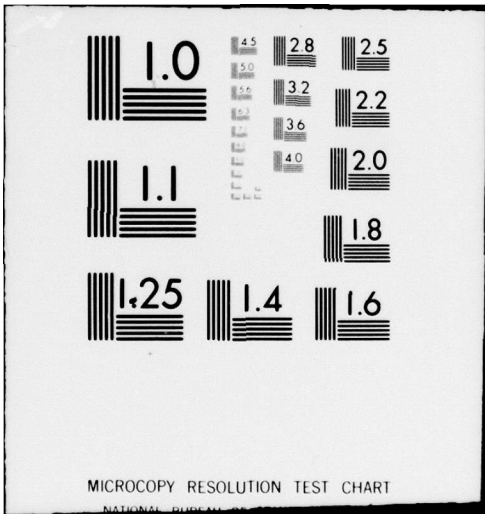
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(6) DEPENDENCE OF FOVEAL VISUAL ACUITY ON THE SIZE OF THE RECEPTIVE FIELDS OF RETINAL GANGLION CELLS.

(12) 26p.

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ABSTRACT

Visual acuity is analyzed in terms of the retinal ganglion cell response to different stimuluses on the receptor matrix. The antagonism between the central and peripheral responses of the ganglion cell receptive field is shown to effect both the sensitivity profile and the Ricco field (Area X Intensity) response. The difficulties with each method of analyzing the receptive field are discussed and an experimental protocol is formulated which derives information by comparisons bewteen the different approaches. Data is presented to show that the ganglion cell receptive fields comprise many receptors even in the portion of the retina where the visual acuity is highest. The experimental data for a similarity between ganglion cell receptive fields in the central and peripheral portions of the retina in the cat is given and compared with similar data for the monkey.

1. INTRODUCTION

The experiments and analysis described in this report are designed to discover something about of the cellular basis of spatial vision. The approach taken is to find and describe the factors limiting spatial vision in a continuation of the work described previously by Wolbarsht and Ringo (1978). The clearest limit to spatial vision is on the resolution of fine detail (acuity) and the experiments discussed are mostly designed to investigate this limit.

The first limit on a visual task is imposed by the optics of the eye. For spatial resolution a complete description of an optical system is provided by its modulation (spatial frequency) transfer function (MTF). In the case of the eye the MTF is known and sets an absolute limit to resolution, a limit human acuity comes remarkably close to achieving (Campell and Green, 1965).

After the optically degraded image is formed on the retina, two new limiting factors come into play. The first is the transducer elements, the receptors. They are usually considered to impose a limit by their size and spacing. The second factor is neural processing which is limiting by the size of the area of summation, any lateral interaction, and any reduction in the number of output channels as compared to the number of receptors. Much less is really known about the transfer function of each of these factors than about the transfer function of the optical portion of the eyes. This is partly because it is very difficult to obtain quantitative information from the electrical recordings from the receptors. The horizontal, bipolar and amacrine cells are, if anything, even harder to record from. As the ganglion cells are fairly easy to record from the most practical approach is to record retinal ganglion cell activity and to deduce what has happened in the earlier stages. Since the ganglion cells produce action potentials (and are probably the only cells in the mamalian retina which do consistantly), extra-cellular monitoring is possible.

A view which is commonly held has acuity limited only by the receptor shape and spacing (Gubisch, 1967). Indeed, most investigators have concluded that the receptor spacing imposes the absolute limit. If the very reasonable assumption is made that the receptor responds to light in the same way no matter what the distribution of this light on the receptor is, then changes in light within regions less than the size of the receptor cannot be signaled. A further development of this theory considers the receptors as sample points for which the inter-receptor spacing limits frequency reception in accord with the Shannon-Nyquist sampling theory (Gubisch, 1967). The Nyquist sampling limit for this case would be a spatial sampling (rather than temporal) rate and must be at least twice the bandwidth of the input in order to achieve resolution of the signal.

There is a rough agreement between the high frequency limit of spatial resolution (with optics by-passed) and the theoretical predication based on the Nyquist limit (twice the receptor spacing). This agreement has lead some workers (Campell and Green, 1965) to believe that we have a sound theoretical understanding of the limits of acuity in the retina. However, there are two serious defects with that analysis. The first is that the Nyquist sampling limit refers to point samples, although the receptors are not points but rather cover most of the available space. Perhaps this causes a certain reduction in resolution when the signal-to-noise ratio is very high, but this local integration is very important in improving the signal-to-noise ratio for lower intensity stimuluses. The second defect is that the receptors form a two-dimensional sampling array, while stimuluses which achieve the Nyquist limit frequency vary in only one dimension. Thus, many samples are taken for any position, and could be averaged to increase resolution. These two defects work in opposite ways. The first implies actual resolution would be below the Nyquist limit and the second, above. Perhaps, it is a coincidental cancellation of these two effects that leads to agreement (Le Grand, 1967) rather than any soundness of strict sampling theory application. When consideration of noise (both noise in light due to local scattering, general scattering, photon fluctuations, and noise in the receptor itself) are added to the two previous points, the situation is very far from one in which sampling theory can be simply applied.

The remaining portion of the visual system which can limit resolution is the integrative, neural network of the retina, and few workers have examined this locale. The prima facie case is that the neural integration of relatively large areas into a ganglion cell receptive field is similar to the earlier, more local, spatial integration which occurs at the receptor level. Since a spot of light in one part of the receptive field can be adjusted in intensity to produce the same response as a spot in another part it seems that spatial information is being lost. However, this is not necessarily true. The difference between these two spots is lost only for that particular ganglion cell. Other ganglion cell receptive fields overlay this same area and a correlation between the responses may allow the two spots to be distinguished. However, a different organization with non overlapping receptive fields is usually postulated for the primate fovea.

Most anatomists consider that the fovea in the primate has a unique midget ganglion cell connection to each cone through a single bipolar cell. If this is true, then the neural organization is simply a point to point relay system and contributes nothing to acuity, increasing or decreasing. However, there is no physiological evidence for a single cone representation in the cortex. In fact, the limited available data on foveal receptive fields Westheimer's (1967) psychophysical test of the effects of background size, and DeMonsterio's and Gouras (1975) rhesus fovea recordings of 15-25 μm fields suggest (weakly) that the foveal receptive fields are composed of at least a few cones. There also a growing body of anatomical data that the neural organization is quite complex and not equivalent to a simple relay network.

ELECTROPHYSIOLOGICAL EXPERIMENTS

An important decision is an electrophysiology investigation is the choice of the experimental animal. There are two obvious candidates in tests in spatial vision: the monkey because of its supposed similarity to humans and the cat because there is already a large body of experimental data on this animal. The best choice is to do enough work on each to bridge the gap between psychophysics and physiology.

The ganglion cells of the retina have been selected since these are the most peripheral cells which can be routinely monitored long enough to complete the experiments. The experiments and their interpretations can be grouped as follows:

1. It is well known that acuity falls with increasing eccentricity from the optical center of the retina. This has often been used to support both the theory of a receptor size limit to acuity, (Green, 1970) and the theory of receptive field size limits to acuity (Harter, 1970) since the receptors and the receptive fields both increase in size with eccentricity.

A comparison between visual acuity and the recordings of receptive field properties (especially the size of the central portion) from ganglion cells of known eccentricity (and known cone density) will distinguish between these two theories. A number of recordings will be necessary since some variation of receptive field size at one eccentricity does occur.

2. The increase in acuity with increase in luminance is also well established. However, its explanation is not. The limit imposed by receptor spacing might explain an increased acuity with increased luminance by the improvement in the signal to noise ratio. This ratio should vary with the luminance, at least where the receptive fields are large. Those theories that limit acuity by receptive field size make the assumption that the receptive field sizes are not fixed, but decrease with increasing luminance (Daitch and Green, 1969). This analysis provides a testable prediction of the receptive field theory. If the fields do not change size with luminance, a receptive field influence on acuity is still possible, but the transform between the contrast sensitivity function in the spatial frequency domain and the shape of the receptive field sensitivity profiles would be shown to be unreliable and falsely predictive (Furukawa and Hagiwara, 1978).

3. The Shannon-Nyquist sampling theory states that the resolution of a system is based on its sampling rate. To apply this theory to the retina raises question of what process in the retina should be considered the sampling rate. For a pattern which varies in only one dimension, such as the standard striped pattern, the effective sampling frequency could be increased by a combination of many rows of receptors. Occurrence of this sort of integration of and its extent, if any, would appear as an effect width (orthogonal to the direction of pattern variation) upon the contrast sensitivity of a cell, and could be measured experimentally.

4. The simplest test of the receptor limit theory would be a measurement of the performance of the system after part of the receptors are eliminated. If receptor density is limiting this would reduce acuity proportionally. In both cats and diurnal primates the available evidence indicates that visual acuity is determined by the red and green cone inputs pooled without distinguishing the spectral differences. As the number of red and greens are approximately equal, a measure of the acuity of the red cones (or green cones) alone can be accomplished by adapting an area with strong green (or red) light then using red (or green) test stimuli. This will show the acuity of the retina with half the normal receptor density with a predictable decrease from the normal visual acuity if receptor density is the limiting factor. This would not work if the pooling occurs before the adaption. Unfortunately, Stiles' π-5 mechamism suggests that just such a type of pooling really occurs (Stiles, 1959).

Another method to accomplish a reduced cone density is to put a stabilized laser speckle pattern of adaptation on an area and compare the reduced acuity this produces with the reduced acuity due to a uniform field. The difference between these two adapting situations should affect only the receptors since the adaptation effects on the ganglion cell would be the same. This again allows a comparison between a normal and a reduced cone density population.

A comparison between a normal and a reduced ganglion cell population can be achieved by use of a moving laser speckle pattern. If the pattern moves faster than the receptors adapt then the adaptation level of all receptors will be the same. Meanwhile, the changing receptor response (the receptor response) change much more rapidly than the receptors adapt) will be led to the ganglion cells and adaptation will take place there. This adaptation will reduce the normal ganglion cell responses. So, if the ganglion cells are limiting in acuity, then the moving speckle pattern will produce a lower acuity than a uniform background at equal average luminance. A uniform background will adapt the receptor to the same extent as the moving speckle pattern, but no differential receptor signals will reach the ganglion cells to adapt them.

5. Scotopic acuity is very much lower than photopic acuity. This is generally attributed to the large integration areas of scotopic vision. However, acuity, as a function of luminance is a smoothly increasing function, with no abrupt transition in the neighborhood of the transition from scotopic to photopic luminance levels. That is, acuity appears to increase with increasing luminance levels, per se, rather than with the rods input or cone input transition which also occurs with increasing luminance. If this explanation is correct then the scotopic acuity should continue to increase smoothly with luminance through mesopic light levels. To measure the constriction in this region, cone intervention must be postponed to higher luminance levels. This can be done in several ways: with a displaced pupil (Stiles-Crawford effect) to favor the rods, or a red background adapting light with a large blue test pattern.

6. Whichever system imposes the limiting point for acuity, a problem still remains in the primate retina outside (and possibly within) the fovea for the coding at the ganglion cell level of all the information received by the more numerous receptoes. For example, overall there are about 10^8 receptors signaling through 10^6 ganglion cells. The estimates for primate foveal place the ganglion cell/receptor ratio at about 0.9 (Missoten, 1974), but all the ganglion cell in this population may not contribute equally to acuity vision. For example, there may be overlapping and somewhat independent systems for both ON and OFF center, and the X, Y, and W cell classes may act independently. Certainly and W cells, which project only to the superior colliculus, must be subtracted from the ganglion cell population in acuity considerations.

ELECTROPHYSIOLOGICAL MEASUREMENTS OF GANGLION CELL RECEPTIVE FIELD PARAMETERS RELEVANT TO VISUAL ACUITY

Our experimental program has been devised to test certain models of ganglion cell coding. This required an analysis and an appreciation of the realistic parameters of ganglion cell receptive fields.

The most important information is the ganglion cell receptive field sensitivity profile. Two methods have been generally used to measure this sensitivity profile, a small exploring spot, and a series of centered progressively larger spots (Ricco plots). However, both methods have drawbacks. The first method uses a small exploratory spot to sample the sensitivity through the receptive field. But this has the drawback that a spot of light small enough to provide the desired resolution still has an appreciable optical spread. To make matters worse white light (with an even larger spread function than monochromatic light) is often (even usually) selected for the stimulus. The second standard method of measuring receptive field sensitivity is to test for complicance with Ricco's Law in which the product of area and log intensity are constant. The optical spread (or scatter) of the stimulus interferes with this method also, but not to such a large degree, as the test spots are larger.

In the cat (by far the most tested animal) the optical spread from a point of white light imaged on the retina has a diameter to 1/e intensity of almost 10' of arc (Wrässe, 1971). Even if a ganglion cell's sensitivity profile were a single receptor, an experimenter exploring with a 6' test spot (perhaps the limit of the test stimulus itself for most tangent screen optical stimulators) would find a receptive field of at least 15' to the 1/e fall in sensitivity of the test stimulus itself. This is shown in Figure 1. It is interesting that this size is the smallest reported for cat ganglion cells to date (Bonds et. al., 1972). More accurate measurements of field size can be made for larger receptive fields, but the 15' integration (optical spread plus physical spot size) smooths the fine details of any sensitivity profile. The Gaussian-shaped sensitivity profiles generally reported could in fact be produced by a great variety of acutal sensitivity profiles if the stimulus had a 15' Gaussian-shaped intensity profile as illustrated in Figure 2.

TABLE I

VARIATION IN RECEPTOR OUTPUT AS A FUNCTION OF THE LUMINANCE

Receptor Group	A	B
Sensitivity	1	1/2
Stimulus (Units of Light)	10	100
Summing Point Response (R)	K log (luminance)	K/2 log (luminance)
R	K log (10)	K log (100)
R	K	(K/2) · 2; or K

Inaccuracies in plotting ganglion cell receptive fields may arise from the case where receptor output equals a constant times the log of the luminance. If all other stages are linear, and the sensitivity of a particular group of receptors (A) is twice the sensitivity of a different group (B), then the receptor responses at the summation point (the input to the ganglion cell) from A and B will be equal when B receives 10 times the illumination of A.

VARIATION IN RECEPTOR OUTPUT AS A FUNCTION OF LUMINANCE

Inaccuracies in plotting ganglion cell receptive fields may arise from the case where receptor output equals a constant multiplied by the log luminance (which is usually the case). As an example of such inaccuracies, even assuming that all other stages are linear, say that the sensitivity of the particular group of receptors A is twice the sensitivity of the different group B then the receptor response at the summation point (the input to the ganglion cell) from A and B will be equal when B receives 10 times the illumination of A. This is shown in detail in Table I. Just this sort of difficulty can arise in Ricco plot experiments. In those types of experiments, sensitivities are compared even though the stimulus luminance levels are very different (in fact necessarily different to compensate for wide differences in stimulus areas). The small exploratory spot method also suffers from this difficulty but to a lesser extent since the luminance levels used do not vary quite so much.

Either the exploratory spot or the Ricco plot method can produce more accurate estimates of the receptive field sensitivity profile if appropriately modified. For the exploratory spot method, this modification is simply to mathamatically deconvolve the experimentally obtained sensitivity profile with the point spread function for the exploratory spot.

It is also possible to modify the Ricco plot method in order to avoid the usual inaccuracies which in this case, are mainly the result of the nonlinear stimulus intensity vs. response function. This modification of the Ricco field plot is to first measure it, and then compensate for its nonlinearities. For this compensation to work, the stimulus intensity vs. response function must be the same everywhere in the receptive field except for multiplication by a constant. This constant will, in general, be different at different places since it is, in fact, the relative sensitivity of at that point, and is the number we wish to find. This requirement, that the form of any nonlinearity be everywhere the same, is not unlikely, since the best known nonlinearity in the system is at the receptor stage, and there is no reason to expect the receptors to have dissimilar forms of nonlinearity as a function of location. The first step then, is to find if these requirements are met by measuring the stimulus intensity vs. response function at various points in the field (using as small a spot as available). If the form of the nonlinearity is the same, then the next step is to make a spot as available). If the form of the nonlinearity is the same, then the next step is to make a measurement of the response (in number of spikes) with different spot sizes (centered spots of an increasing diameter) for a fixed intensity, followed by measurements of the response (in spike numbers, again) as a function of intensity for a fixed spot size. A Ricco plot (intensity vs. spot size for a constant response) is obtained with the points which produce equal number of spikes (Fig. 3). The cell sensitivity profile can be derived from this.

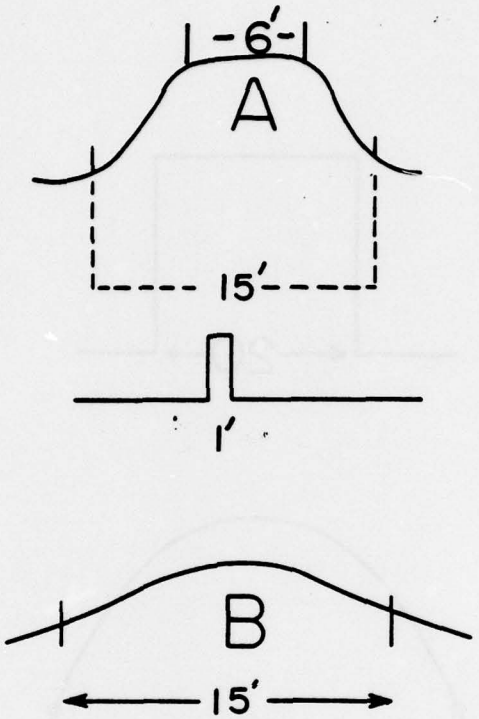

Figure 1

Receptive Field of a Single Receptor as Mapped with a Point Spread Function

Optical spread of 6' spot on the cat retina convolved with a 1' sensitive field due to one receptor. The response gives the optical spread of the 6' spot. Since the receptor diameter is very small compared to the optical spread the receptor acts like a Dirac function.

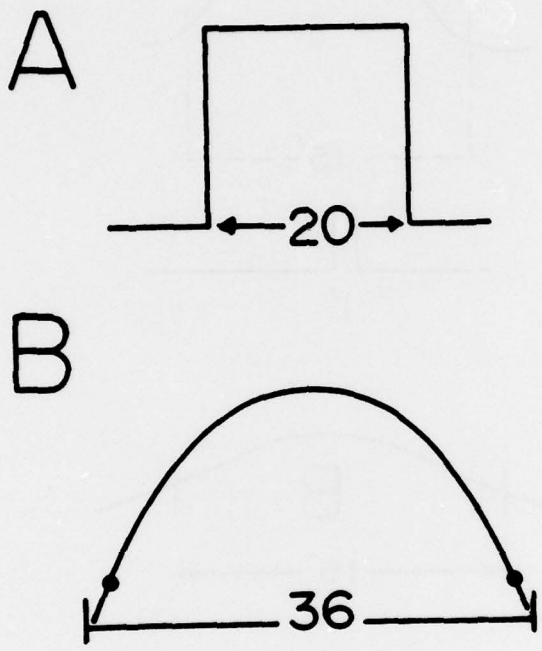

Figure 2

Distortion of a ganglion cell sensitivity profile when tested with a Gaussian point spread function stimulus. The true sensitivity profile (A) is convoluted with a Gaussian point spread function to give the measured sensitivity profile (B).

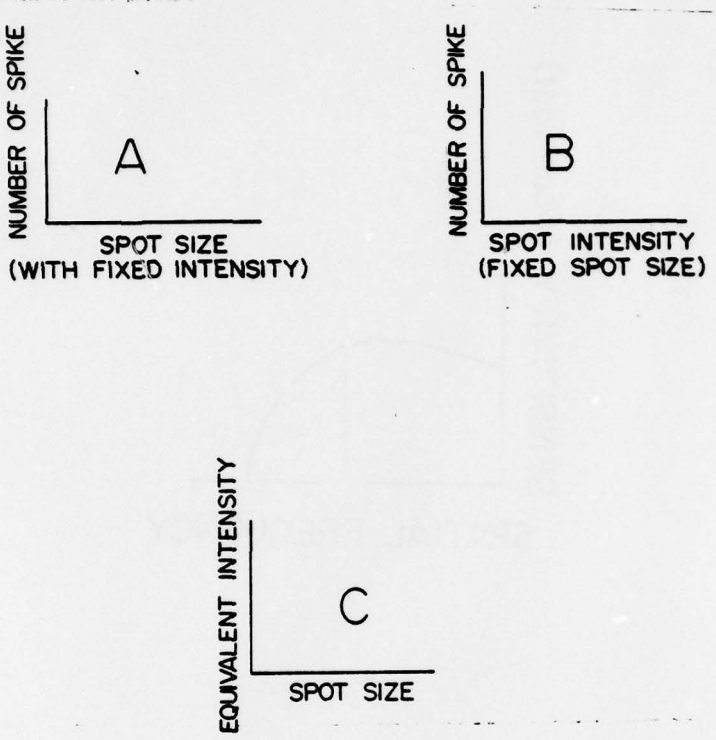

Figure 3

Response from Ricco Field Plot (Area vs. Intensity)

Graph C takes as equal those stimuluses which produce equal responses from graphs A and B. This approach assumes only that equal output implies equal input. It assumes nothing else about the nature of the response - stimulus relation, except that the form of the relation is fixed.

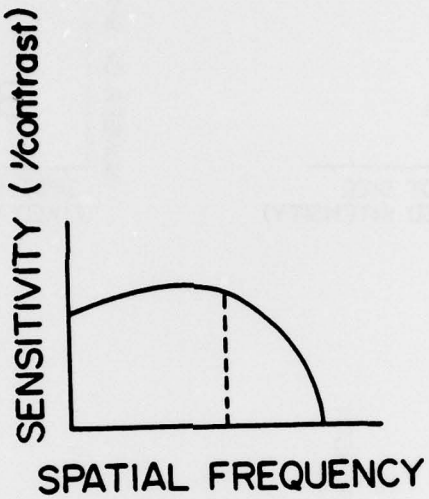

Figure 4

Spatial Frequency as a Function of Sensitivity

The frequency peak might be determined by a stimulus width which matches the receptive field center and reverses polarity at the same place the cell's sensitivity profile reverses polarity.

The experimental work proposed above has its main value in the limitations it places on acuity by the receptor density, the ganglion cell receptive field organization, and by modifications to the various models of visual acuity. As pointed out earlier the receptors are two dimensional arrays of extended (as opposed to point) detectors. Strict sampling theory does not necessarily apply to extended sampling processes, but some numerical methods can closely mimic the actual receptor sampling. The receptor may be considered as integrating light over a certain area with an output (response) which is a function of the integral. When a receptor array is set up, its response to an acuity target must be convoluted with the optical transfer function which will represent the actual intensity variation on the retinal receptors. This, then, will give the maximum theoretical acuity as a function of the receptor density. Receptor outputs can then be combined by a weighted summation to produce the theoretical ganglion cell output. A particular attempt will be made to find the area of summation and the weighing function which preserves as much information as possible from the receptors. However, in any case where there are more receptors than ganglion cells, the weighting function and the area of summation will have their boundary conditions imposed by the data from the electrophysiological experiments.

Another important characteristic of the retinal ganglion cell receptive field is the center-surround antagonism. In certain respects the effect of the surround antagonism on the center is similar to the well known lateral inhibition in the Limulus eye although the neural mechanism is quite different. Also, as in the Limulus, under some conditions, the spatial properties of the surround antagonism could contribute to the production of Mach bands. This surround antagonism might be the basis for the lumped nature of the sensitivity versus spatial frequency curve (Fig. 4). The spatial frequency peak might be determined by the stimulus width which matches the receptive field center and reverses polarity at the same place that the cell's sensitivity profile reverses polarity. This surround influence might also explain the changes in the spatial frequency, CSF, with Luminance. If the peak of the CSF is indeed due to the surround antagonism, then the surround can be supposed to diminish with luminance fall. Since the CSF curve flattens with fall in luminance, it is known that at very low luminances the surround effects do vanish. This might be the extreme luminance effect on the surround strength. If changes in overall luminance level produce a different surround effectiveness, then spot stimulation of the receptive field will not clearly demonstrate receptive field changes with the luminance (Fig. 5). A bar stimulus, however, with a large integrated area in the surround field would give an easily detectable change in the response function with changes in the luminance level.

As unexpected complication in matching the spatial distribution profile of the ganglion cell receptive field sensitivity changes with intensity related changes in visual acuity arises from the fact that the wavelength sensitivity of the response is location dependent within the receptive field. This means that simple changes in sensitivity to test stimuluses are not sufficient to describe the receptive field, but variations in wavelength sensitivity must also be considered. Also, some properties of the receptive field which have previously been

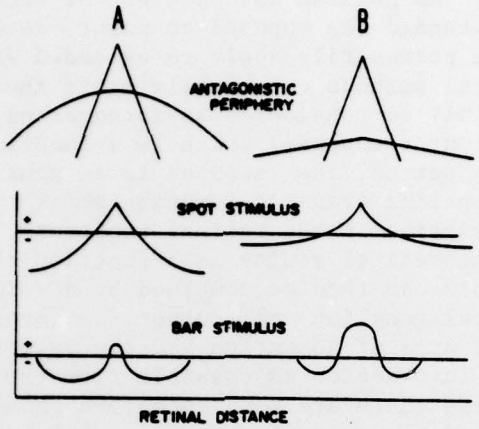

Figure 5

Receptive field profile response to spot and bar stimuluses of a retinal ganglion cell similar to those in the cat and monkey.

Even though the surround in A is stronger than B, the change in the profile of the surround antagonism does not produce much difference in the size of the center response when explored with a small spot stimulus. However, when the same receptive fields are explored with a bar stimulus with its long axis perpendicular to the plane of the plot, the height of the center responses are very different. The width of the center response is much narrower when the peripheral antagonism is stronger. This is due to the larger stimulus integration of a bar in the peripheral field. Thus, the peripheral antagonism makes larger contributions to the central area stimulus with the bar.

considered as enhancing color discrimination may introduce an inhibitory factor to sharpen up the receptive field. On the other hand, the same factor in other ganglion cells may foster the opposite effect on visual acuity. Overall the result should be an even smearing of the signal, at best, as regards visual acuity. That is, some cells will have their spatial frequency characteristics helped by it, others will be degraded by it.

The area centralis of the cat retina is almost ideal for this analysis. The visual acuity is high in this region, yet measurements of its ganglion cells show much larger receptive fields than the visual acuity seems to warrant. Also, the anatomical relations of the ganglion cells to their underlying receptors in it are easier to map as there is no foveal depression to displace the ganglion cells and other neural elements. A simple examination of the number of ganglion cells easily shows that there must be an enormous overlap of receptive fields. Thus, even where visual acuity is the highest, overlapping receptive fields suffice for visual signal processing in the cat retina. We feel that a similar overlapping fields, nor will there be any point to point information transfer within the retina or higher visual centers, even for the fovea.

EXPERIMENTAL PROCEDURE

Foreword

The animals involved in this study were procured, maintained, and used in the accordance with the Animal Welfare Act of 1970, and the "Guide for the Care and Use of Laboratory Animals" prepared by the Institute of Laboratory Animal Resources-National Research Council.

TYPES OF ANIMALS USED

Cats and three types of monkeys were used in the present study, rhesus (Macaque), the Himalayan Macaque (Macaca assamensis), and the crab-eating or cynamolgus (macaca fascularis). All were essentially identical in terms of the recordings from the eye. However, the bone structure of the head differed among them, especially in the older animals. The younger animals had less prominent brow structures which made recording from the central portion of the eye much easier.

ANESTHESIA AND SURGERY

All experiments were carried out under general inhalation anesthesia as described. Animals were initially anesthetized with ether. When a suitable depth of anesthesia was obtained, an intravenous infusion of gallamine triethiodide (Flaxedil) was initiated. The animal was then intubated

and respired artificially with a ventilator (Harvard Apparatus Company Model 661). Surgical anesthesia was maintained with 70% nitrous oxide/30% oxygen mixture in all animals throughout the experiment. Expired pco_2 was monitored continuously by a Beckman Model LB-1 medical gas analyzer with the aid of an indicator alarm (Electrodyne MS-25). In addition to the control of gas mixture flow furnished by the anesthesia machine (Ohio Chemical and Surgical Instrument Company, Model 212B), a manometer was installed to avoid any damage to the animal's lung from over-pressure during the inspiration and exhalation parts of the respiratory cycle.

The infusion of Flaxedil with dextrose and saline was continued throughout the experiment to assist in fixing the eyes. A local anesthetic (5% Lidocain ointment) was applied to the surface of the conjunctiva before an incision was made to insert the electrode into the eye, and to all other incision margins and pressure points. Animals were maintained at normal body temperature by means of a heating pad. These life support systems were adequate to maintain a cat in satisfactory physiological condition for 24 to 48 hours. The experiment with monkeys was never more than eight hours long.

Although nitrous oxide, even at high pressures, does not produce surgical anesthesia (Brown et al., 1927, Venes et al., 1971), it has been established that 60% nitrous oxide in oxygen produces a high degree of sedation and analgesia in the cat and monkey and is an adequate anesthetic where only mildly noxious stimulants are present; for example, the direct electrical stimulation of peripheral nerves at frequencies up to 3 Hz or foot pad shock (Vense et al., 1971). In our experiments, the animals are under deep ether anesthesia during all surgical procedures. The level of ether anesthesia was sufficient to terminate spontaneous respiration and the animal required artificial ventilation. In addition, all cuts were infiltrated with a local anesthetic. Only after surgery was ended was the ether discontinued and 70% nitrous oxide/30% oxygen used. The insertion of the electrode through the pars plana involved no pain and is similar to operations that are often carried on in humans with only a local anesthetic. The heart rate was continuously monitored and at no time were heart rate changes detected which could be associated with pain perception.

The gallamine triethiodide (Flaxedil) drip is not required to relax the animal. It assists in establishing the high degree of eye immobility required for single cell retinal recordings (Enroth-Cugell and Robson, 1966). It has also been established that Flaxedil has no effect on retinal ganglion cell responses (Enroth-Cugell and Pinto, 1970). Because of these considerations nitrous oxide and Flaxedil have been routinely used by all workers in this field.

Nitrous oxide is used by us and others because it has been shown to have only slight effects on evoked CNS responses as compared to the

strong central depression produced by other bolatile anesthetics and barbituates (Van Norren and Padmos, 1977). A depressive action in the retina has been seen with some of these anesthetics as well (Van Norren and Padmos, 1977). It is obviously important to minimize drug effects on the CNS when studying the activity of the visual system.

OPTICAL STIMULUS

The optical stimulator has been described previously (39) and has two channels with essentially equivalent pathways. Each channel could be varied independently and included a collimated region to allow the use of interference filters. The characteristics of the interference filter are shown in Table I.

A Maxwelliam view was used for the stimulus, and the field aperture of the optical stimulator was focused on the retina. The stimulus beam was approximately normal to the retina to eliminate any changes in the stimulus-response relations from the Stiles-Crawford effect. A third channel is available, which is suitable for chromatic adaptation of the entire retina through the series of Wratten filters given in Table II.

The optical system output was calibrated with a Epply thermopile (Type 12 junction linear with a quartz window). The sensitivity of this thermopile, in turn, was calibrated against a secondary standard lamp, Epply Type NALCO A-10, whose initial calibration is traceable to the National Bureau of Standards.

The electrophysiological recording equipment has been described previously (Wagner et al., 1960 and Wolbarsht, 1978).

EXPERIMENTAL DESIGN

Most data points were measured with a constant response technique. That is, when any selected parameter of the stimulus was changed the intensity was varied sufficiently to obtain a response equal to the criterion one at the original test conditions. Some data points were obtained by a silent substitution techniques in which the stimulus was alternated from a new wavelength to the original one, or from one spatial distribution to another while the intensity of the altered position was changed to minimize or eliminate the response. Although this technique has problems, as some ON responses maybe confused with OFF responses, a selection of the proper type of chromatic adaptation ususally allow a balance to be reached, and in this way quite accurate data can be obtained. Spatial isolation of the stimulus can also be used to assist in elucidating the spectral sensitivity within a ganglion cell receptive field as composed of the various cone systems in addition to the rod contribution.

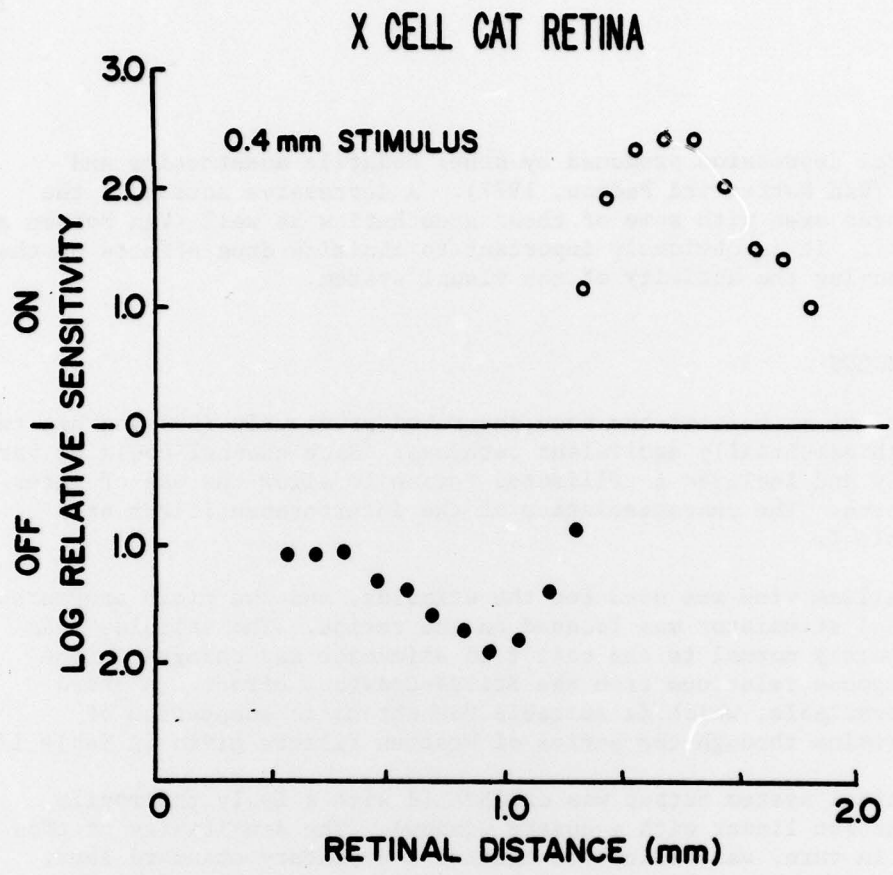

Figure 6

Sensitivity profile of an X type ganglion cell in the cat retina.

The data points indicate the intensity required to give a criterion response. The ON response in the center has a dome shaped sensitivity profile. The stimulus is 400 μm on the retina, or approximately 2 degrees of arc in the visual field. The sensitivity profile of the peripheral OFF response should be compared with the central ON response loss of sensitivity with distance. More information on the central ON response is given in the Ricco field plot in Figure 7, which suggests that the top of the sensitivity profile should be flatter.

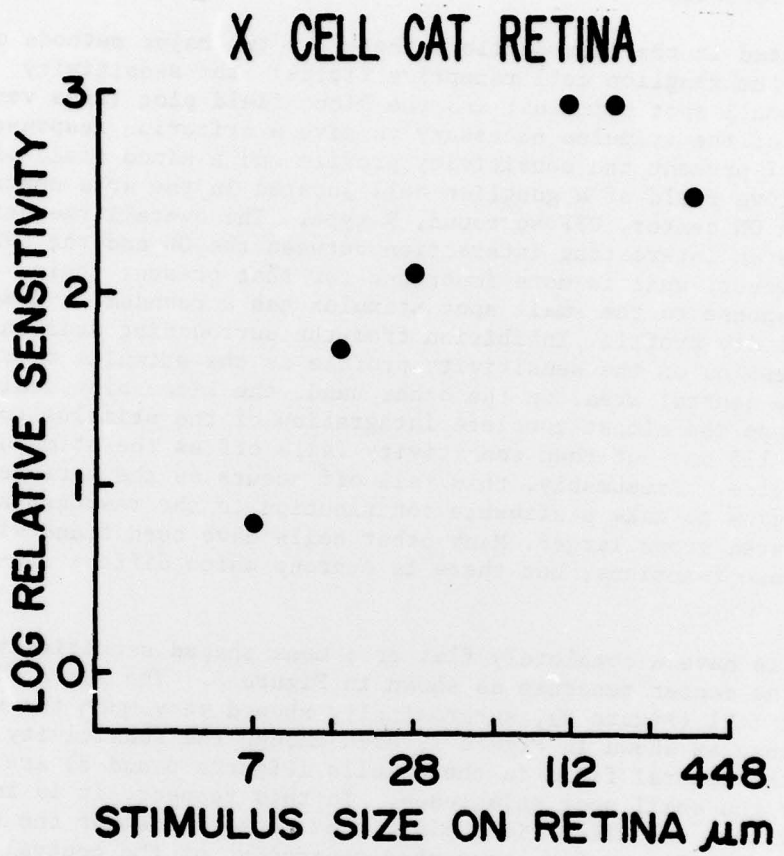

Figure 7

The Ricco field plot (Area X log intensity)

The data points indicate the intensity required to give a criterion response fot the ON response of a cat retinal ganglion cell (X type). The sensitivity profile of the central ON and peripheral OFF responses of this cell are shown in Figure 6. This Ricco field plot shows complete intefration within the central ON response for approximately 110 µm. The fall off of sensitivity with increased stimulus area is probably dur to the recruitment of inhibition from the antagonistic surround.

RESULTS AND DISCUSSION

As indicated in the Introduction, there are two major methods of investigating the ganglion cell receptive fields: the sensitivity profile to a small spot stimulus; and the Ricco field plot (area versus the intensity of the stimulus necessary to give a criterion response). Figures 6 and 7 present the sensitivity profile and a Ricco field plot for the receptive field of a ganglion cell located in the area centralis. The cell is an ON center, OFF surround, X type. The overall receptive field presents an interesting interaction between the ON and the OFF responses. However, what is more important for that present topic, the central ON response to the small spot stimulus has a rounded or dome shaped sensitivity profile. Inhibition from the surrounding area only makes an impression on the sensitivity profile as the stimulus moves outside of the central area. On the other hand, the Ricco plot indicates by its 45^{o} slope the almost complete integration of the stimulus to approximately 115 μm, but then sensitivity falls off as the stimulus increases in size. Presumably, this fall off occurs as the peripheral inhibition begins to make a sizeable contribution to the response as the stimulus area grows larger. Many other cells have been found with similar response functions, but there is a group which differs significantly.

Some cells have a completely flat or a mesa shaped sensitivity profile for the center response as shown in Figure 8. The Ricco field plot for this cell (Figure 9), surprisingly, showed very much the same type of response as shown in Figure 7, even though the sensitivity profiles of the central field in these cells (Figures 6 and 8) are much different for the small spot stimuluses. In this respect, it is interesting that neither than the Ricco field plots from these cells nor the responses to small spot stimuluses show any marked sharpening of the central response from lateral inhibition. This data is in contrast to most models of the mammalian retina. However, there does not seem to be sufficient lateral inhibition in the retina to play an important role in either acuity or color vision.

Figures 6 and 7 show an X cell response. The data available from the primate visual system seems to be consistent with the proposed that X cells are the basic units of acuity. It has been suggested that all mammalian retinals have the same basic organization (Wolbarsht, 1978; Ringo et al., 1977). From this, it would appear that all information on visual acuity in the cat retina would be passed on to the higher visual centers through this particular type of ganglion cell.

An examination of the slopes of the Ricco field plots of cells in and around the area centralis as well as those for more peripheral cells, shows a remarkable similarity in shape between them, Also, the over all sizes of the central area of total integration are nearly the same. The variation between Ricco field plots in different parts of the cat retina seems to be quantitative rather than qualitative. This is true even when the area centralis is compared with the most peripheral regions. Although the cells illustrated here are typical of our data,

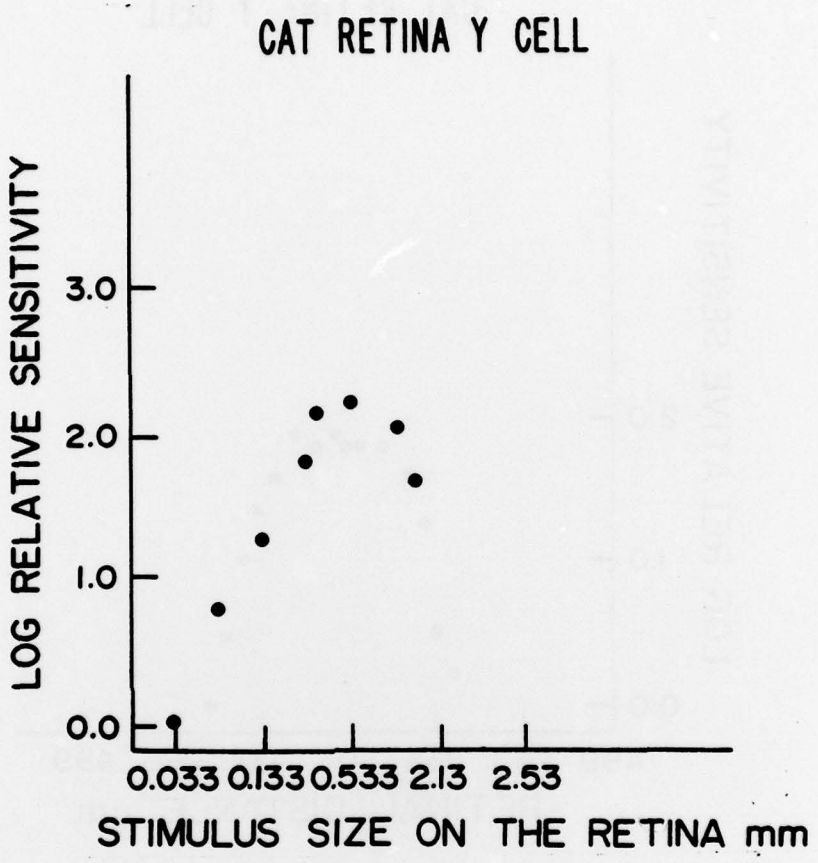

Figure 8

Sensitivity profile for central OFF response of a Y cell in the cat retina.

The data points indicate the intensity required to give a criterion response. The flat top of the central response here should be compared to the profile of the cell shown in Figure 6. Although the central responses of those cells have quite different sensitivity profiles, their Ricco field plots are almost identical, as shown in Figures 9 and 7 respectively.

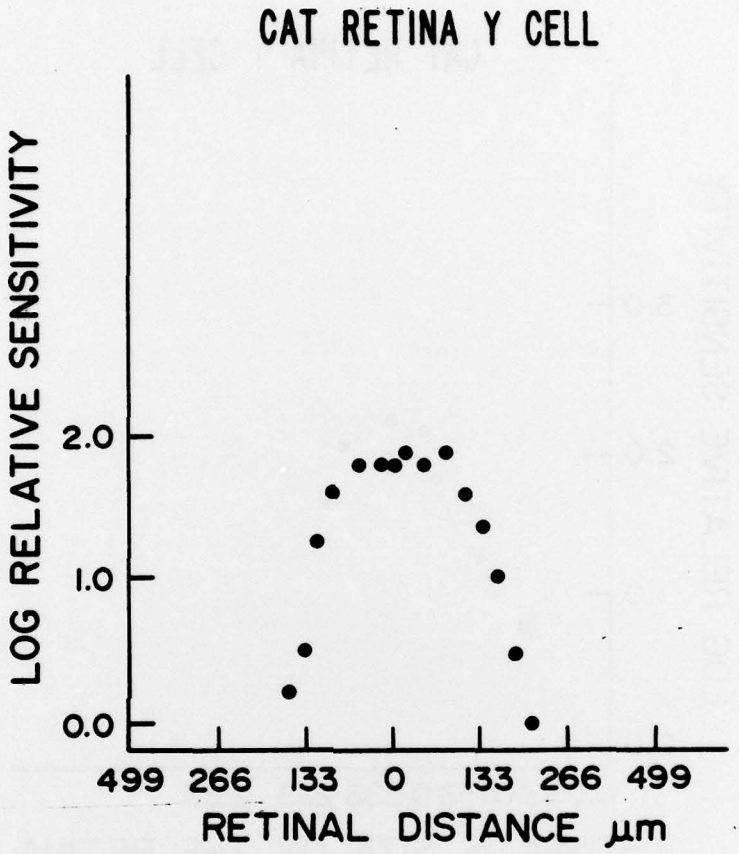

Figure 9

Ricco field plot (Area X log intensity).

The data points indicate the intensity required to give a criterion type response for the OFF response of a Y cell in the cat retina. The sensitivity profile for the central OFF response of this cell is shown in Figure 8. Complete integration is shown up to about 400 µm, which is sloghtly larger than the flat part of the sensitivity profile for this cell.

only a small number of cells are known in this much detail. For example, we have only the sensitivity profile to a small spot stimulus on many cells, while on others we have only the Ricco field plot. Our data leaves two questions still open:

(1) Whether the sensitivity profile is flat, with complete integration taking place in the center of the field, as indicated by the Ricco plot?
(2) Whether there is actually a locus containing a very few (or even a single) receptors of maximum sensitivity in the center of the receptive field?

The receptive fields we have found have inputs from many types of cones. Similar data has been found in the monkey retina. Based on our own work, and the data shown in the literature (DeMonasterio and Gouras, 1975), the center response area seems to be fairly large. That is, it always includes more than the single receptor, and probably more than one cone type, even in the foveal area of primates. However, the Ricco field plots and the map of the sensitivity profile of the receptive field found with a small spot stimulus give us additional information about the spatial response properties of ganglion cells in relation to the stimulus pattern on the retina.

In a pilot series of experiments we have turned up possibly another useful approach to this problem by using the movement of small spots within the receptive fields of retinal ganglion cells. The spot is moved very quickly in the receptive field of a cell whose sensitivity plot is similar to those shown in either Figure 6 or Figure 8. In our experiments the maximum sensitivity to movement occurred at the border between the central and surround responses, indicating that the surround mechanism contributes to visual acuity, possibly by detecting smaller changes in light intensity. This increased sensitivity may be used in conjunction with saccades, or may enhance the response to a particular part of a pattern. Which, is used is not at present clear. However, it is interesting that the 450 nm (blue) cone contribution to a ganglion cell does not show the center surround organization responses to moving targets even though other cones connected to the same ganglion cells do. This may indicate why the visual acuity at the blue end of the spectrum is much lower that it is in other parts. It also suggests why the blue cone is not part of the visual acuity mechanism.

Only through those approaches, both new and old, can we find out the basic information necessary to formulate a model of the neural network within the retina responsible for maximum visual acuity.

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