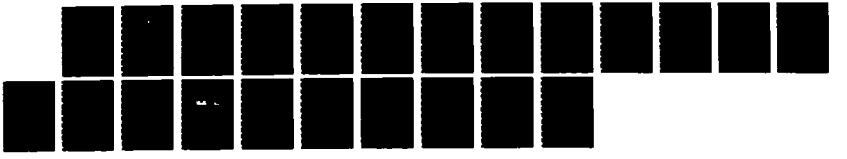
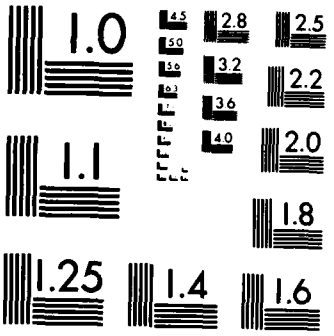
AD-A172 594 STATIC AND DYNAMIC REPPONSES OF RETINAL GANGLION CELLS 1/1
(U) DUKE UNIV DURHAM NC DEPT OF PSYCHOLOGY M WOLBARSHT
AUG 85 NADC-86017-60 N62269-84-M-3152

UNCLASSIFIED F/G 6/16 NL





REPORT NO. NADC-86017-60

AD-A172 594

STATIC AND DYNAMIC RESPONSES OF RETINAL GANGLION CELLS

Myron L. Wolbarsht
Department of Psychology
Duke University
Durham, NC 27706

AUGUST 1985

Final Report
Contract No. N62269-84M-3152

Approved for Public Release; Distribution is Unlimited

Prepared for
NAVAL AIR DEVELOPMENT CENTER
Department of the Navy
Warminster, PA 18974

NOTICES

REPORT NUMBERING SYSTEM - The numbering of technical project reports issued by the Naval Air Development Center is arranged for specific identification purposes. Each number consists of the Center acronym, the calendar year in which the number was assigned, the sequence number of the report within the specific calendar year, and the official 2-digit correspondence code of the Command Office or the Functional Directorate responsible for the report. For example, Report No. NADC-86015-20 indicates the fifteenth Center report for the year 1986, and prepared by the Systems Directorate. The numerical codes are as follows:

CODE	OFFICE OR DIRECTORATE
00	Commander, Naval Air Development Center
01	Technical Director, Naval Air Development Center
02	Comptroller
10	Directorate Command Projects
20	Systems Directorate
30	Sensors & Avionics Technology Directorate
40	Communications and Navigation Technology Directorate
50	Software Computer Directorate
60	Aircraft & Crew Systems Technology Directorate
70	Planning Assessment Resources
80	Engineering Support Group

PRODUCT ENDORSEMENT - The discussion or instructions concerning commercial products herein do not constitute an endorsement by the Government nor do they convey or imply the license or right to use such products.

UNCLASSIFIED
SECURITY CLASSIFICATION OF THIS PAGE

AD-A172594

REPORT DOCUMENTATION PAGE

1a REPORT SECURITY CLASSIFICATION Unclassified	1b RESTRICTIVE MARKINGS
2a SECURITY CLASSIFICATION AUTHORITY	3 DISTRIBUTION/AVAILABILITY OF REPORT Approved for Public Release: Distribution is Unlimited
2b DECLASSIFICATION/DOWNGRADING SCHEDULE	
4 PERFORMING ORGANIZATION REPORT NUMBER(S) NADC-86017-60	5 MONITORING ORGANIZATION REPORT NUMBER(S)
6a NAME OF PERFORMING ORGANIZATION Duke University 6b OFFICE SYMBOL (*If applicable*)	7a NAME OF MONITORING ORGANIZATION Naval Air Development Center
6c ADDRESS (*City, State, and ZIP Code*) Durham, NC 27706	7b ADDRESS (*City, State, and ZIP Code*) Warminster, PA 18974
8a NAME OF FUNDING SPONSORING ORGANIZATION Naval Air Systems Command 8b OFFICE SYMBOL (*If applicable*) 320R	9 PROCUREMENT INSTRUMENT IDENTIFICATION NUMBER
8c ADDRESS (*City, State, and ZIP Code*) Washington, D.C. 20361	10 SOURCE OF FUNDING NUMBERS PROGRAM ELEMENT NO: PROJECT NO: TASK NO: 04101001 WORK UNIT ACCESSION NO: DG157

11 TITLE (*Include Security Classification*)
STATIC AND DYNAMIC RESPONSES OF RETINAL GANGLION CELLS.

12 PERSONAL AUTHOR(S)
Dr. Myron Wolbarsht

13a TYPE OF REPORT Final	13b TIME COVERED FROM Jul 84 TO Jul 85	14 DATE OF REPORT (*Year, Month, Day*) Aug 85	15 PAGE COUNT 28

16 SUPPLEMENTARY NOTATION

17 COSATI CODES		
FIELD	GROUP	SUB-GROUP

18 SUBJECT TERMS (*Continue on reverse if necessary and identify by block number*)
Vision; Retinal Model; Edge Detection; Discontinuity Detection

19 ABSTRACT (*Continue on reverse if necessary and identify by block number*)

In this report, experimental work on a model based on information processing in the retina for global processing of the information gathered by individual detectors in a focal plane array is described. The model gives edge or discontinuity detection for pattern recognition under minimal contrast conditions. As the resolution achieved by the retina under some conditions is much better than the first order Rayleigh criterion, the model should have similar high performance. Measurements of small movements of the image in the focal plane, such as due to vibration, were made a part of the performance. The data indicates that more rapid movements enhanced the responses at the center-surround junction, while the sensitivity in the center remained depressed. A key part of the system is the preservation of analogue data until discontinuity and gray (color) scale information have been separately encoded. Future tests on model systems to determine other optimum circuit configurations are described.

20 DISTRIBUTION/AVAILABILITY OF ABSTRACT ☐ UNCLASSIFIED/UNLIMITED ☒ SAME AS RPT ☐ DTIC USERS	21 ABSTRACT SECURITY CLASSIFICATION Unclassified
22a NAME OF RESPONSIBLE INDIVIDUAL Phyllis E. Morway	22b TELEPHONE (*Include Area Code*) (215) 441-1871 22c OFFICE SYMBOL 60B1

DD FORM 1473, 84 MAR — 83 APR edition may be used until exhausted. All other editions are obsolete.

SECURITY CLASSIFICATION OF THIS PAGE
UNCLASSIFIED

TABLE OF CONTENTS

INTRODUCTION

A description of the characteristics of the human visual system indicates that it performs considerably better than any present detector array. Histological investigations of the anatomy of the photoreceptor layer and data from optical measurements (Gubisch, 1967;Snyder and Miller, 1977) of the characteristics of the retinal image (point-spread, line-spread functions) indicate that the human visual system can detect separate sources whose angular sublenses are much less than the width of a single receptor (Westheimer, 1977). This is an apparent violation of the first order Rayleigh criterion for the lower limit of resolution of a detector array where the illuminated and unilluminated portions of the image form the basis for detectability. When consideration is given to several factors, the analysis of the threshold performance is made more puzzling :

(1) The detectors in the retinal array are the same order of magnitude as the wavelength of light;

(2) The limits of resolution require defraction-limited images;

(3) Visual performance is as good in white light as in monochromatic;

(4) Image movement due to head and body tremor and small amplitude eye rotation is present during the known integration time for the optimum detection of the image.

The factors involved in visual acuity and the quality of the visual image have been reviewed in detail by Gubisch (1977), Ditchburn (1973), Le Grand (1967), and most recently by Wolbarsht (1985) with a detailed discussion of the particular points listed above.

Prior models of visual system information processing have tended to conclude that there is an orderly point-to-point representation of the retinal receptor array in the cortex (Helmholtz, 1924). Although both the anatomical and neurophysiological studies have suggested for some time that this view is too simplistic, nevertheless, no model has been based on anything other than the match between the defraction image and the receptor array, the performance limit of the system. Polyak (1941) and others have suggested a direct connection between the detectors and the cortex in the area of best vision, the fovea. However, the extensive interconnections which have been demonstrated between the retinal neurons processing the information gathered by the detectors (Kolb, 1977), as well as the limited number of fibers in the optic nerve (always less than the number of detectors) have either been ignored, or the view has been taken that the system achieves its high performance by pattern recognition. That is, the neural representation is poor, but the brain guesses as to what source might have caused the degraded pattern represented at the cortical level.

On the other hand, evidence has been accumulating about the nature of the information processing in the retina. The most recent experiments have led to a radically different theory of information handling that suggests a model which seems to avoid the limitations discussed above. The model that we have formulated is based on several aspects of the information processing in the retina, and suggests that the high overall performance does not depend on pattern recognition, but it is rather pre-processing of the neural information that is the limit to the detection performance of the system. This is especially significant because the overall visual acuity seems to extend beyond that which is usually considered the acuity limit by optical considerations alone (Wolbarsht et al, 1985).

Whether or not the visual system uses the information in the way the model suggests is not important as yet, for much information about how the retinal output is used by succeeding stages is still missing. It is important, however, that the present model can be examined to determine if the processing types of information will improve the detectability of targets imaged upon retinal photoreceptor array. First, it must be clear that the model, of course, does not gain its improvement of detectability without certain trade-offs or losses. That is, information, of course, can not be manufactured and there are real limitations, but these limitations themselves may have certain advantages when the retina is organized for surveillance, as will become evident.

The present model for the visual system can be best thought of as a discontinuity detector operating within a color framework which gives a highly nonlinear representation of all edges independent of color with an exaggerated contrast scale. A linear representation of the various intensities of color is filled in between the discontinuities. This linear part of the system depends upon the use of feedback to adjust the mid-point of the intensity scale to the ambient lighting level. The present model of the visual system incorporates the large amount of evidence which suggests that there is also some compression of size representation, particularly at the low end of the scale. Thus, small objects have a certain minimum representation, and there may be many fewer locations (pixels) in the display array than in the detector array.

For modeling purposes, as in the real system, the most convenient place to represent the coded information from the detector array before it is decoded in the cortex is as it leaves the retina in the optic nerve. The individual optic nerve fibers are the output of the retinal ganglion cells which represent the third stage of computation in the retina.

The details of the human visual system which are incorporated in the model are as follows:

1. The visual system in common with most, if not all, other sensory and motor systems in animals has analogue information processing and transfer. The nerve impulses, so popularly viewed as digital information, are really pulsed-coded analogue data. The impulse spacing or instantaneous frequency and the bunching patterns are the analogue information for the next stage. In general, the impulse patterns are translated into decremental slow potentials and summed with incoming information from other normal channels to form the basis for the next stage of computation.

2. No receptor in the retina has a unique transmission line to a specific neuron in the cortical representation of visual space.

3. Each computing unit in the retina, beginning with the photodetectors, has a positive and negative output, possibly through interneurons, to its succeeding stages of neurons. The information from each unit has a lateral spread in passing to the next stage. Thus, by the time the third level of neural units, the ganglion cells, is reached, a large area of the retina is contributing information into each unit. These spheres of influence at the ganglion cell level are termed receptive fields and they have a large amount of overlap, although the optimum amount of overlap is not known. The retinal ganglion cell reception fields have a complicated structure whose transfer functions can be represented in profile as shown in Figure 1. These receptive fields can be represented as the sum of two Gaussian curves, one representing the positive input to the ganglion cell, the other representing the negative input. As the input Gaussian curves are not the same width, the summed output for steady state input from the two Gaussian curves is represented by a triphasic curve often termed "the Mexican hat" or sombrero.

The use of the triphasic curve (or Mexican hat) as a substitute for a simple step function profile allows both integrating and correlation functions to be incorporated in the computations for edge detection and localization. Nevertheless, as so far shown, this model is only a more sophisticated version of the point-to-point representation of the detector array. The location of any discontinuity still involves finding the ganglion cell whose receptive field center coincides with the detector indicating the location of the discontinuity. Basically, it requires an identification of a specific ganglion cell with each photoreceptor and possibly a one-to-one ratio between ganglion cells and detectors.

4. Under physiological conditions, the image upon the detector layer is in continual motion due to the frequent small amplitude and random direction tremor resulting from head, body, and ultimately eye translations (Bengi and Thomas, 1973 .and van Buskirk et al, 1966). Eye rotations, if small, may add to these (Ditchburn, 1973).

As mentioned above, the detection of visual information is a dynamic process, and the retinal image is always in motion due to small amplitude tremor of the head and body and, to some extent, to eye rotation. Whatever the source of the motion, there is a semi-periodic movement of the retinal image, random in direction about a common location. Large or saccadic eye movements do not contribute to vision and are omitted in the present model. The frequency of the tremor (up to 50 Hz) is well within any integration time for detection of the retinal image under ordinary ambient lighting conditions. Thus, the transient response of the system to such small amplitude image motions on the retinal detector array must be considered as a part of the ganglion cell output during discontinuity detection. Such retinal image motion responses are shown in Figure 2. In this case, the interplay between the positive and negative responses produces a cup-shaped transfer function profile rather than the Mexican hat profile shown in Figure 1 and as a solid projection in Figure 2. The center has a minimum output flanked on all sides by maximum responses in the region where the positive and negative inputs are approximately equal.

When the data in Figure 1 and Figure 2 are combined, the response from a single ganglion cell under normal in vivo conditions can be understood. The portion of the retinal image in the center of the receptive field is averaged for wavelength distribution and intensity. This results in a more or less steady output from the ganglion cell. Superimposed on this steady background are the bursts of high frequency which accompany any discontinuity moving within the annular region where the central (restricted) and peripheral (diffuse) groups of inputs have an equivalent sensitivity, and thus, a combined high sensitivity to slight motions. In the neural analogue system (simple or pulse coded), both types of information can be carried along the same transmission line, as they have different frequency domains.

The portion of the information carried by the burst of high frequency transient can be used to localize discontinuities in the following manner. The maximum output from a single ganglion cell in response to a small displacement of a discontinuity within its receptive field is eccentric to the center of its receptive field as shown in Figure 2. From this, the motion of a discontinuity at a particular retinal location would give a maximum signal in the ganglion cells located eccentrically in a circular fashion about the locus of the motion in the detector array. Thus, the problem of locating the discontinuity on the detector array is not one of finding a single ganglion cell whose output is different from the others. It is rather, one of finding the ring or cluster of ganglion cells whose output is different from other ganglion cells. Succeeding stages can localize the discontinuity to the weighted average of ganglion cells whose center of gravity is those detectors at the center. Obviously, in such systems, the precise location of the detector might not be represented in the output. Only the presence of the discontinuity itself needs to be represented. Indeed, since motion is involved in the detection, the exact location can not be specified.

In fact, the overall performance of the system can be considered to be represented by a sort of "Heisenberg Uncertainty Principle" applied to vision. This means that at threshold, the loss of the knowledge of the exact location of a discontinuity is traded for the certainty of its presence. In this system, it is obvious that small discontinuities can be detected more reliably, yet with less certainty about their location in space relative to the position of the eyes. Since the presence of a discontinuity is represented only as the center of gravity of a cluster of ganglion cells outputs, accurate analysis of size may be also lost for very small discontinuities. However, relative judgments between two small discontinuities of similar contrast may still be given with precision.

The information coming from the ganglion cells is analyzed in the higher visual centers by splitting it into high and low frequency components. As described above, the high frequency or transient component signals a discontinuity located eccentrically to the receptive field center. The low frequency component would be representative of the center of the receptive field and will give intensity information. Also, if detectors with different wavelength sensitivity are included in the detector array, color discrimination can be achieved by a comparison of responses from the ganglion cells with different types of detector connections which are included in the cluster make-up. The actual ganglion cells found in the retina have varying types of detectors with both positive and negative inputs to the central and peripheral portions of the receptor field, as explained in the legend to Figure 1. Since the vast majority of the detectors are summed equally for detection of discontinuity information, the presence of color detectors does not seriously degrade the performance of the system for discontinuity detection. Different channels connect the detectors to the ganglion cells for discontinuity detection and for color and intensity information. The gain of each transmission line can be adjusted separately before combination at the ganglion level to depend upon ambient light conditions. In this way, the intensity scale of the system can be fairly linear over a factor of about 100 with reference to ambient lighting over the entire range of human vision (a factor of a million or more). In an electronic system, feedback biasing of gain and adjustment of the current through the detectors could accomplish the same task.

In order to get such electronic systems to work, many interconnections must be made between the detectors and the pre-processing units representing the ganglion cells. For any reasonable sized detector array, such large scale types of interconnections can only be done by integrated circuit technology with a special chip. A simplified model with only a few detectors in order to determine the parameters forming the basis of a large scale integrated circuit in a pre-processing detector array to represent the retinal portion of the visual system is the obvious first step in such a process.

The actual decoding procedure used by the retina in the geniculate and at the cortical level is not known at the present. Even though much information is available, it is not sufficiently organized to allow formulation of a model with the same precision as for the retina. However, certain general features of the model can be highlighted.

1. Since motion is an integral part of the detection process, the array can be set up to process only information when there is image motion. In this case, only a portion of the image is in motion, the rest is held constant. Manipulation of the size of the receptive field relative sensitivity to small motions could render the overall performance insensitive to vibrational movement of the entire detector array and only detect differential motion of discontinuities within the image on the detector array. Alternatively, the whole image may be moved to simulate the image motion on the retina, thus giving high detection capability over the entire detector array to images which are essentially still or at least moving slowly. Also, portions of the image which move rapidly could be ignored while those that are stationary could be resolved with high precision.

2. Proper selection of wavelength sensitivity of the detectors could allow detection of small discontinuities against various types of backgrounds with a high degree of precision with either wavelength or intensity contrast as the basis. Also, intensity and color information could be obtained simultaneously in the same detector array without seriously compromising the ability to detect discontinuities.

3. The sharper the discontinuity on the detector array, the larger the ganglion cell response to movement. Thus, an indication of proper focus is easily found when the imaging optics are moved in relation to the detector array. A signal indicating the achievement of focus in the plane of the detector array can be derived simply from the total output or from any portion of the detector array analogously to that from the retinal ganglion cells.

4. In the visual system of a human or one with a similar visual system such as the eagle, fewer ganglion cells than receptors are needed for detection of even small discontinuities (the ratio may be 1:10). As point-to-point representation is not necessary, there can be many fewer transmission lines to the decoding representation than there are detectors (pixels) in the detector array.

5. Modern detector arrays are essentially analogue in output, and the present computing system may, thus, make full use of the analogue model without necessarily changing it into digital information immediately. The pre-processing can have a very compressed gain range for the gray scale representation of discontinuities, it can even be non-linear or digital, while the intensity and color scales near the area of discontinuity can be preserved in a linear non-compressed fashion with a single transmission line sufficing for both components of the signal. However, the output stage in the electronic system analogous to the ganglion cell to optic nerve can be digitized and processed by conventional pattern recognition technology.

RESEARCH METHODS AND RESULTS

The collection of data from the retina used essentially the same techniques as described in previous reports (Wolbarsht and Ringo, 1981). The description that follows shows how the plots in Figures 1 and 2 were made. The responses of single ganglion cells from the retinas of adult cats were recorded. The methods used in this study were generally the same as those described in a previous work (Wolbarsht and Ringo, 1979).

FOREWORD

The animals involved in this study were procured, maintained, and used in 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.

ANESTHESIA AND SURGERY

All experiments were carried out on healthy adult cats under general inhalation anesthesia. 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 artifically with a ventilator (Harvard Apparatus Company Model 661). 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 animals' lungs from over-pressure during the inspiration and exhalation parts of the respiratory cycle.

The infusion of Flaxedil with dextros 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.

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 (Venes et al., 1971). In our experiments, the animals were under deep ether anesthesia during all surgical procedures. The level of ether anesthesia was sufficient to terminate spontaneous respiration and the animals 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 volatile anesthetics and barbiturates (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 CMS when studying the activity of the visual system.

OPTICAL STIMULUS

The optical stimulator has been described previously (Wolbarsht, 1978) 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.

A Maxwellian 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.

However, for the present series of experiments, three changes were made in order to make spatial measurements as accurately as possible. First, the exploratory spot used to map the receptive fields had a diameter of 3.5 minutes of arc. Second, a Wratten # 21 filter was used in the stimulus beam to convert the white light to orange light (Wratten # 21 blocks light of 520 nm and shorter wavelengths). Third, a two dimensional micromanipulator was used to position the exploratory spot to specified locations within the object plane of the stimulus beam. The smallness of the spot allowed for the measurement of localized sensitivities within the receptive field. The chromatic restriction of the stimulus beam further localized the spot image by reducing chromatic aberration. The micromanipulator insured accurate and repeatable positioning of the stimulus spot. It was attached to an electro-mechanical link that allowed small movements of known amplitude and excursion of the spot as explained below.

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 technique 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 may be confused with OFF responses, a selection of the proper type of chromatic adaptation usually allows 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.

RESULTS AND DISCUSSION

In order to determine if the ganglion cells responses were, in fact, compatible with the motion of a tremor, an attempt was made to find the frequency spectrum of the response. Table 1 shows the kind of ganglion cells from which most data was accumulated. Two things are evident. The first is that there is very little difference between so called X and Y or brisk and sustained types of cells. The major difference is that the X cells have a more restricted central process than the Y cells. This correlates with the data found by Shapley (as reported in Ratliff, 1985). In Ratliff's paper his Figure 2 represents a 3 dimensional plot of the sensitivity of the receptive fields both in X and Y cells in a manner similar to Figure 1 in the present report and is adapted for the top half of Figure 2.

We found many cells which had in-between types of responses and distributions of sensitivity in their receptive fields, indicating that to some extent X and Y were overlapping types of populations. However, this may not indicate that X and Y are a complete homogeneous group of cells. It is of much greater importance to which group of cells in the genicular higher visual centers each of those types project. That alone will decide if they are from the same or different portions of the population. If the portion closest to the classical X cell projects to one group of genitulate neurons, while another closest to the Y group projects to a different layer or cell type, then they indeed represent two different population of cells. In this case, the determination of them as possibly separate groups is important and should be refined to a greater degree. However, these projections must also be described in terms of the other characteristics of the retinal ganglion cells such as color, intensity, receptive field movement representation, etc. Any correlation must await the more extensive data which will certainly be available in the future.

In order to find the time constants of the movement response in the retinal ganglion cells, data was gathered on the optimum speed with which the stimulus spot could be moved to give a most vigorous response at the threshold sensitivity. However, for all the cells tested, the optimum response was given by the fastest motion that was possible by our equipment, approximately 1 millisecond to move approximately 50 um. This is well above any physiological translation of a retinal image, as this is in the neighborhood of a thousand degrees per second, whereas a comparable translation due to tremor would be a tenth or more less than that. Tremor is in the neighborhood of 75 to 100 degrees per second, and the amplitudes could be slightly less than used in our test stimulus. The cells in Table 1 are all in or near the area centralis.

Data from the cells in other parts of the retina seem to indicate that for all cells, the optimum velocity remains also very high, certainly beyond the limits of the present testing equipment. Indeed, it probably would be the maximum speed available, that is if the stimulus did not really move, but the stimulus spot would be turned off in one place and turned on in another, perhaps even with an overlap. This is the so called silent substitution method. In future experiments, this technique will be used to find the minimum amount of motion that can be detected. Preliminary data for this type of protocol seems to indicate that any motion, however small, can be detected if the intensity is high enough. The problem is in matching the two optical channels exactly, so that the retina cannot tell the difference when given sufficient intensity. In practice, of course, the stimulus spots are slightly different sizes and have slightly different wavelength distributions due to the difference in the transmitting and reflecting characteristics of various combining elements within the system. However, this is a further indication of the exquisite sensitivity of the detection process for any discontinuities within the retina which seems to be the main objective of this retinal information processing.

Our series of well characterized ganglion cells (now well over 100) seems to indicate that all have the characteristics reported here except for those few incorporating the blue cone system. In these cases, the blue cone seems to contribute little to the small motion response. Thus, small

TABLE I

STATIC AND MOTION RESPONSES FOR RETINAL GANGLION CELLS

Type	Test	Types of Cones Center (Surround)	Motion Response; Depression in Center	Number of Cells
X	Rotating Prism	555 (556)	Best with 1000^2/sec; ½-3/4 dip	10
X	Standing Contrast	500,556 (556)	Best with 1000/sec; 3/4-full dip	2
Y	Standing Contrast	450 (556)	No motion response for blue cone	8
Y	Standing Contrast	556 (556)	Best with 1000/sec; ½-3/4 dip	15
	Rotating Prism	556 (556)	Best with 1000/sec; ½-3/4 dip	7
	Standing Contrast			
	Rotating Prism	500 (556)	Best with 1000/sec; 3/4-full dip	3
	Standing Contrast			
	Rotating Prism	450, 556/586	No motion response for blue cone	3

Selected characteristics of ganglion cells in the cat retina. All were from the area centralis or slightly nasal to it.

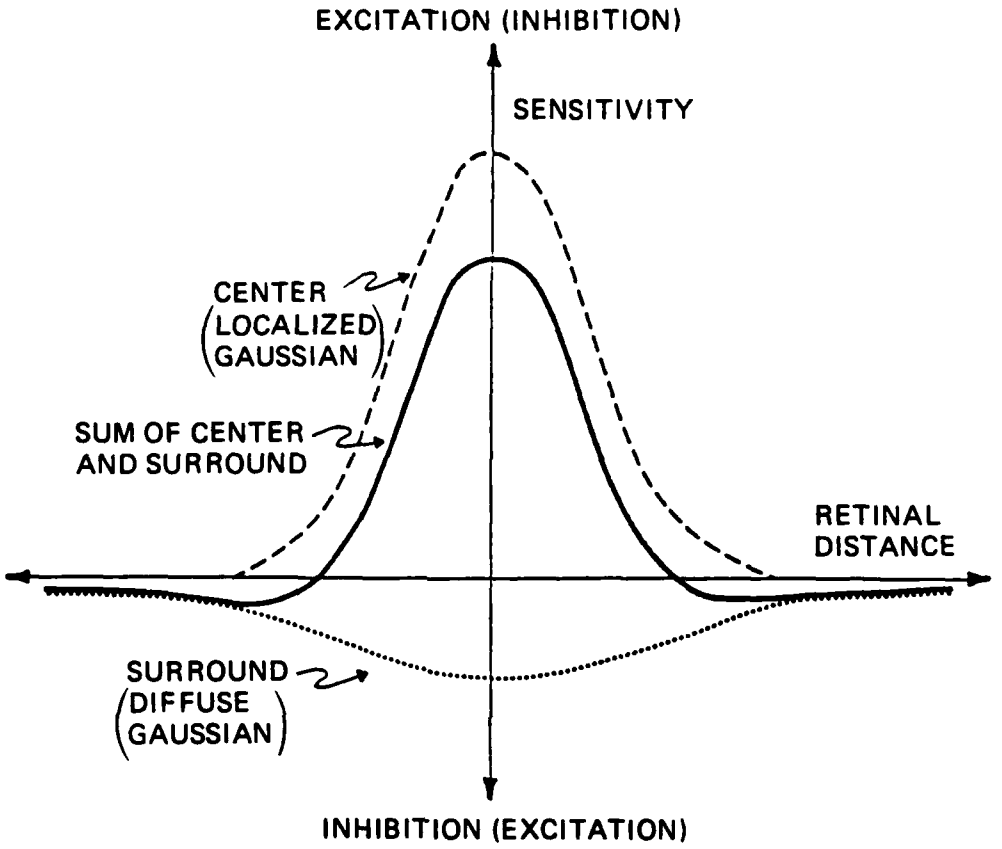


Figure 1. Receptive field sensitivity profile of a retinal ganglion cell to ON/OFF stationary retinal image stimulation. (Sensitivity is the inverse of the intensity needed to give a standard response.) The receptor input reaches the ganglion cell through 2 input channels. The first (center) is a rather restricted central area of receptors having positive (or negative) input through the intermediate neuronal layers to the ganglion cell. This profile is Gaussian and may arise from more than one type of receptor. The second input (surround) has an opposing type of input in a more diffuse Gaussian. The solid curve is the summed input from a stimulus which activates both inputs (based on Wagner et al, 1963 and Rodieck, 1965).

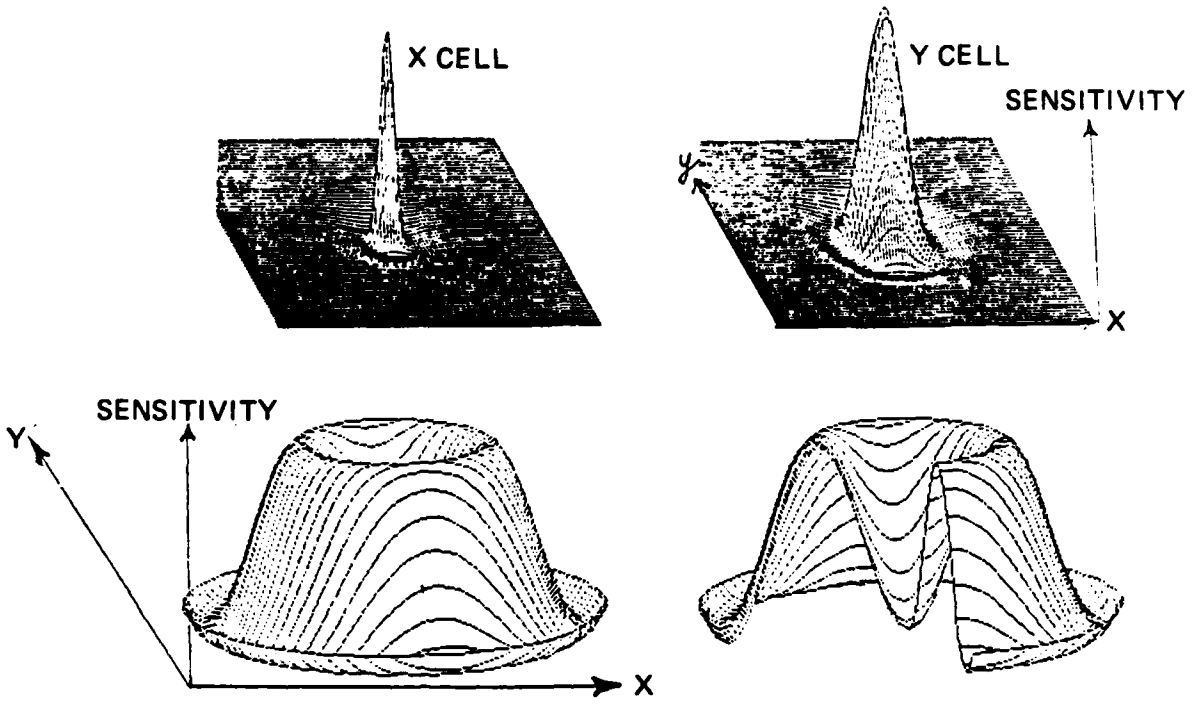


Figure 2. Three dimensional plots of single retinal ganglion cell sensitivity as a function of location. The upper figures show the excitatory center and inhibitory surround of an X cell and a Y cell. The peak sensitivities of the excitatory centers are adjusted so that they are approximately equal. In absolute terms, the peak sensitivity of the X center is about ten times that of the Y center. The widths of centers and surrounds of the two cells are shown in their proper relation to one another: the radius of the excitatory center of the X cell is one-third that of the Y cell; the radii of the inhibitory surrounds of the two cells are equal. The overall strengths of the center and surround of the X cell are equal; the strength of surround of the Y cell is about two-thirds that of the center. These plots are based on actual physiological measurements of the dimensions of the receptive fields of X and Y cells in the cat retina. The lower figures are similar to plots of the motion response from an X cell (see text for details). The figure on the right has a pie section removed to show the lack of sensitivity in the center of the receptive field. The top figures are adapted from Ratliff (1985).

motion detection or visual acuity in the cat is either due to the red cone system alone or a combination of the red and green cone systems. It is presumed that in the monkey, the red-green combination is the main one and that the same exclusion from visual acuity of the blue cone will hold. This data seems to be correlated with psychophysical data in humans which indicates that the blue cone contributes little to visual acuity. However, that may be due to the lower density or infrequent distribution of the blue cone in the retina, such that they do not have discontinuities moving across them often or in a regular fashion in order to generate the proper kinds of input signals to the ganglion cells.

The responses to small motions of almost all types of ganglion cells known suggests that the presence of the center-surround organization within the ganglion cell is itself an indication that this is the basic feature for information processing, and even that it is the most important feature. It is somehow possible that this organization grew out of the scallop (Pectin) which has dual retinas, with one retina giving ON responses and the other OFF. A combination of these two, with interlaced cells, could in time produce such an organization as we see it. However, that may not be the proper way to consider the evolutionary process. In any case, whatever the line of development, it seems very likely that primative vertebrate retinas had some such organization for motion detection as the visual system moved toward greater and greater complexity.

REFERENCES

Bengi, H. and Thomas, J. G. Studies on Human ocular tremor. pp 281-292. In: "Perspectives in Biomedical Engineering" (ed. by R. M. Kenedi) London, MacMillan, 1973.

Brown, W. E., Lucas, G.H.W. and Henderson, V.E. (1927). "Anesthetic value of N_2O under pressure"; J. Pharmacol. Exp. Ther. 31:269-289.

Ditchburn, R.W. "Eye Movement and Visual Perception". Oxford, Oxford University Press, 1973.

Enroth-Cugell, C. Robson, J.G. (1966). "The contrast sensitivity of retinal ganglion cells of the cat"; J. Physiol. 187:517-552.

Enroth-Cugell, C. and L.H. Pinto (1970). "Gallamine triethiodide (Flaxedil) and cat retinal ganglion cell responses"; J. Physiol. 208:677-689.

Gubisch, R.W. Optical performance of the human eye. J. Opt. Soc. Am. 57, 407-415, 1967.

Helmholtz, H.V. "Treatise on Physiological Optics". (Ed. by J.P.C. Southall) New York: Optical Society of America, 1924.

Kolb, H. The organization of the outer plexiform layer in the retina of the cat: electron microscopic observations. J. Neurocytol. 6:131-153, 1977.

LeGrand, Y. "Form and Space Vision". (Translated by M. Millodot, and G.G. Heath). Bloomington: Indiana University Press, 1967.

Polyak, S. "The Retina". University of Chicago Press, Chicago, IL. 1941.

Rodieck, R.W. Quantitative analysis of cat retinal ganglion cell responses to visual stimuli. Vision Res. 5, 583-601, 1965.

Snyder, A.W. and Miller, W.H. Photoreceptor diameter and spacing for highest resolving power. J. Opt. Soc. Am. 67, 696-698, 1977.

Van Buskirk, C., Wolbarsht, M.L., and Stecher, K., Jr. The nonnervous causes of normal physiologic tremor. Neurology 161, 217-220, 1966.

Van Norren, D. and Padmos, B. (1977). "Influence of anesthetics ethyl alcohol and freon on dark adaptation of monkey cone ERG"; Invest. Ophthal. 16:80-83.

Wagner, H.G., MacNichol, E.F., Jr., and Wolbarsht, M.L. Functional basis for "ON" center and "OFF" center receptive fields in the retina. J. Opt. Soc. Am. 53. 66-70, 1963.

Westheimer, G. Spatial frequency and light spread descriptions of visual acuity and hyperacuity. J. Opt. Soc. Am. 67:207-212.

REFERENCES (Continued)

Wolbarsht, M.L. (September 1978). "Electrophysiological determination of retinal sensitivity to color after intense monochromatic light adaptation"; Report SAM-TR-78-9, USAF School of Aerospace Medicine, Brooks Air Force Base, Texas.

Wolbarsht, M.L. and Ringo, J. (April 1979). "Dependence of foveal visual acuity on the size of the receptive fields of retinal ganglion cells"; Final Report on Naval Air Systems Command Contract N0019-78-C-0431.

Venes, J.L., Collins, U.P. and Taub, A. (1970). "Nitrous oxide: an anesthetic for experiments in cats"; Am. J. Physiol. 220:2028-2031.

DISTRIBUTION LIST (Continued)

Report No. NADC-86017-60

	No. of Copies
Commander, Naval Air Test Center, Patuxent River, MD 20670	1
Air Force Aerospace Medical Research Lab., AMRL/DAL Library, Wright-Patterson Air Force Base, OH 45433	2
Science & Technology Div., Library of Congress, 110 2nd St., S.E., Washington, DC 20540	1
Dr. James A. Bynum, US Army AMRL, P.O. Box 476, Fort Rucker, AL 36362	1
Mr. John K. Crosley, US Army AMRL, Fort Rucker, AL 36362	1
Mr. Dennis Breglia, Naval Training Equipment Center, Code N-731, Orlando, FL 32813	1
Mr. John H. Allen, Naval Training Equipment Center, Code N-731, Orlando, FL 32813	1
Prof. Aaron Lewis, School of Applied and Engineering Physics, Cornell University, Ithaca, NY 14853	1
Dr. Myron L. Wolbarsht, Department of Ophthalmology, Duke University Medical Center, Durham, NC 27710	1
Dr. Herschel W. Leibowitz, Moore Bldg., Pennsylvania State University, University Park, PA 16802	1

DISTRIBUTION LIST

Report No. NADC-86017-60

	No. of Copies
Director, Defense Technical Information Center, Bldg. 5, Cameron Station, Alexandria, VA 22314	2
Chief of Naval Operations (OP-98E) Navy Department, Washington, DC 20350	1
Chief of Naval Research, 800 N. Quincy St., Arlington, VA 22217 (1 for Code 440) (1 for Code 441)	2
National Library of Medicine, Bethesda, MD 20014	1
Commanding Officer, Naval Medical Research and Development Command, National Medical Center, Bethesda, MD 20014 (Code 40-2)	2
Command Officer, Naval Aerospace Medical Research Laboratory, Naval Air Station, Pensacola, FL 32508	2
Command Officer, Naval Aerospace Medical Institute, Naval Air Station, Pensacola, FL 32508	1
Commander, Operational Test & Evaluation Force, Naval Base, Norfolk, VA 23511	1
Commanding Officer, Naval Training Equipment Center, Orlanda, FL 32813	2
Commanding Officer, Naval Submarine Medical Center, Naval Submarine Base, New London, Groton, CT 06340	1
Commander, Naval Air Systems Command, Washington, DC 20361 (00D4) (2 for retention) (8 for AIR-03D) (1 for AIR-340B) (1 for AIR-531) (1 for AIR-5311C) (1 for AIR-5313)	14
Commanding Officer, Naval Health Research Center, P.O. Box 85122, San Diego, CA 92138	1
Commanding Officer, Naval Air Development Center, Warminster, PA 18974 (3 for Library Code 8131) (4 for Code 60B1)	7
Commander, Naval Safety Center, Naval Air Station, Norfolk, VA 23511	1

END

11-86

DTIC