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A MODEL OF THE AVIAN RETINA

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FOREWORD

This report was prepared by personnel of the Astropower Laboratory, Advanced Systems and Technology, Missile & Space Systems Division, Douglas Aircraft Company, Inc., Newport Beach, California 92663, under Air Force Contract AF33(615)-3726 in support of Project Number 7233 and Task Number 7233-05. The contract was administered by the Aerospace Medical Research Laboratories, Aerospace Medical Division, Air Force Systems Command, Wright Patterson Air Force Base, Ohio, with Dr. Hans L. Oestreicher as Project Director.

This is a final report covering the work performed during the period May 1966 to January 1967. The report was prepared by R. G. Runge, S. S. Viglione and M. Uemura, all of the Astropower Laboratory, under the supervision of S. S. Viglione. Dr. R. L. Binggeli of the School of Medicine at the University of Southern California contributed substantially to the specification and understanding of the retinal neuroanatomy and physiology contained in this report and in the model.

This Technical Report has been reviewed and is approved.

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ABSTRACT

The specific objective of this contract was to construct an electronic model of the avian retina based upon reported physiological and anatomical findings and capable of replicating the specific ganglion functional responses. A critical review of the pertinent physiological and anatomical literature relating to the retina was performed. The electronic model of the pigeon retina containing the six functional classes of ganglion detectors reported in the literature was constructed. In addition the model incorporates two hypothetical detectors to demonstrate the selective performance that can be achieved with artificial neuron networks. The development of the model has shown that the complex data processing of the retina can be functionally duplicated. The results of this work could lead to the design of an effective visual data preprocessor which would operate into a self-organizing decision network to yield a multilayer optical pattern recognition system.

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INTRODUCTION

The neuron networks of the pigeon retina have been investigated by physiologists[1, 2] by stimulating the retina with various light patterns and observing the corresponding output activity of single retinal ganglion cells by means of a microelectrode inserted in the optic nerve. The optic nerve is normally severed and eye tremor removed by anesthetics. Figure 1 is a simplified drawing of the experiment and the basic neural anatomy of the retina.

These physiological experiments have shown that ganglion cells of the pigeon retina perform complex and specific functions as opposed to those observed in the cat and monkey.[3] The fundamental elements of form (points, edges, corners), movement intensity and color are detected by the pigeon's retinal ganglion cells. In the maze of the 2,230,000[4] optical ganglion fibers emanating from the pigeon retina, Maturana's monitoring of single fibers has indicated that only six functionally unique ganglion cells are present, classified in accordance with the visual stimulus which yielded a maximum response. Table I lists the six classes of ganglions and a brief description of the functional performance of each class.

It is apparent from the description of the functional performance of the various ganglion detectors of the pigeon that considerable processing of visual information occurs in the retina. The high degree of specific visual data processing, and consequent data reduction, retains ample information for dealing with the environment. This monogamous animal can find its mate from hundreds of similar birds. It can recognize a turkey vulture from a hawk. It can see a hawk at such distances that a breeder requires field glasses. It can find food while avoiding hazards — man made and natural. It searches for and recognizes nesting material. It can recognize receptacles for water or feed and relocate the container quickly if it is moved. The pigeon recognizes its own nest from a number of others after being away from a loft for long periods of time. It is known to view distant objects with one eye and to utilize its binocular vision for nearby objects. In some experiments the pigeon has even been shown to be capable of recognition of objects from photographs.

The pigeon obviously possesses a highly discriminating visual system in spite of the fact that the retina performs very specific transformations on the input visual information. The transformation from spatially oriented, luminous points appearing at the receptors to the pulse coded outputs of the ganglion layer constitutes a major reduction on the input visual data in a precise and meaningful manner.

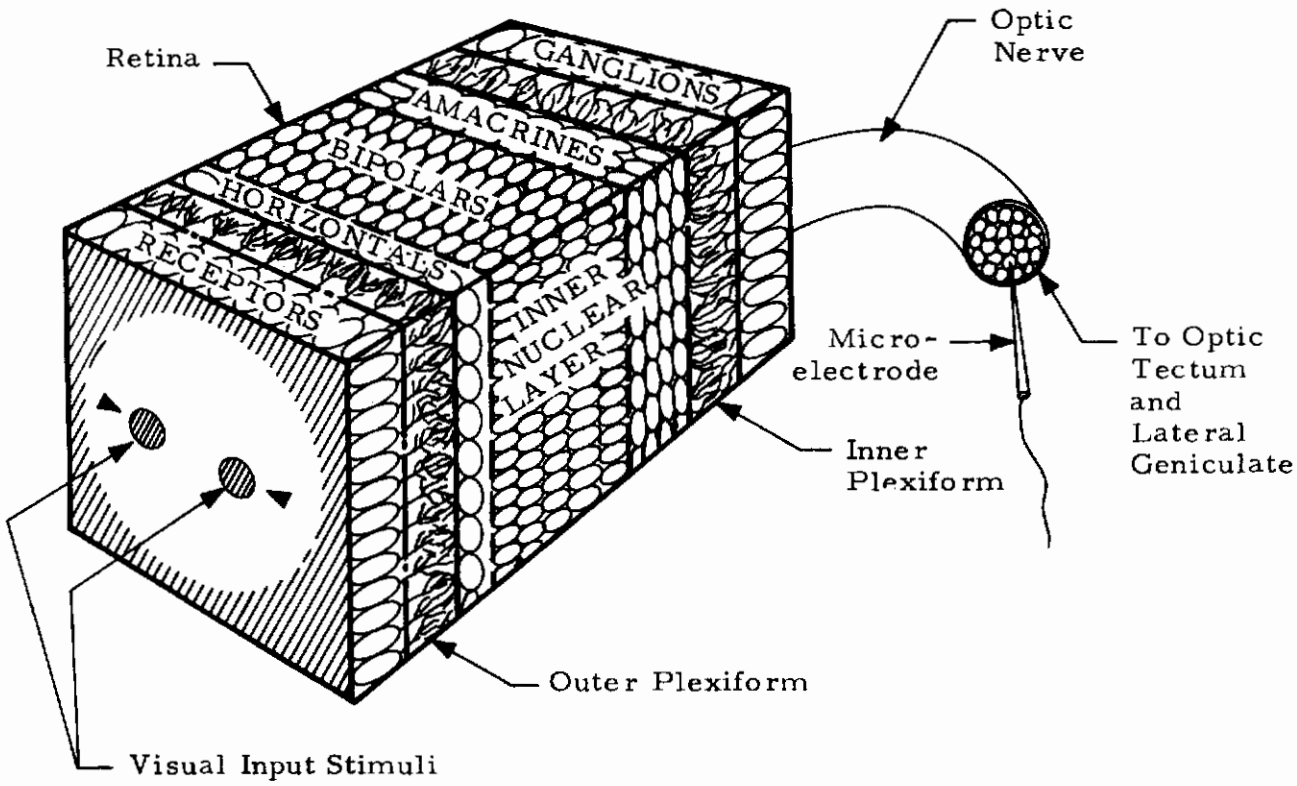


Figure 1. Retinal Flow Diagram

TABLE I. GANGLION CELL CLASSES

Ganglion Classification	Functional Performance	
	Response	No Response
Luminosity Detector	Intensity, color	
General Edge Detector (Type I)	Moving spot or edge, "ON/OFF" of a spot	Diffuse light Multiple moving edges
General Edge Detector (Type II)	Moving spot or edge "ON/OFF" of a spot	Diffuse light
Convex Edge Detector	Moving spot or convex edge, "ON/OFF" of spot	Diffuse light Long straight edges
Directional Moving Edge Detector	Spot or tongue moving from a specific direction, "ON/OFF" of a spot	Diffuse light Simultaneous spots
Horizontal Edge Detector	Long moving horizontal edge	Diffuse light, "ON/OFF" of a spot
Vertical Edge Detector	Long vertical edge (stationary or moving)	Diffuse light "ON/OFF" of a spot

Armed with a knowledge of the visual transformation performed by the pigeon retina and aware of the useful visual discrimination performed by this avian, an electronic retina model was constructed with the objective of gaining insight into the actual mechanisms of the retina. For example, of the five major anatomically distinct neurons in the retina (receptors, horizontals, bipolars, amacrines, and ganglions) speculation still arises as to which neurons are excitatory and which are inhibitory. The spatial arrangement of specific receptors, horizontals, bipolars and amacrines influencing a single ganglion cell can not be attained with current neuroanatomical staining techniques. Even in electron-microscopic investigations of the synaptic interconnection arrangement of the retina it is often difficult to distinguish amacrines from bipolars, horizontals from bipolars, and nerve axons from dendrites. In addition, only limited knowledge is available concerning the stimulus/response characteristics of individual neurons, since it has been found impossible to monitor individual receptors, horizontals, bipolars, and amacrines.

By restricting the model to perform the same transformation from visual input to ganglion output and by constructing an electronic analog of each anatomically unique neuron in the retina, interconnected to replicate known retinal anatomy, it is hoped that the model can provide a possible answer to some of the physiological and anatomical conjectures.

A further objective of this work is to investigate methods for constructing an electronic system capable of performing visual discrimination similar to that of living systems. In this light the pigeon retina would act as a preprocessing network supplying selected inputs to an adaptive decision network, yielding a multilayer recognition system as illustrated in figure 2.

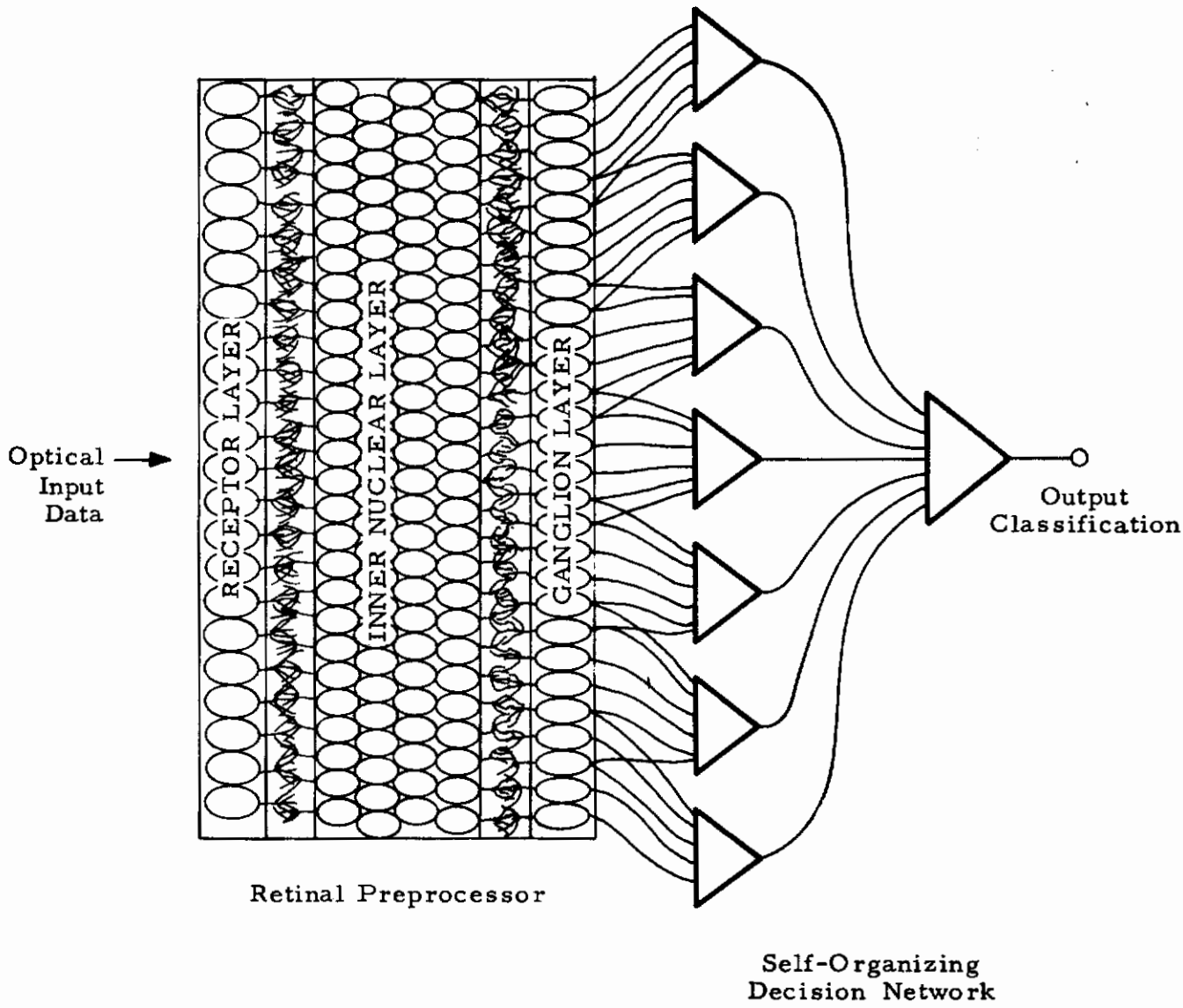


Figure 2. Multilayer Recognition System

SECTION II

THE RETINAL MODEL

The constructed model contains one or more of each of the six reported detectors for a total of ten functionally unique ganglion cells. The detectors incorporated are (1) Luminosity, (2) General Edge (two ganglions for the two types), (3) Convex Edge, (4) Directional Edge (three ganglions for three independent directions), (5) Vertical Edge, and (6) Horizontal Edge. One additional ganglion is used to model a hypothetical object detector which distinguishes a specific object from others independent of translation or rotation of the object.

Figure 3 shows the model operating in conjunction with a motion picture projector and animated film which provides the input stimulus. Various methods of optical stimulation may be used. However, to assure that each detector is thoroughly, and properly, evaluated, the animated film was prepared containing a variety of visual stimuli. The visual patterns are a replication of the stimuli reported to be used by physiologists on live animals to test both the major and minor response of each detector.

Figure 4 shows the sensory array which monitors the projected stimuli. Each cadmium sulfide light sensor has a viewing angle of approximately ±20 degrees. The sensors are simple two-terminal devices having a resistance which decreases as the light intensity increases. One terminal of each sensor is supplied by a positive voltage while the second provides the input to the receptor signal conditioning circuit. The 1.414 centimeter spacing of the array is considered to be equivalent to 0.177 visual degrees or about 21.2 microns as projected on the pigeon retina. The equivalent square area occupied by a sensor is 450 square microns. In an area of this size the average of 10 receptors would be found in the pigeon retina. In the interests of economy, wiring complexity, and size, receptors of the pigeon are represented by one in the model. The necessary reduction in receptor population may be somewhat overcome by employing high quality uniform sensors. Since the equivalent visual angle seen by each modeled sensor is 0.177 visual degrees and the actual field of view of each sensor is ±20 degrees a disparity occurs. If the sensors were caused to observe such a narrow field of view, it would be impossible to stimulate many of them by means of the projector. The equivalent visual angle on the pigeon retina as seen by the entire array is 2-1/2 degrees.

The electrical output of the sensors then provides the input to the 381 neural analog circuits housed on fifty printed circuit boards as shown in figure 5. These neural analog circuits are interconnected, as shown in figure 6, by means of taper pin connectors. The model also contains a speaker so that response or lack of response of each ganglion detector may be monitored. An audio monitor is employed rather than visual since an

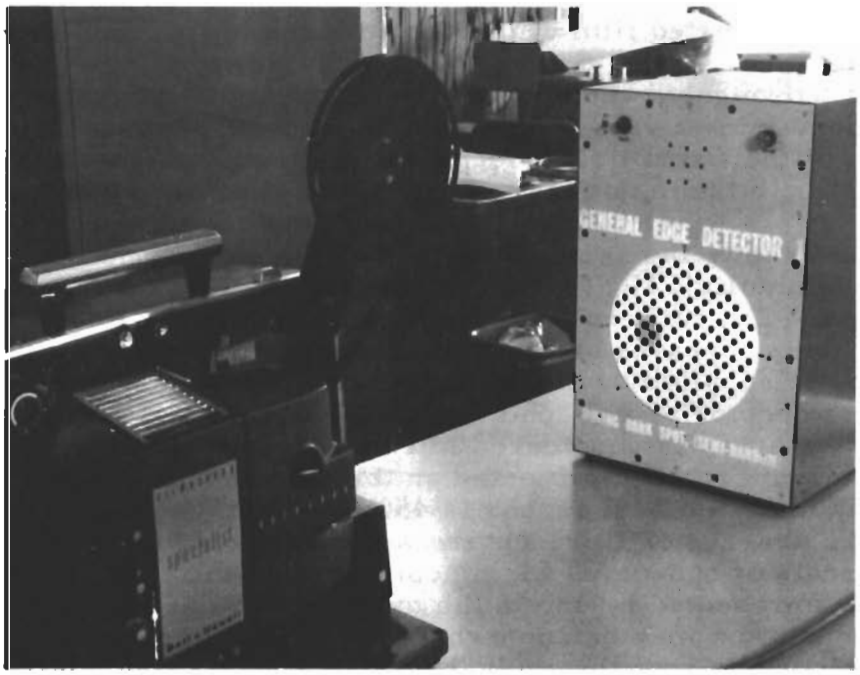


Figure 3. Avian Retina Model

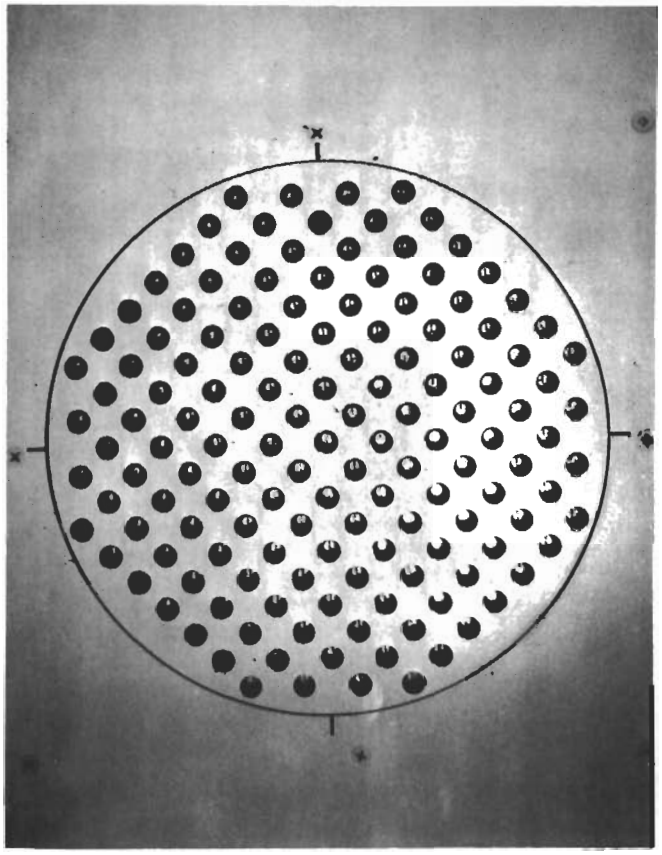


Figure 4. Sensory Array

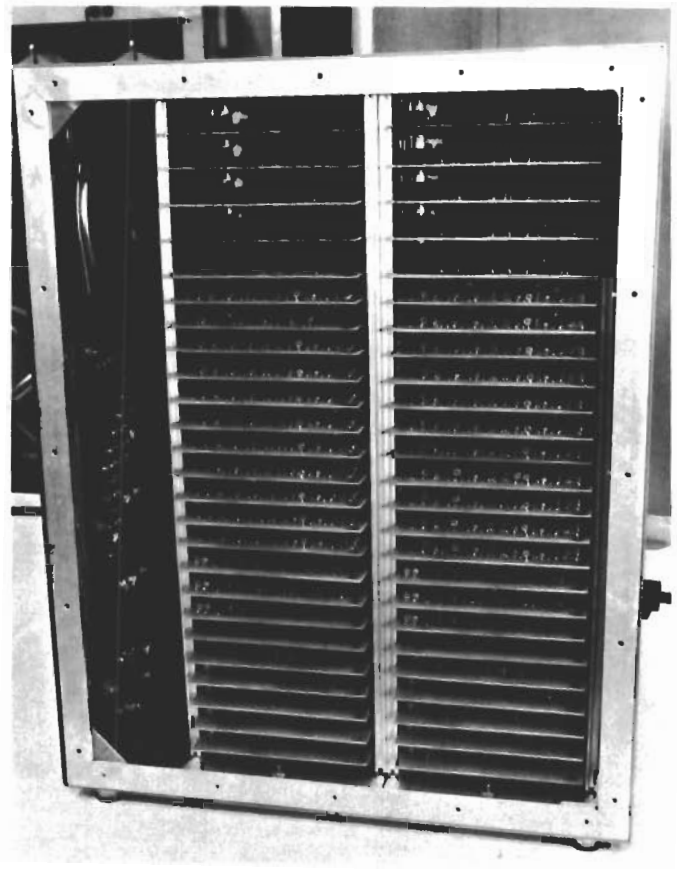


Figure 5. Neural Analog Circuit Boards of the Model

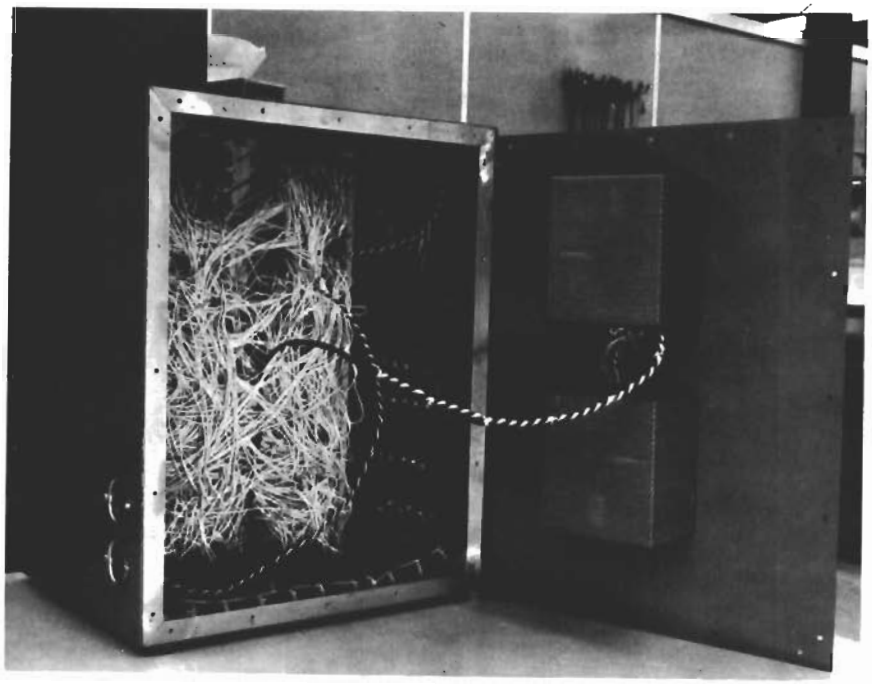


Figure 6. Physical Interconnections and Related Components

observer might have some difficulty in observing the projector stimuli and visual response simultaneously. Since the model contains 10 functionally distinct ganglions a selector switch is interposed between the speaker and the 10 ganglions.

The major title or classification, for example General Edge, for each detector is projected immediately above the sensory array on the front panel of the retina simulator (see fig. 3). For each major title a corresponding set of test functions occur. For each detector it is necessary to maintain the ganglion selector switch to the position of the major title being projected.

The various neural analog types, general performance characteristics of each neural analog, allowable interconnection arrangement, and quantity of each neuron type contained in the model are given in table II. For each nerve cell analog in the model a positive neuron output polarity exerts an excitatory effect and a negative neuron output polarity exerts an inhibitory effect on its connecting neurons.

TABLE II. NEURON SPECIFICATIONS

Neural Analog Type	General Performance Characteristics	Outputs to	Quantity
Receptors (+)	Analog voltage approximately proportional to the logarithm of the incident light flux density. 20 neurons/board.	Bipolars, Horizontals	160 (15 spare)
Horizontals (-)	Analog voltage equal in magnitude to the average of the three receptor inputs. 10 neurons/board.	Bipolars	60 (2 spare)
Bipolars (+)	Provides for spatial/temporal summation for a maximum of five inputing receptor and horizontals. Provides a pulse frequency modulated output proportional to the magnitude of the input sum. Provides a positive pulse width of 1 msec. Has the capability of self-adaptation. Has the capability of being inhibited by amacrines. 4 neurons/board.	Amacrines Ganglions	84 (4 spare)
Amacrines (-)	Receives excitation from bipolars. Produces an output identical to that of the bipolar except delayed in time and of opposite polarity. May be inhibited by other amacrines. Pulse width may be modified from standard 1 msec. Two types: 4 neurons/board and 8 neurons/board.	Amacrines Ganglions	92 (4 spare)
Ganglion (+)	Accomodates a total of 36 inputs from various arrangements of bipolars and/or amacrines. Has weighted temporal summations. Provides for amplification of weighted temporal sum. Has adjustable threshold. Capable of self-adaptation. Has a pulse frequency modulated output. Provides a positive 1 msec pulse width. 1 neuron/board.	Speaker	10

SECTION III

PRELIMINARY INVESTIGATIONS

Useful modeling depends on understanding the object to be modeled. In the course of development of the avian retina model a survey of retinal physiology and anatomy in the available literature has been made. In addition, Dr. R. L. Binggeli, a Neuroanatomist of the University of Southern California School of Medicine, has made a quantative investigation of the retinal structure of the pigeon as a part of this modeling effort. The purpose of Dr. Binggeli's work was to supplement the available anatomical information. The following paragraphs present some of the findings of the literature survey and Dr. Binggeli's work.

1. RETINAL ANATOMY OF THE PIGEON

Figure 7 shows a cross section of the pigeon eye.[5] The avian eye has all the structural components of the reptilian eye and differs principally from the mammalian eye in that it has a pecten. The earliest effort at studying the structure of the eye was concerned with verifying the camera analogy.

More careful analysts began to probe the business end of vision, the retina, and by using simple microscopy described and classified the basic laminations of the retina. Figure 8 is a drawing of the neural layers of the retina and the corresponding anatomical designations.

In the latter part of the nineteenth century detailed investigation of the structural components of the retina was begun and has continued to the present. Four types of anatomical investigations have been conducted to date in an effort to define the structure of the retina.

1. Structure of individual neurons by silver stains
2. Determination of cell density of the various neurons as a function of distance from the fovea by staining techniques
3. Determination of the population of the ganglion layer by optic nerve fiber counts
4. Specification of synaptic interconnection arrangement by electron microscopy.

a. Structures of Individual Neurons

The structure of individual neurons and general relationship to other neurons is illustrated in figure 9. Reduced to its most essential elements the retina of all vertebrates may be considered as consisting of

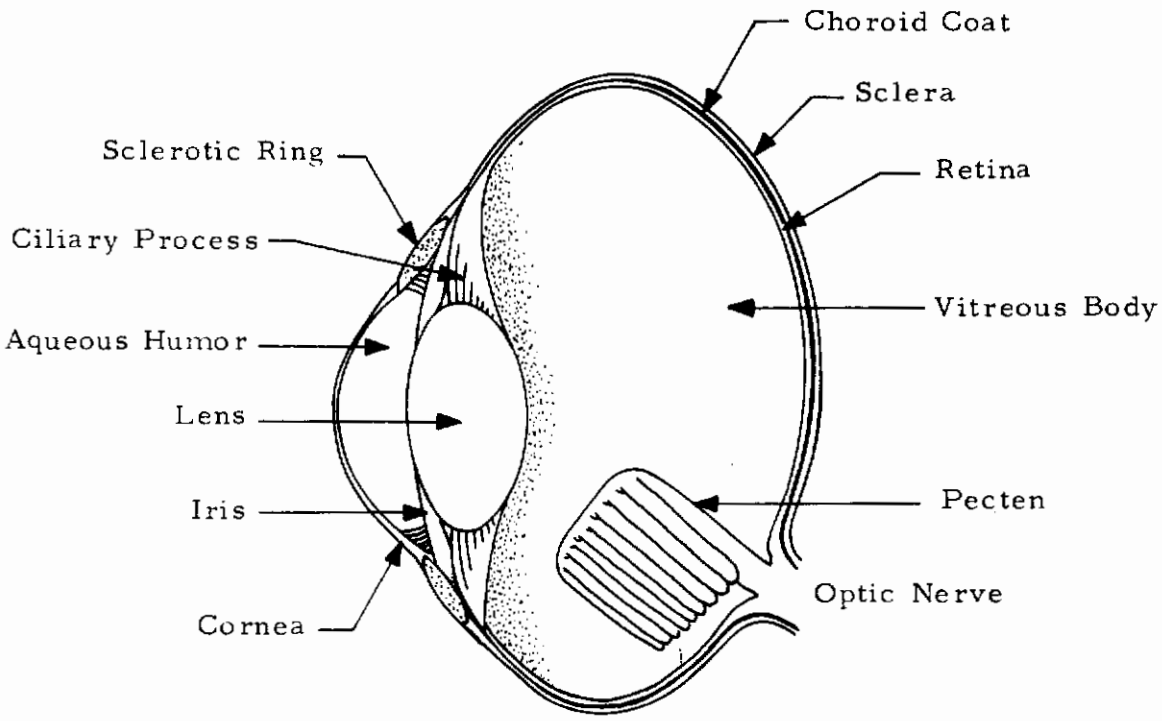


Figure 7. Cross Section of a Pigeon Eye

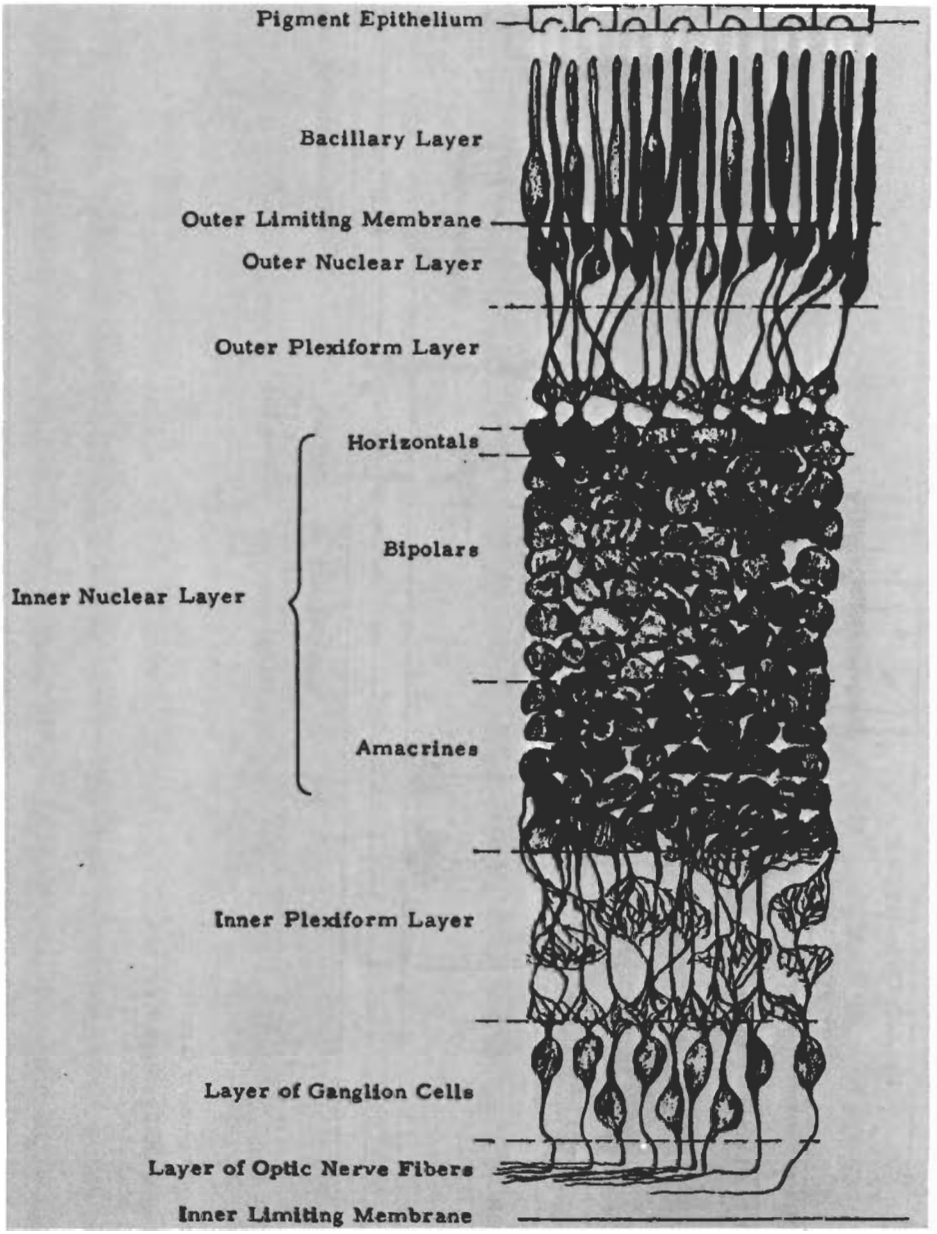
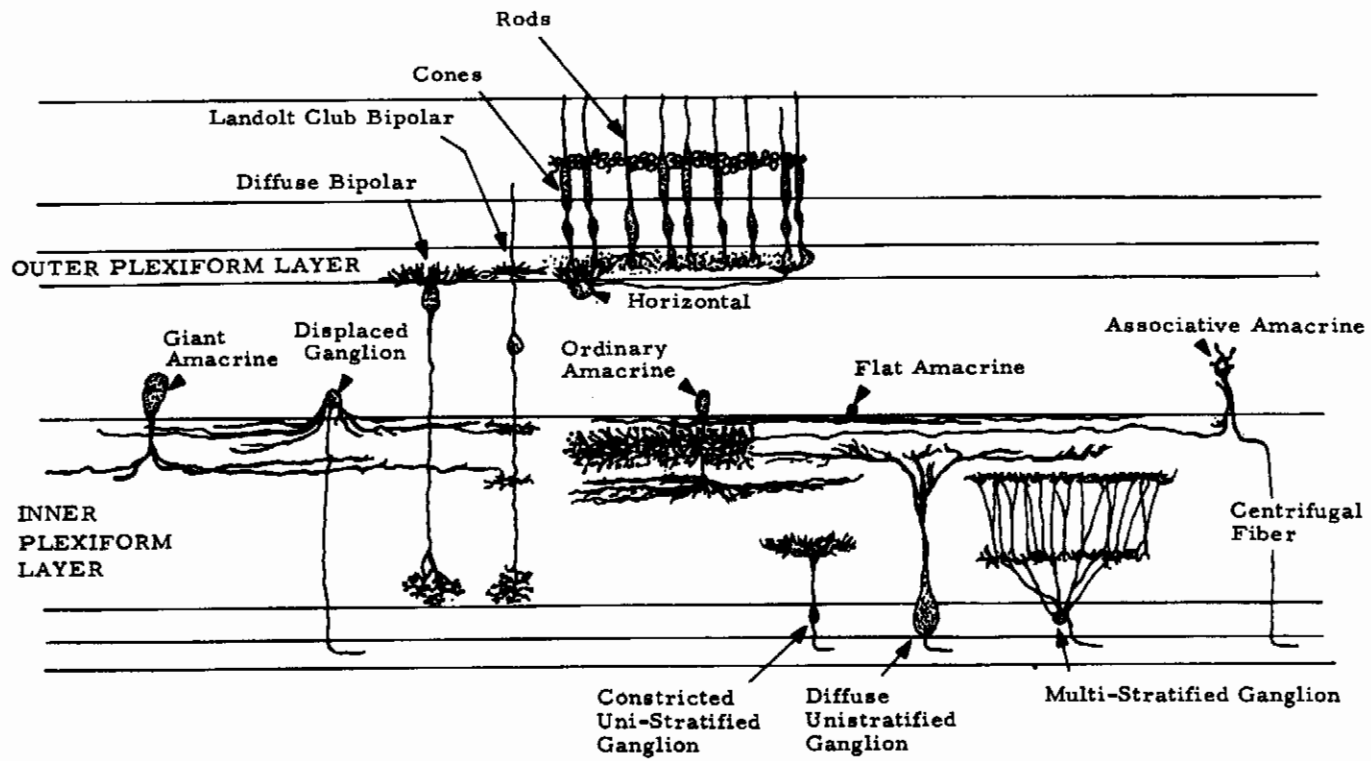


Figure 8. Neural Layers of the Retina



(Courtesy Ramon y Cajal)

Histologue Du Systeme Nerveux
Paris; Maloine 1909-1911

Figure 9. Structure and Arrangement of Individual Neurons of the Avian Retina

three superimposed layers of neurons which form synaptic connections in two plexiform layers. Figure 9 illustrates that two layers of receptors — rods and cones — form synaptic contacts in the outer plexiform layer with horizontals and bipolars. The retina of avians, such as pigeons, ducks, chickens, and canaries, is predominantly composed of cones.

Adjacent to the outer plexiform layer lies one very regular layer of horizontal cells. The output axons of these cells run parallel to the plane of the retina. Two types are found in the avian — the long axon and the short axon horizontal — with the short axon type being most predominant.

At 3 mm from the fovea (located near the optical center of the eye), seven layers of bipolars are found lying primarily between the horizontal cell layer and the amacrine cell layer.[6] Cajal[7] divides the bipolars of birds into two classes — those with and those without Landolt's club. The Landolt club type of bipolar is very abundant in the pigeon. In general, the more diffuse type of bipolar (without the club) is thought to be associated with rods. The axonal output of the Landolt bipolar stratifies at various levels of the inner plexiform.

Between the outer limit of the inner plexiform and the bipolar layers are the amacrine layers. The bipolar/amacrine separation is formed by the Mueller fibers. The amacrine cells, with the exception of the associative amacrine, are difficult to distinguish which are the input dendrites and which the output axon. In birds the quantity of amacrines is large relative to that of monkey and man. At 3 mm from the fovea they occur in five layers. The amacrines, like the horizontals, have a lateral input/output arrangement. At least four structurally distinct types of amacrines are found. They include ordinary or parasol amacrines, flat amacrines, giant amacrines, and associative amacrines. The associative amacrine is unique in that it has both a dendritic input and an axonal output in the inner plexiform layer. Notice that all amacrines have a stratification in the inner plexiform layer with a spread considerably larger than that of the Landolt type bipolar. Hence, an amacrine will more likely synapses on a ganglion's dendrites even though its cell body center is considerably removed from the ganglion dendritic spread. For a bipolar to make synaptic contact with a ganglion its cell body must lie in the immediate vicinity of the ganglion dendritic spread. In the layer of the amacrines displaced ganglions occasionally occur.

In the optic nerve, in addition to the different fibers outputing to the optic tectum and lateral geniculate, there are efferent fibers received by the retina from the neurons in the ismo-optic nucleus.[8] These fibers terminate in the amacrine layer on ordinary amacrines, flat amacrines, associative amacrines, and displaced ganglions.[9] (The model does not provide for these fibers since in the reported laboratory experiments of the functional performance of the retinal ganglions the optic nerve was severed, excluding this feedback from influencing the retinal responses.)

The ganglions project primarily to the optic tectum of the pigeon. The majority of the ganglions may be broken into three classes. Some of these cells are singly stratified and constricted, others are single stratified and diffuse and still others are multistratified. The dendritic spread of a particular cell is reasonably constant, however if all types are included, ganglion spreads from about 30 to 300 microns (0.25 to 2.5 visual degrees) occur. The latter figures are estimated from the qualitative data of Cajal and are confirmed by Maturana's physiological findings.

b. Cell Density and Optic Fiber Counts

Dr. Binggeli has recently investigated the regional variations in the population of the various neuronal layers of the pigeon. In his investigation he employed silver-pyridine to stain the retinal layers. Using this stain only the nucleous, a small spot within the cell nucleus, is stained. The nucleous is such a small structure compared to the thickness of the retinal section (0.3 μ compared to 20 μ) that the counting error is minimized. Figure 10 is a plot of the neuronal cell density as a function of distance from the fovea taken toward the nasal or anterior direction of the right eye.

Since each ganglion is currently believed to yield only one fiber in the optic nerve, and these fibers constitute greater than 99% of the optic nerve fibers (only about 10,000 efferent centrifugal fibers come from the ismo-optic nucleus to the retina), a count of the optic nerve fibers provides a means of determining the total ganglion population of the retina. For Binggeli's count of the optic nerve fibers 150 sample areas, 10 μ by 10 μ, from three different pigeons were stained. The measured area of the optic nerve fiber was 2.014 mm^2. The resulting count showed that 2,230,000 fibers exist in the retina. Seventy-eight percent were thinly myelinated and twenty-two percent were unmyelinated. The average ganglion axon diameter was found to be 0.5 to 1.5 microns for the myelinated cells (some were as large as 3 microns). The diameter of the unmyelinated fibers were found to be from 0.2 to 0.3 microns. Breusch and Arey[10] also made counts of the optic nerve fibers and indicated a population of approximately 988,000 ganglions. This discrepancy is probably due to the fact that Breusch and Arey employed a light microscope while Binggeli utilized an electron microscope. Binggeli also measured the area of the whole retina of 10 pigeons and found the mean area of the retina to be 314.6 mm^2 with a range of 269 to 360 mm^2.

c. Synaptic Interconnection Arrangement

The electron microscope has made it possible to observe the detailed synaptic interconnection arrangement of the retina. However, it is often difficult to determine the types of neurons making synaptic contact. This is particularly true for the horizontals and amacrines since it requires following the cell processes long distances.

Recent electron microscope studies have shown that the outer plexiform receptors synapse on dendrites of bipolar and horizontal cells.[11] In

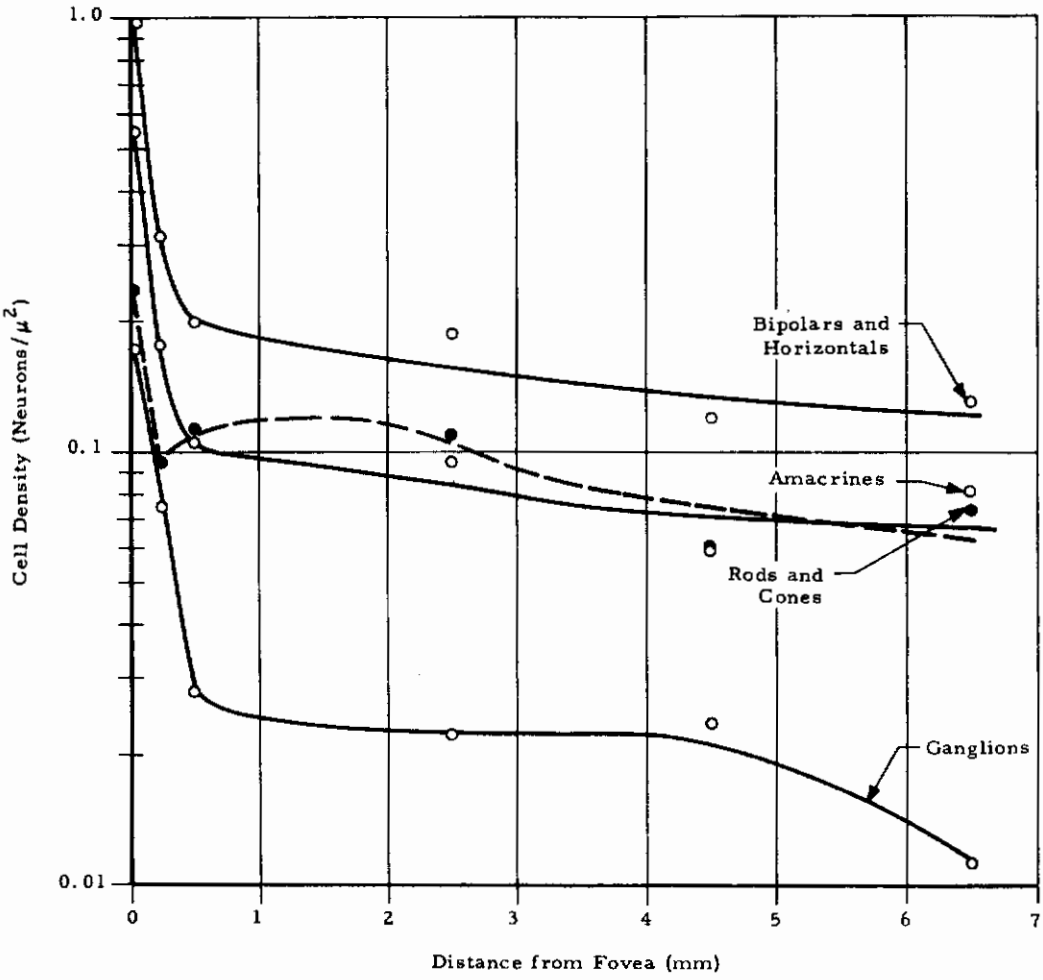


Figure 10. Neuron Density vs. Distance from the Fovea [Right Eye, Anterior (Nasal) Direction]

addition inter-receptor contacts have been found between adjacent receptors.[11] Morphologic evidence that the laterally extending horizontal cells are postsynaptic to receptor (receive input from receptors) and presynaptic (supplying an input) to bipolars has been found.[12] It is probable that horizontal to horizontal synapses exist but this requires further confirmation. In the inner plexiform layer the bipolar cell synapses with two postsynaptic processes — one is a ganglion cell dendrite which presumably transmits visual excitation centrally, and the other is ordinarily an amacrine process.[11] In addition it is found that adjacent bipolars functional contact one another.[11] The amacrine cell process extends laterally in the inner plexiform layer and end presynaptically on adjoining bipolar cell terminals.[11] In addition amacrine processes synapsing onto ganglion dendrites have been found.[11] One feature of the avian retina is that amacrine-to-amacrine synapses frequently occur.[13] No evidence of these synapses has been found in the primate retina. This fact is likely to be of major importance in explaining the differences in the functional response of avians and primates.

Table III summarizes the synaptic arrangement of the retina as presently reported. All of these connection arrangements are employed by the model with the exception of local receptor to receptor and local bipolar to bipolar connections.

TABLE III. SYNAPTIC ARRANGEMENT OF THE RETINA

Cell Type	Source of Input (Postsynapses)	Supplies (Presynapses)
Receptors	(Light)	Bipolar, Horizontals, Local Receptors
Horizontals	Receptors	Bipolars, Horizontals
Bipolar	Receptor, Horizontals	Amacrines, Ganglions Local Bipolars
Amacrines	Bipolars	Amacrines, Bipolars Ganglions
Ganglion	Amacrines, Bipolars	Tectum & Lateral Geniculate

SECTION IV

NEURAL NETWORKS OF THE MODEL

1. GENERAL CONCEPT

This section describes some of the general concepts used to develop the model. As was indicated in the previous section only the input/output function of the pigeon retina is known implicitly. The specific properties of receptors, horizontals, bipolars and amacrines are derived as a result of the input/output relationship and a knowledge of the neural anatomy.

a. Neuron Characteristic

For the purpose of this discussion, it is assumed that a neuron can be represented by a "black box" as far as its electrical characteristics are concerned. The properties of this black box are abstracted from physiological neuron behavior such that the data processing capabilities of the biological neuron are preserved. In particular, the following neuron properties are considered.

(1) Linear, Weighted Summation of Inputs

This accounts for the spatial summation characteristics of the neuron, in which inputs are weighted according to the value of the corresponding synaptic strength and summed linearly at the cell body.

(2) Standard Signal Shape

The output signal generated by a neuron is a pulse frequency. The frequency of these pulses is a function of the input signal. The shape, duration and amplitude of the individual pulse, however, is independent of the input signal.

(3) Threshold Phenomenon

A neuron will produce an output signal only if the summation of its input signals exceeds a certain threshold level.

(4) Refractory Recovery

Immediately after firing there is a recovery period during which the neuron exhibits reduced sensitivity to input stimulation. This period is called the refractory period. The reduced sensitivity is explained by an increase in threshold level during firing. After firing, the threshold level decays exponentially to the normal state.

(5) Signal Delay and Temporal Summation

A neuron exhibits a time delay between excitation and firing. The delay is an exponential function of the excitation amplitude (i.e., higher input levels are associated with shorter delays). Temporal summation can be described as follows: an excitatory input pulse that does not reach the firing threshold cannot cause a neuron firing but it will condition the neuron to be more sensitive to a subsequent pulse by effectively lowering the threshold potential. The conditioning effect decays exponentially.

(6) Excitatory and Inhibitory Input Signals

Excitatory input signals are those that tend to fire the neuron (generate an output pulse). Inhibitory input signals are signals that tend to restrain a neuron from generating an output and may be treated as excitatory signals with a negative prefix.

(7) Self-Adaptation

Many neurons, when stimulated with a constant input, respond with an initially high rate of impulses which decreases with time.

b. Excitatory/Inhibitory Arrangement of the Retina

Histological inspection of the receptor shows that it has two parts, the outer and inner segment. The structure of the receptor, like all sensory neurons is unique from the neurons of the retina. The outer segment is suitable for absorbing light-energy. The inner segment, adjacent to the outer plexiform layer, contains the receptor nucleus. The inner segment of the receptor in turn provides excitation to the neurons of the inner nuclear layer.

In the fovea single receptor to bipolar to ganglion arrangements have been observed in many animals. If the retinal ganglion cells of the foveal area are to report the light activity as seen by receptors it is essential that bipolars are excitatory since any neuron, other than a primary sensory neuron, requires excitatory synaptic action in order to generate impulses.[14] Thus it is assumed that the model of the retina should employ excitatory bipolars and receptors.

The nature of the remaining two neurons, horizontals and amarines, influencing the response of the retinal ganglions remains to be defined. The electronic model postulates that amacrines are inhibitory. Dowling's electron microscopy has shown that amacrines form presynaptic inputs to the axonal end feet of the bipolar and that the bipolar is presynatic to the amacrine and the ganglion (see figure 11).

The dotted area in figure 11 represents the presynapse of the amacrine with the bipolar. Notice also that the bipolar is presynaptic to the

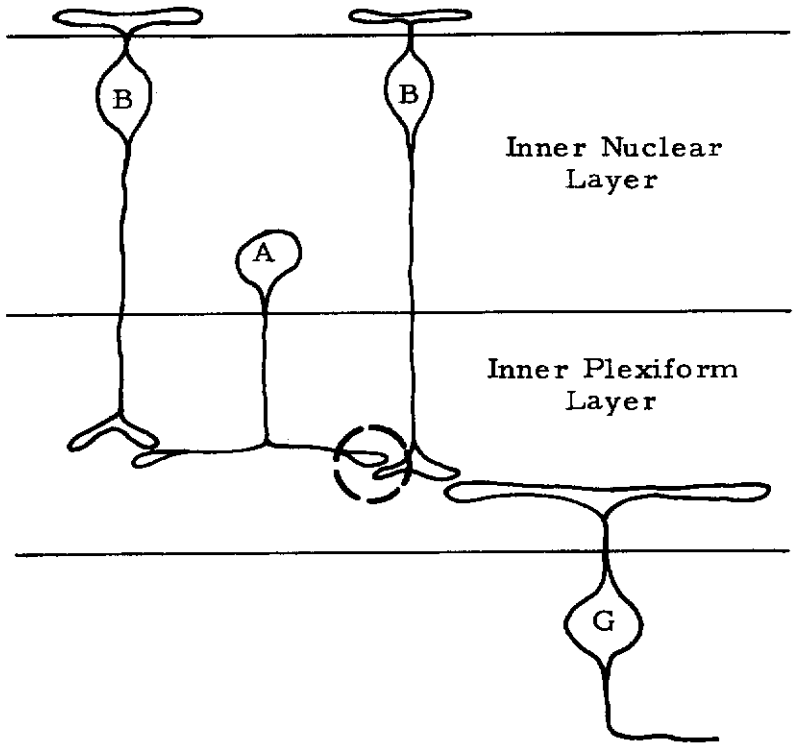


Figure 11. One Common Synaptic Structure of the Inner Plexiform Layer (Simplified Drawing)

ganglion. Hence an amacrine forms a presynaptic interaction. Presynaptic interaction has been found to be characteristic of afferent systems and is usually inhibitory,[15] thus supporting the postulate that amacrines are inhibitory.

The horizontal is also postulated to be inhibitory primarily because of its structural similarity to the amacrine in the fact that both of these neuron types project lateral to the plane of the retina.

c. Weighting

The model postulates that all weighting in the retina is accomplished in the inner plexiform layer and is the result of the dendritic branching of the ganglion cells. A rapid inspection of the outer and inner plexiform layers (see the Appendix for photographs of the pigeon retina) reveals that the outer plexiform is less than one-fifth thickness of the inner plexiform layer. Golgi stains of the avian retina indicate that bipolar and horizontal dendritic branching is quite restricted in the outer plexiform relative to that of the ganglions dendrites in the inner plexiform.

In keeping with this postulate each receptor or horizontal inputting to a bipolar has an equal effect on the linear input sum of the bipolar (postsynaptic potential). That is, all inputs to the bipolar are equally weighted. In addition, all receptors inputting to a horizontal are equally weighted.

The amacrine, in the interest of modeling simplicity, is not provided with spatial summation capabilities except through its corresponding spatially located bipolar. If a bipolar firing occurs the corresponding amacrine responds unless it is inhibited by another amacrine (serial synapse of Kidd 1962).

d. Number of Inputs

In the model it is assumed that the number of receptors acting upon a bipolar is essentially equal to the number of receptors acting on a horizontal. This implies that the bipolar and horizontal dendritic branching are essentially equal. In addition the model postulates that any bipolar receives the output of at most one horizontal and that the number of inputs to an amacrine or ganglion are dependent upon its size, increasing as its dendritic spread increases.

e. Threshold

In designing the analog neurons for the model it was assumed that all neurons of the pigeon retina are essentially zero threshold neurons. The threshold value of the neural analogs is not precisely zero volts; however, with respect to the pulse amplitude of the bipolars, amacrines and ganglion (12 volts), and the maximum analog output the receptors and horizontals, the thresholds are essentially zero. For example the average bipolar will yield a response for an input of about +0.3 volts. The ganglion circuit has a

manually adjustable threshold which subtracts or adds a constant to the ganglion input sum. No ganglion threshold setting greater than 0.5 volt in magnitude is required for any of the modeled detectors.

f. Terminology

In describing various neural arrangements of the model the following designations apply.

R = receptor
H = horizontal
B = contrast bipolar
B^* = intensity bipolar
A = contrast amacrine
GA = group contrast amacrines
A^* = intensity amacrines
G = ganglion

The pair of numbers (i.e., $R_{9,9}$) immediately below the letter designator indicates the location of the center of the modeled cell body. The first number is the column location, the second the row location. The column and row location are separated by a comma. All spatial locations are with respect to the light sensor array. Figure 12 shows the location of each of the available photoreceptors of the model.

A letter designator followed by one or two X's (i.e., $AXX_{8,9}$) indicates that more than one neural analog is modeled at the designated spatial location. A letter designator preceded by an S indicates that this neuron is special, that is, it has been modified to function in a manner different from the typical neuron. If the letter designator for a group of contrast amacrines has a prime superscript this indicates that it may be joined together at its output terminal with others of the same type.

g. The Intensity and Contrast Bipolar

The intensity bipolar is simply a bipolar without a horizontal input. Figure 13 illustrates the connection arrangement of one of the intensity bipolars of the model as seen from a top view. The input voltage sum to the bipolar, neglecting temporal properties, is equal to the average receptor output voltage. The receptors which synapse on a bipolar are in physical proximity to the bipolar cell body center. This is true for all bipolars and horizontals of the model.

It is further assumed in the model that the majority of bipolars in the pigeon retina, and possibly in all cone eyes (avians, reptile, ground squirrel, etc.) are contrast bipolars. Figure 14 illustrates the connection arrangement of one of the contrast bipolars employed by the model and a

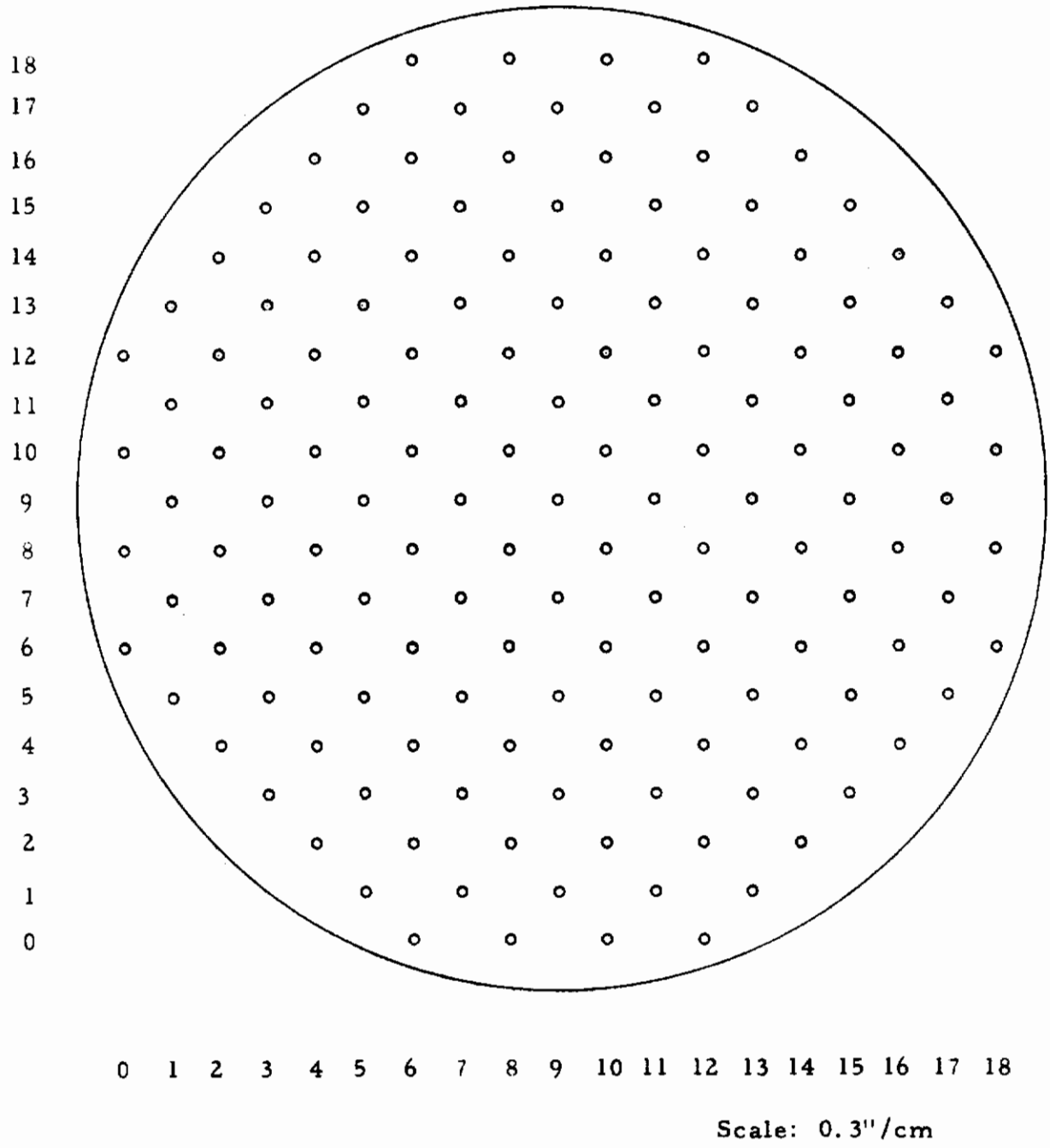


Figure 12. **Photoreceptor Spatial Arrangement**

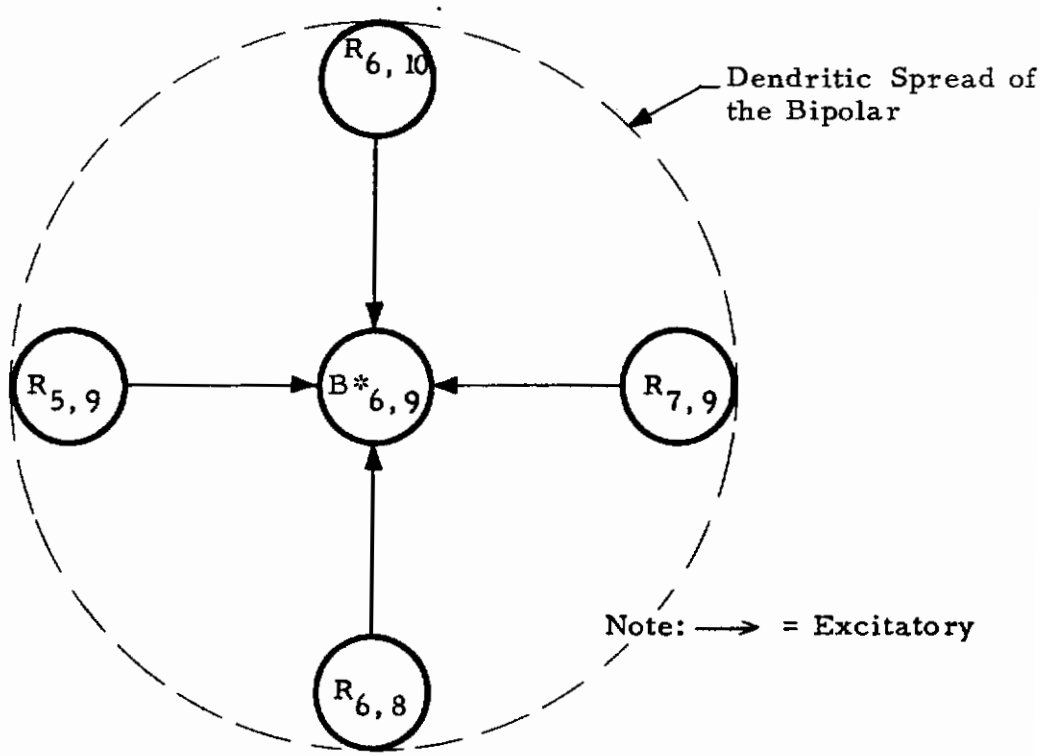


Figure 13. Intensity Bipolar Analog

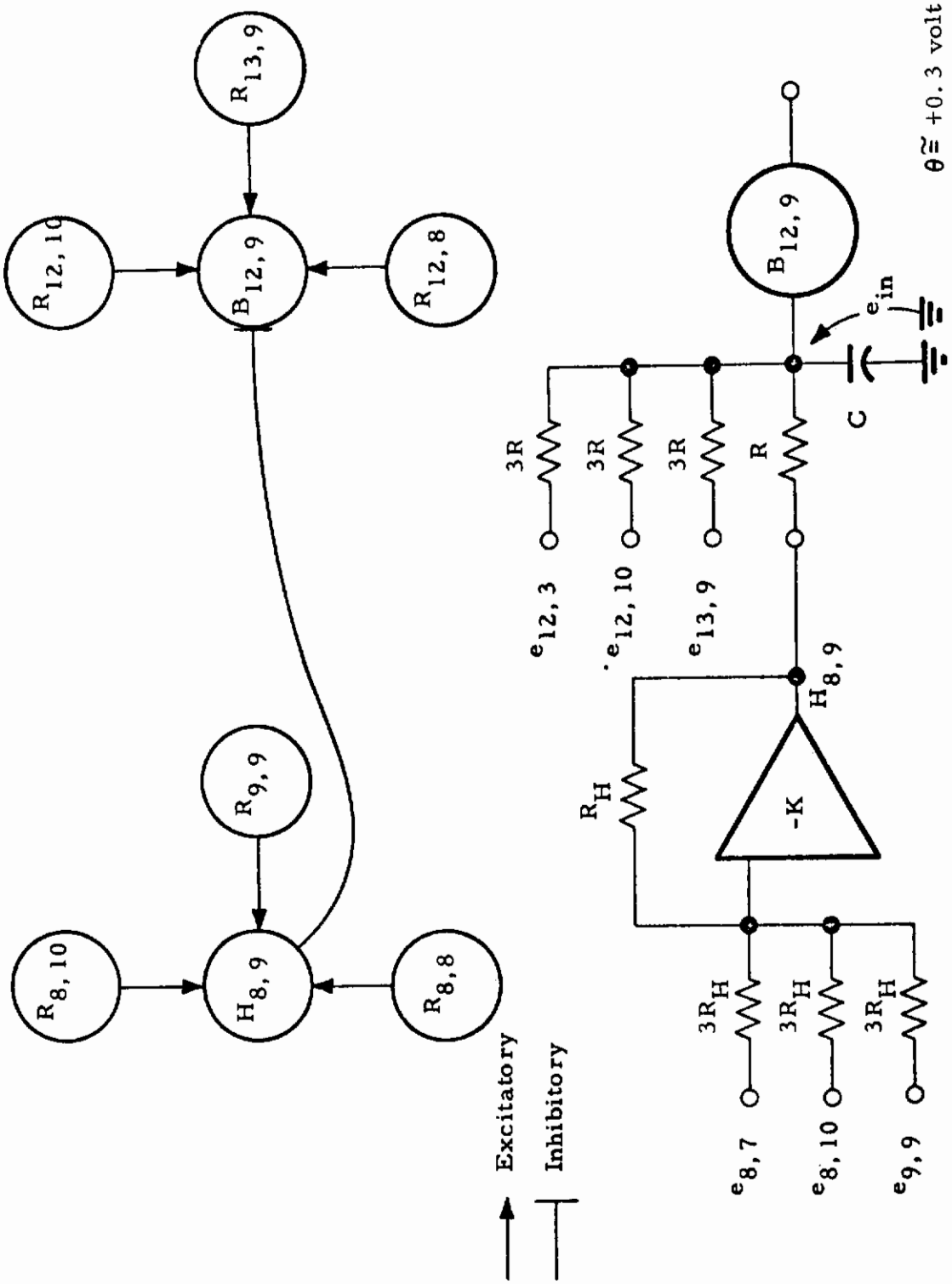


Figure 14. Contrast Bipolar Analog

simplified drawing of the electronic analog. All contrast bipolars are unresponsive to diffuse changes of light projected uniformly across the sensory array. In the illustrated example $B_{12,9}$ will produce a response if the receptors supplying $H_{8,9}(R_{8,8}, R_{8,10}, R_{9,9})$ are dark relative to the receptors immediately surrounding $B_{12,9}(R_{12,8}, R_{12,10}, R_{13,9})$.

In the model the neural generators of the outer plexiform layer do not produce a pulse frequency modulated output. Rather the receptors simply produce an analog voltage approximately proportional to the logarithm of the light stimuli. The horizontal is implemented with a simple operational amplifier which provides summation and polarity inversion of the receptor outputs.

Effectively all connections of the outer plexiform layer are equally weighted, that is, all receptor to bipolar and horizontal, and all horizontal to bipolar connections have equal weight. Hence the model assumes that the function of the horizontal is to provide an input to the bipolar equal but of opposite polarity to the sum of the receptors inputting on the horizontal. The equivalent form shown in figure 15 is used by the model to avoid saturating the horizontal operational amplifier. In the equivalent form the magnitude of the horizontal output is equal to the average receptor output rather than the receptor sum.

The majority of contrast bipolars employed by the model use reciprocal inhibitory horizontal pairs. Figure 15 is an illustration of one of the reciprocal contast bipolar analogs. Consider a spot of light centered at 12, 9. At the onset of the spot, $B_{12,9}$ will respond. For a dark spot centered at 12, 9; $B_{8,9}$ will fire. If the light spot is now recentered at location 8, 9 then at the onset of the spot, $B_{8,9}$ will fire. For a dark spot centered upon 8, 9, then $B_{12,9}$ will respond.

If a large group of such reciprocal contrast bipolars are input to a ganglion the resultant ganglion will have an ON-OFF center. This characteristic is common to several of the ganglion detectors of the pigeon.

h. Long Duration Amacrines or Group Amacrines

Figure 16 is a schematic drawing of an inhibitory amacrine acted upon by a group of bipolars. The amacrine in turn tends to inhibit the ganglion. The ganglion is also acted upon by a group of excitatory bipolars.

If the bipolars of figure 16 are excited sequentially from a left to right direction they would cause the amacrine to repetitively fire. This in turn would cause successive and repetitive inhibition of the ganglion. The effect upon the ganglion would be a build up in inhibitory postsynaptic potential. In the model this amacrine effect is implemented by modifying the amacrine circuit to provide a single long duration pulse. The long duration amacrine could be likened to a group of amacrines sequentially operating into an electronic "or" gate.

Notice that if the ganglion retains the inhibitory build-up from the amacrine, it would not respond as the right hand bipolars are excited. If

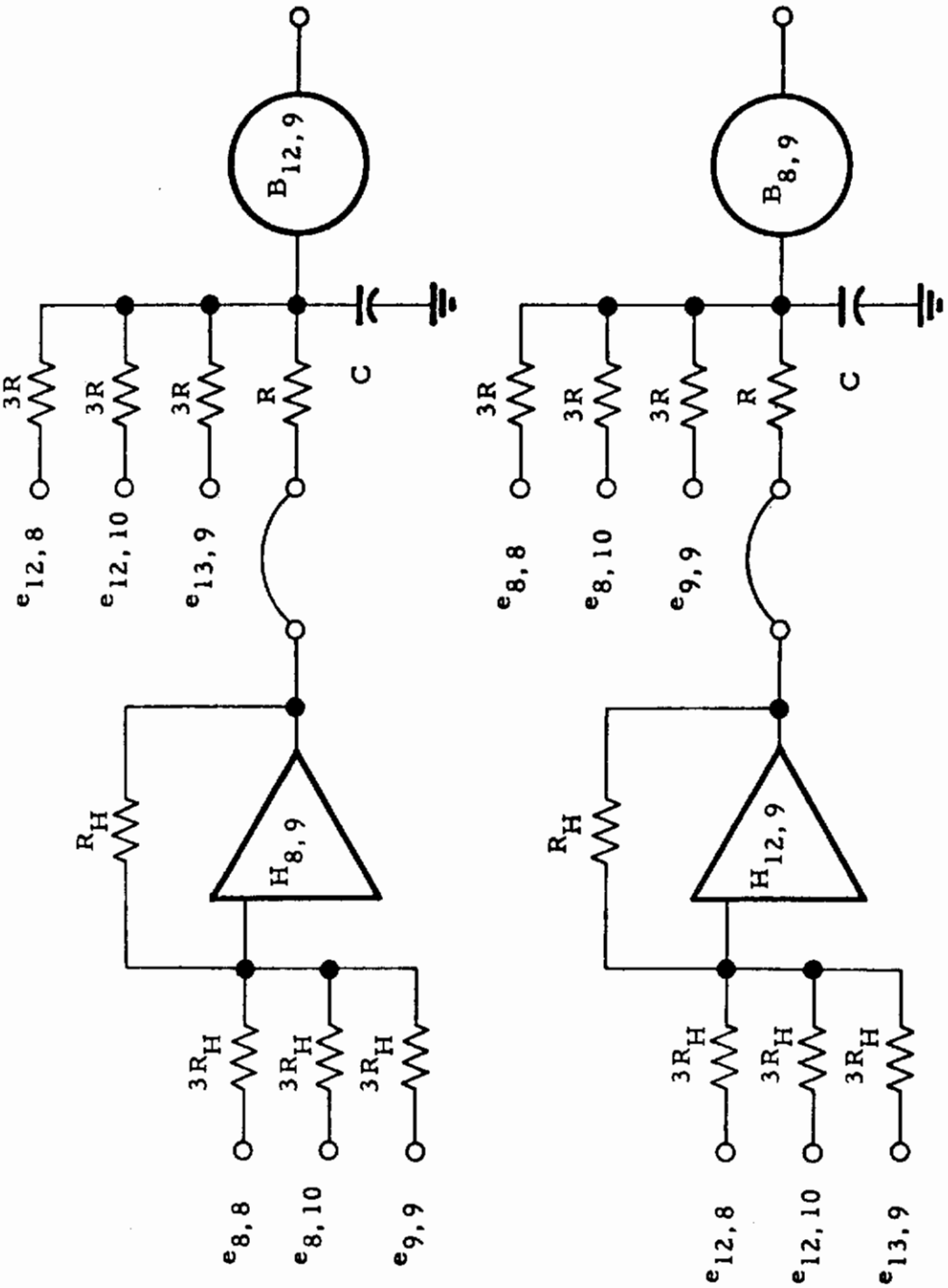


Figure 15. Reciprocal Contrast Bipolar Analog

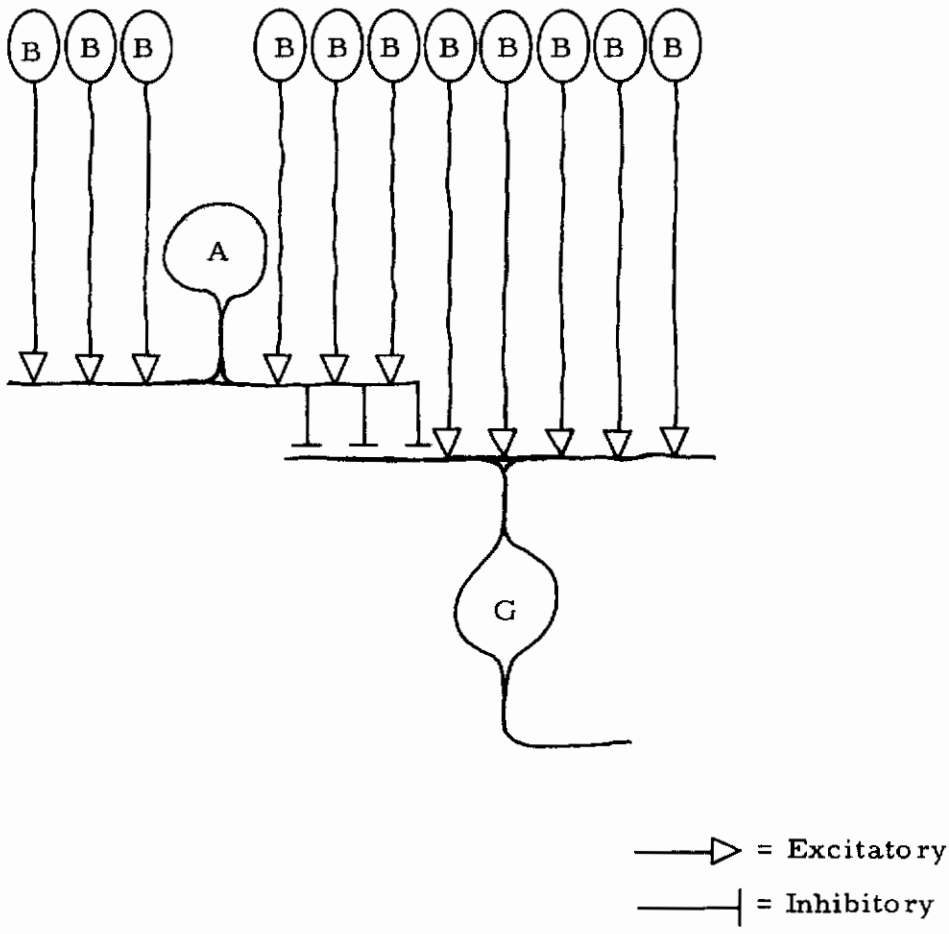


Figure 16. The Group Amacrine Postulate

on the other hand bipolars are excited from right to left then bipolar excitation will lead amacrine inhibition and the ganglion will respond. This simple example shows the importance of the spatial inputs to the retinal ganglions as well as the importance of temporal summation at the ganglion.

i. Bipolar Adaption

Impulses from neurons can be obtained by either exciting the soma (direct stimulation), exciting the synaptic inputs, or stimulating the axon or axonal endings of a nerve cell. The presynapse (see figure 11) of inhibitory amacrines on end feet of the bipolar axon has been suggested by Dowling[16] as a likely mechanism for bipolar adaptation. Bipolar adaption has been implemented in the model by feedback of the corresponding amacrine output, after integration, to the bipolar input sum.

j. Simplifications of the Model

This section describes the major simplify assumptions used in developing the electronic model of the pigeons retinal ganglions.

(1) Visual Field Represented by the Sensory Array

The visual field represented by the sensory array is thought of as being equivalent to 2-1/2 degrees on the pigeon retina. Each ganglion cell body is considered to be located in the center of the sensor array. From a review of the neural anatomy it appears unlikely that the majority of the retinal ganglions will be strongly influenced by receptors over an area greater than 2-1/2 visual degrees. This simplification may be somewhat in error for ganglions having a large dendritic branching but appears reasonable for the majority of ganglions.

(2) Localized Effects

The synapses of receptor to receptor and bipolar to bipolar are neglected since both the receptor end feet and bipolar axonal branching are quite limited. The localized nature of this type of synapse is assumed to be of limited importance due to the extensive branching of the ganglion.

(3) Surrounding of the Ganglion

In the area outside of or surrounding a ganglion's dendritic branching, only inhibitory amacrines can synapse on the ganglion. This simplification is based on the fact that bipolars have a relatively restricted axonal spread relative to amacrines. This means that if any influence comes from the area surrounding a ganglion's dendrites it must be inhibitory.

(4) Receptor

The model employs only one neural analog for the receptors, the cone. This simplification is based on the fact that the majority of receptors in the pigeon retina are cones. Each receptor of the model represents approximately 10 cells in the pigeon retina.

(5) Bipolars

The bipolars of the model are thought of as the Landolt Club type. This simplification is based on the fact that the pigeon retina is predominantly composed of the Landolt type bipolar and since the diffuse bipolar is normally associated with rods.

2. MODELING SPECIFIC DETECTORS

This section describes the neural interconnections and interactions incorporated into the model to electronically duplicate the functional response of the pigeon s optical ganglion cells as specified by H. R. Maturana's physiological measurements. In addition a velocity sensitive directional detector and an object detector built into the model are also described. These latter two detectors are presented only to show some of the capabilities of neural networks and do not form a part of Maturana's findings.

The detailed input stimuli presented to each detector are described prior to describing the connective arrangement employed to model each ganglion. The test stimuli bear a one-to-one correspondence with the reported tests performed by physiologist. All cell arrangements are to be regarded as top views.

The number of neurons employed by the model is considerably less than would occur in the retina; primarily in the interest of economy, model size and hardware limitation. Nevertheless, it is felt that the general arrangements employed are adequate to demonstrate basic neural mechanisms of the retina.

Maturana found that many of the individual ganglions monitored yield no response to stationary pattern with the eye anesthetized. The importance of this property in the actual visual system of the pigeon is questionable in lieu of the fact that the pigeon eye has a high frequency tremor at a frequency of one to two bursts per second. However the lack of response to stationary patterns does give additional clues regarding the operation of this avian's retina.

a. Luminosity Detector

The pulse repetition rate of this ganglion increases as the light intensity increases. Figure 17 shows the four bipolars, $B_{6,9}$, $B_{12,9}$, $B_{9,12}$, $B_{9,6}$, connected to the ganglion. The X's denote the cell bodies of the bipolars. The square around each bipolar cell body denotes the receptors which input to each bipolar. The circle around this area denotes the ganglions dendritic field, the area from which bipolar to ganglion connections are made.

The bipolars for this detector are the intensity type bipolar and do not adapt. The lack of self-adaptation of these bipolars is associated with the lack of presynaptic inputs from amacrines terminating on bipolar end feet. This situation could occur in the fovea or any area of limited amacrine population.

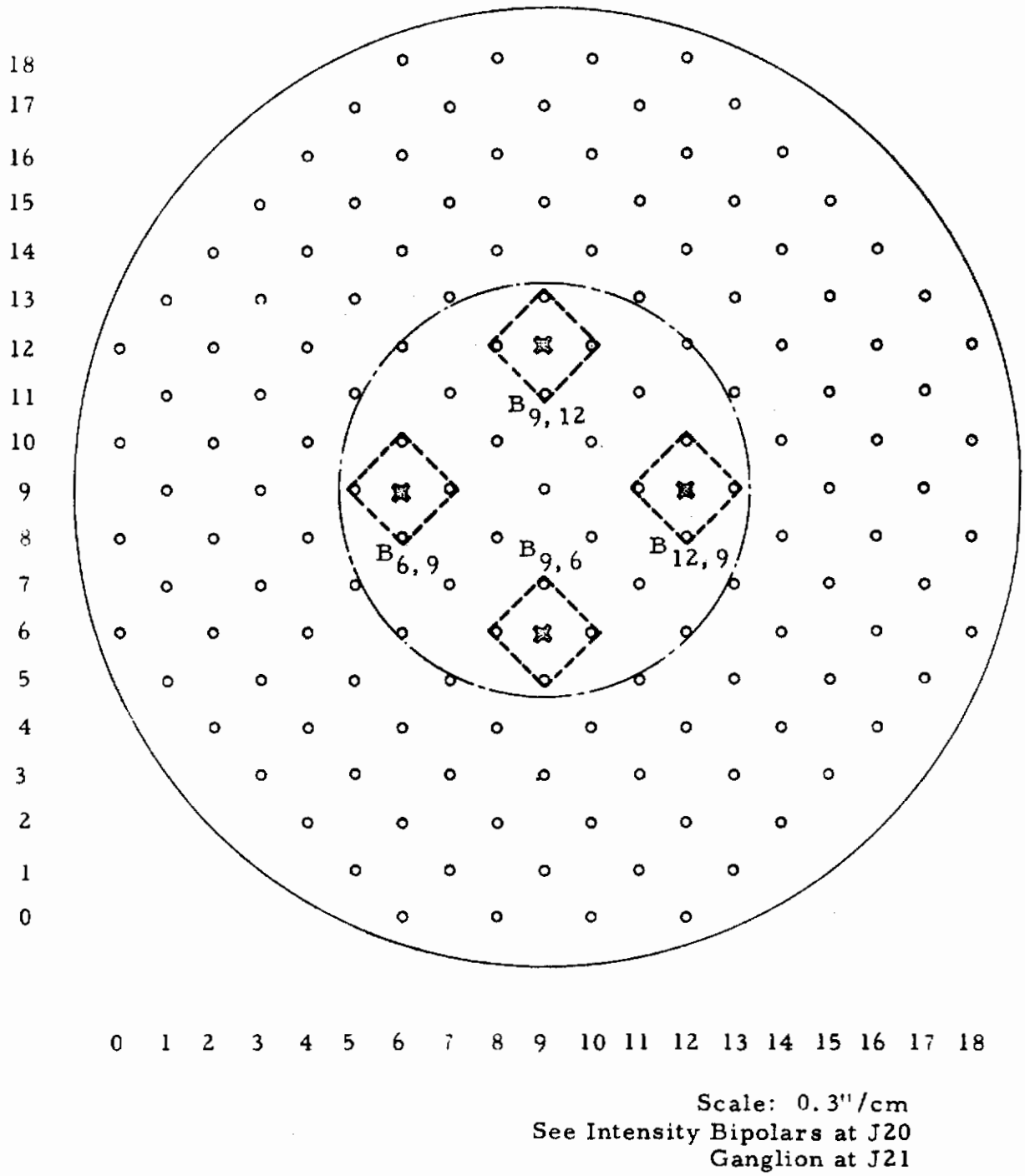


Figure 17. Luminosity Detector

b. General Edge Detector (Type I)

The required performance for this detector is:

Stimulus	Response
Diffuse Light	No
Small Light Spots	Slight
Moving Dark Spot (semi-random)	Yes
Moving Dark Edge (semi-random)	Maximal
Moving Grating	No

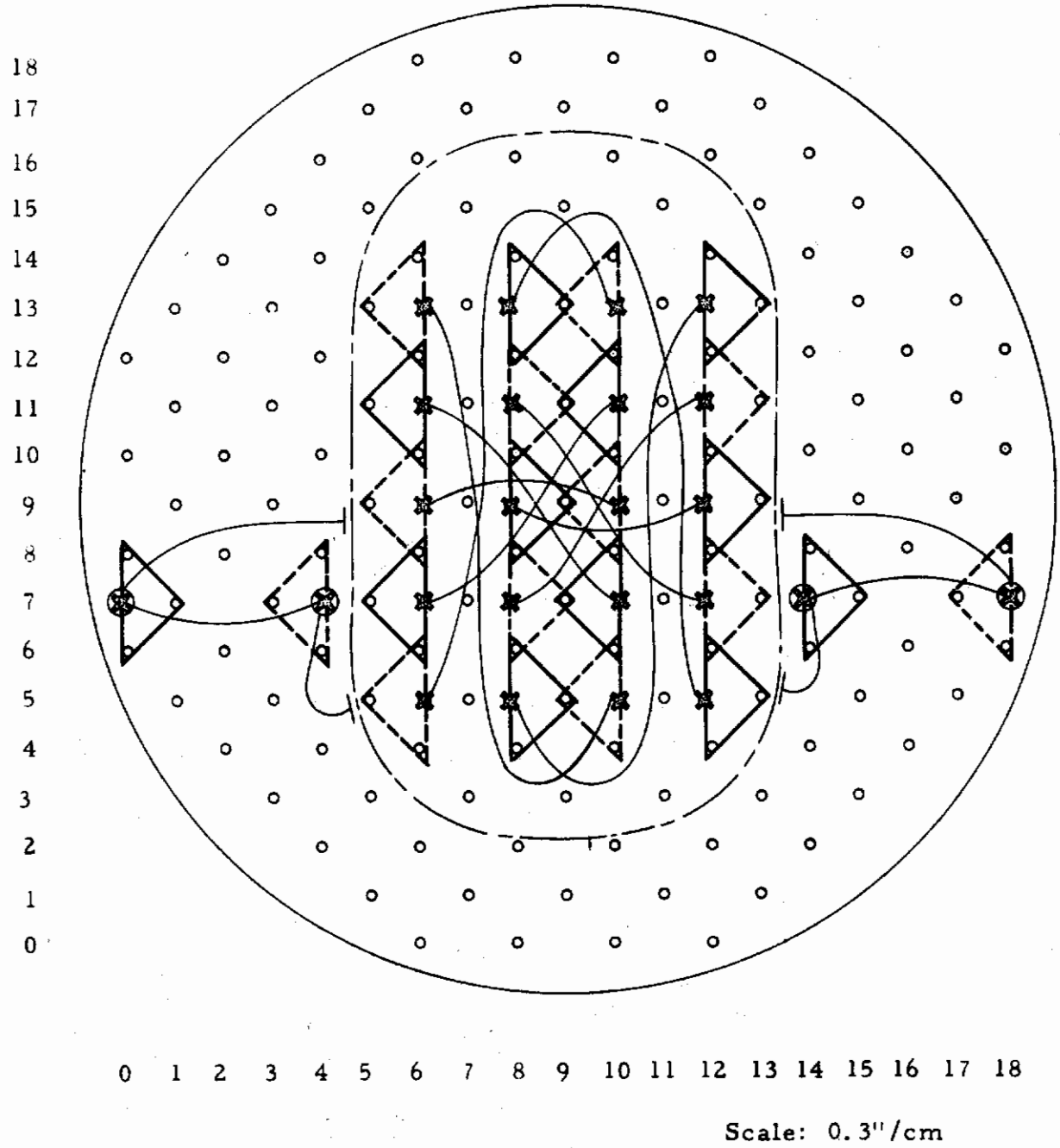
The connection arrangement is shown in figure 18. This ganglion receives twenty reciprocal contrast bipolar inputs and four reciprocal contrast amacrine inputs. As before, the bipolar cell body locations are designated by X's. The receptors inputting to each bipolar are contained by the triangles. Each bipolar cell body location is also the site of a horizontal cell body. Mutual contrast areas are shown by the interconnecting lines between bipolar X's. The area enclosed by the broken line represents the ganglions' input dendritic spread. The lines running from the surrounding amacrines $A_{0,7}$, $A_{4,7}$, $A_{14,7}$, and $A_{18,7}$ designate the amacrine outputs contacting the ganglion dendrites. Notice that $B_{0,7}$, $B_{4,7}$, $B_{14,7}$ and $B_{18,7}$ do not contact the ganglions' input dendritic field.

This detector cannot respond to diffuse light since only contrast bipolars provide the ganglion excitation. A light or dark spot interior to the ganglions' dendritic field will produce a response from the ganglion since one or more bipolars will be excited, depending upon the size of the spot. A moving spot will excite bipolars in sequence causing a build-up in the ganglion input sum, so that a moving spot produces a slightly stronger response than an ON-OFF spot. A moving edge produces the largest response since several bipolars are simultaneously excited.

A grating is essentially a multiplicity of edges which extend both into the ganglions' excitatory dendritic field and into the inhibitory surrounds containing the amacrines. If sufficient contrast is obtained in the inhibitory surrounds then the excitation of the central region does not cause a response. This is the situation which occurs for the moving grating. To obtain a maximum of inhibition with a limited number of neurons the self-adaptation of the bipolars exciting the four inhibitory amacrines has been removed.

As a vertical edge enters the field, for example moving left to right, the inhibitory amacrines cease firing when the edge reaches column four. When the vertical edge reaches column six a group of five bipolars respond. If the entering edge is dark the response is from the column ten bipolars. A light edge causes the column six bipolars to respond. In either event the ganglion receives excitation as a vertical edge approaches column six.

If a vertical edge is maintained in this position the ganglion firing rate decreases significantly. This is due to the self-adaptation of the bipolars.



See Contrast Bipolars at J10, J11, J12, J13, J14
and Contrast Amacrines at J39
and Ganglion at J22
Note: Self adaptation of J39 removed.

Figure 18. General Edge Detector (Type I)

c. General Edge Detector (Type II)

The anatomical difference between general edge Type I and Type II lies in the smaller responsive area of the Type II detector. Functionally, the Type II ganglion responds to a moving grating whereas Type I does not.

The required performance of this detector is:

Stimulus	Response
Diffuse Light	No
Small Light Spots	Slight
Moving Dark Spot (semi-random)	Yes
Moving Dark Edge (semi-random)	Maximal
Moving Grating	Yes

The connection arrangement for this ganglion is shown in figure 19. Operation of this detector is identical with that described for General Edge (Type I) except that the ganglion does not receive inhibition from surrounding contrast amacrines causing it to respond to a moving grating.

d. Convex Edge Detector

The required response of this ganglion is:

Stimulus	Response
Diffuse Light	No
Small Light Spot	Slight
Moving Dark Spot (semi-random)	Yes
Moving Dark Wedge (semi random)	Yes
Moving Dark Edge (180^{o}; 90^{o})	No

Notice that although the detector responds to a convex edge, no response is obtained for a long straight edge inclined vertically.

Figure 20 illustrates the connection arrangement used to model this detector. No response occurs for diffuse light since all bipolars are of the contrast type. Small light or dark spots inside the ganglion dendritic spread cause a response by exciting the bipolars. As in the General Edge Detectors, the moving spot causes successive bipolar firing which, when integrated by the ganglion, produces a larger response than the ON or OFF of a spot.

The ganglion does not respond to a long vertical edge, light or dark, since inhibitory contrast amacrines of rows 1 and 17 are simultaneously excited. This combined inhibition is weighted such that it overcomes the excitatory bipolars inside the ganglions dendritic spread.

A response does occur, however, for a pointed or convex edge since the row 1 or 17 amacrines do not simultaneously respond. A response

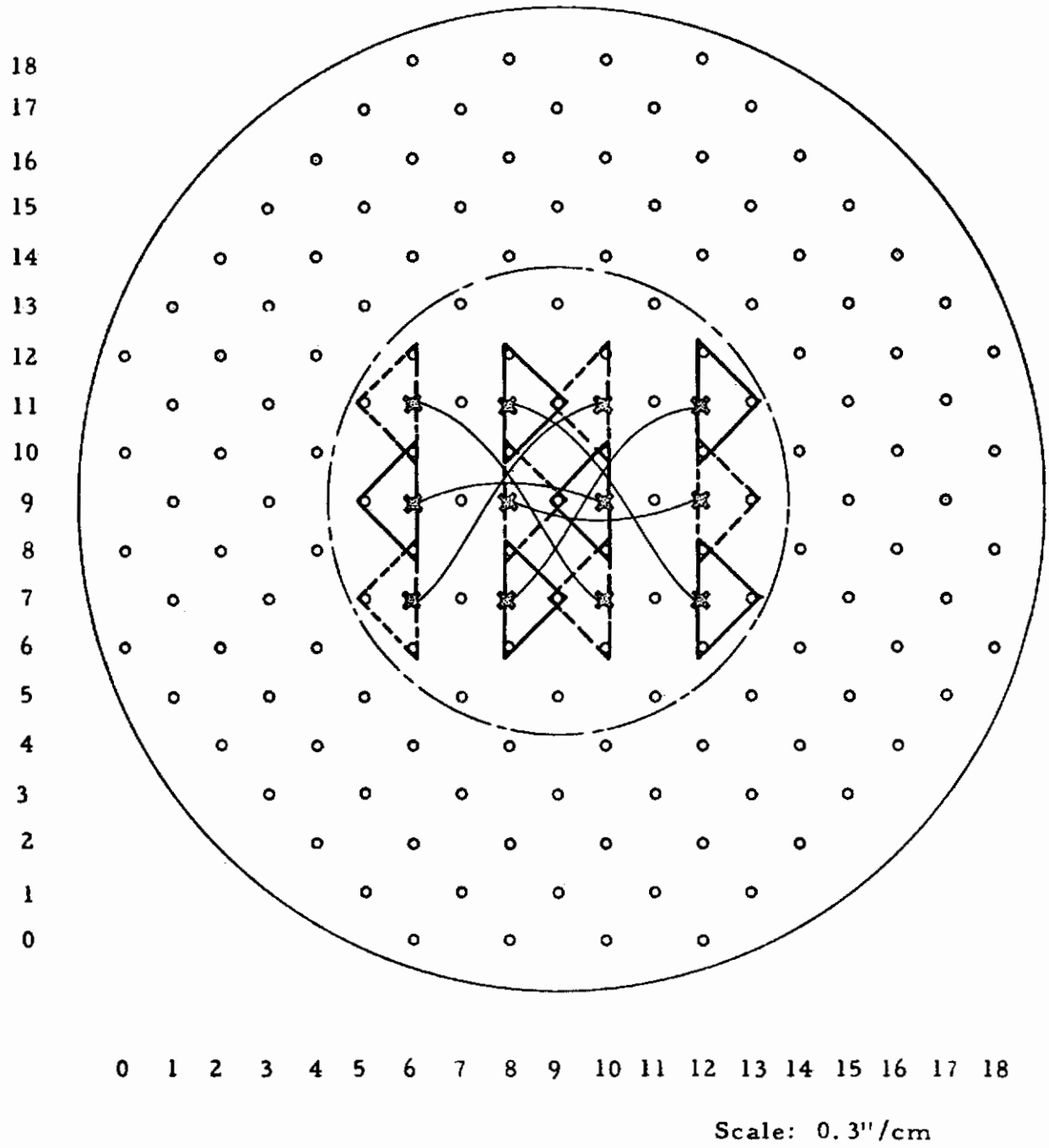
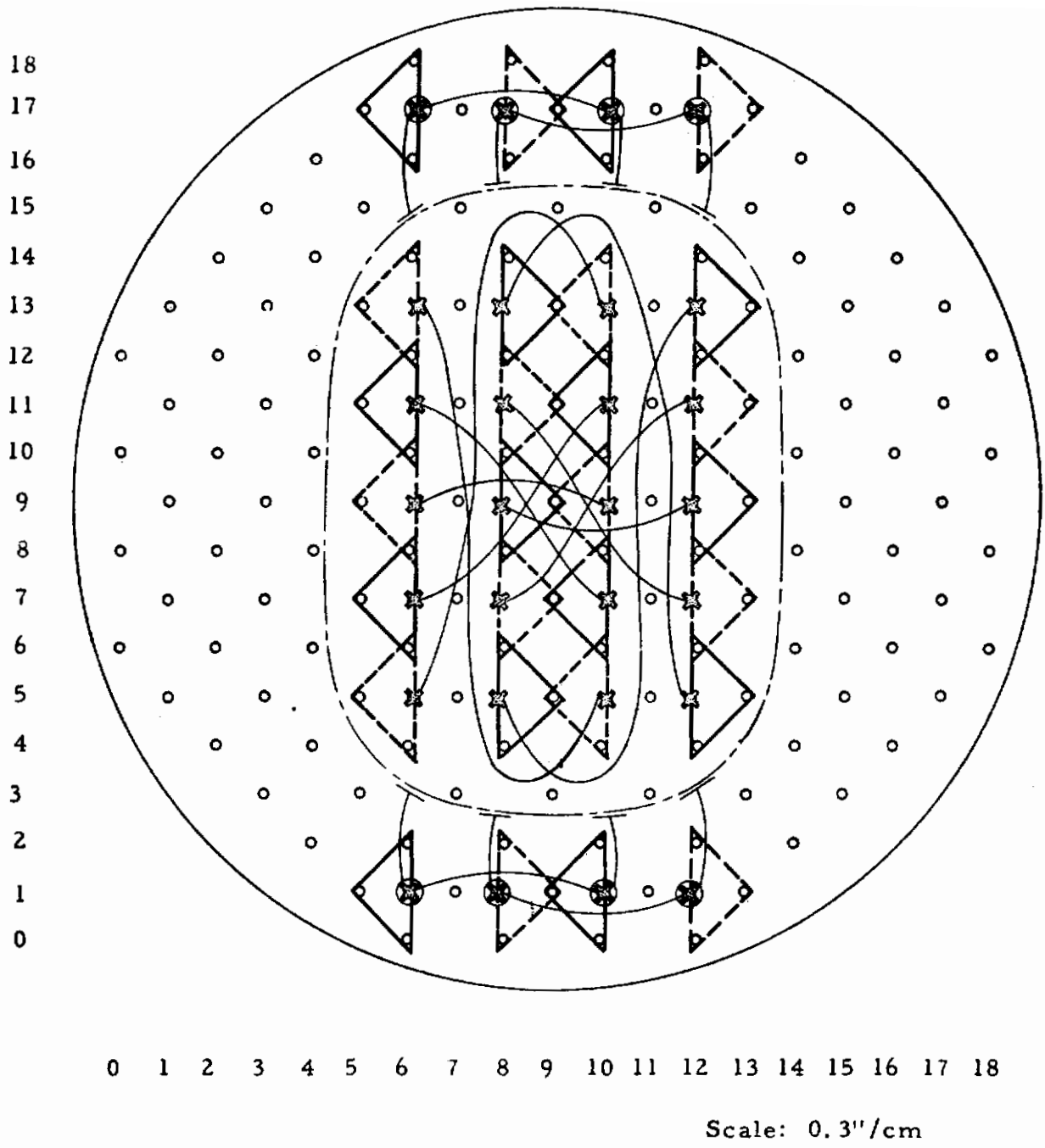


Figure 19. General Edge Detector (Type II)



See Contrast Bipolars at J10, J11, J12, J13, J14
and Contrast Amacrines at J40, J41
and Ganglion at J24.

Figure 20. Convex Edge Detector

to a stationary convex edge is strongly diminished by virtue of the bipolar adaptation.

e. Vertical Edge Detector

The desired response for this detector is:

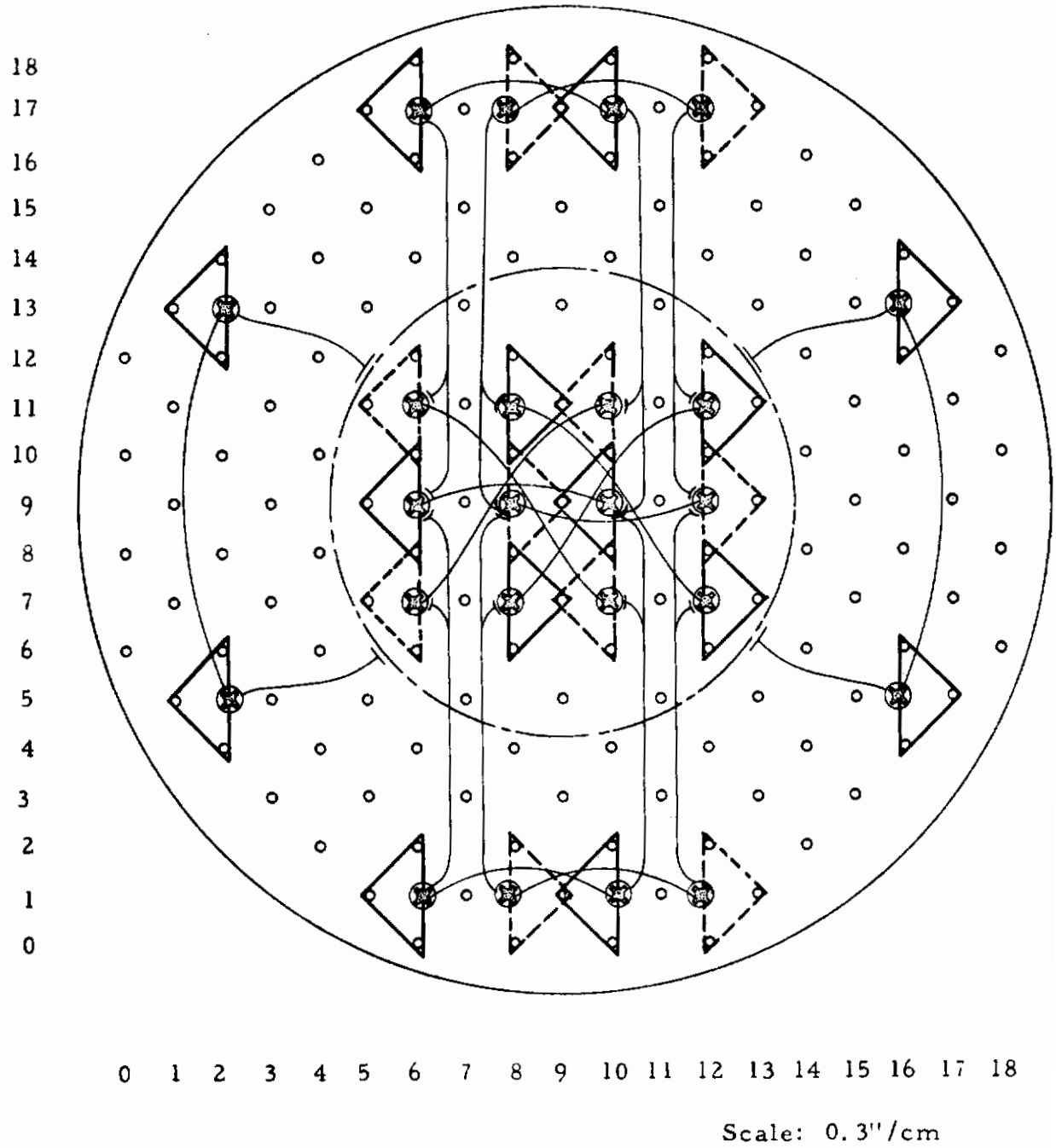
Stimulus	Response
Diffuse Light	No
Small Light Spots	No
Small Dark Spots	No
Moving Dark Spot (180°)	No
Moving Light Spot (180°)	No
Moving Dark Edge (180°; 90°)	Yes
Moving Dark Edge (180°; 60°)	No
Moving Dark Edge (180°; 120°)	No
Moving Dark Edge (0°; 60°)	No
Moving Dark Edge (0°; 120°)	No
Moving Dark Edge (0°; 90°)	Yes
Moving Light Edge (0°; 90°)	Yes
Stationary Dark Edge	Yes

This ganglion does not respond to diffuse light or to small light spots. It responds exclusively to a light or dark vertical edge.

Figure 21 shows the connection arrangement used to model this detector. Twelve contrast bipolars and their associated amacrines are positioned internal to the ganglions dendritic spread. In the area surrounding the ganglion dendrites are contrast amacrines (four in row 1 and four in row 17). The output of these cells act to inhibit the twelve central amacrines for a vertical edge. For a response to occur, it is necessary that like column neurons be simultaneously excited. The four contrast amacrines $A_{2,5}$, $A_{2,13}$, $A_{16,5}$, and $A_{16,13}$ act directly upon the ganglion input sum. They provide additional inhibition for off angle edges in excess of that given by the central amacrines.

No response to diffuse light occurs since all ganglion inputs originate from contrast bipolars. No response occurs for spots in the central region since each bipolar firing is followed immediately (1 msec) by the corresponding amacrine activity. The ganglion integration interval is such that bipolar excitation is cancelled by the amacrine inhibition. This ganglion has a maintained response for a stationary edge. When row 1 and row 17 amacrines inhibit the central amacrines this concurrently releases the adaptation of the bipolars. The lack of bipolar adaptation in conjunction with a lightly adapted ganglion causes the continuous response for a stationary vertical edge.

To insure that the central amacrine inhibition is released when row 1 and 17 amacrines are excited the pulse width of the latter neurons is made



See Contrast Bipolars at J15, J16, J17, J40, J41,
Contrast Amacrines at J18, J19, and
Ganglion at J25.

Note: The Amacrines of J19 have a pulse duration of approximately 200 msec.

Figure 21. Vertical Edge Detector

long (200 msec). This in effect simulates simultaneous excitation of a group of amacrines.

f. Directional Detector No. 1

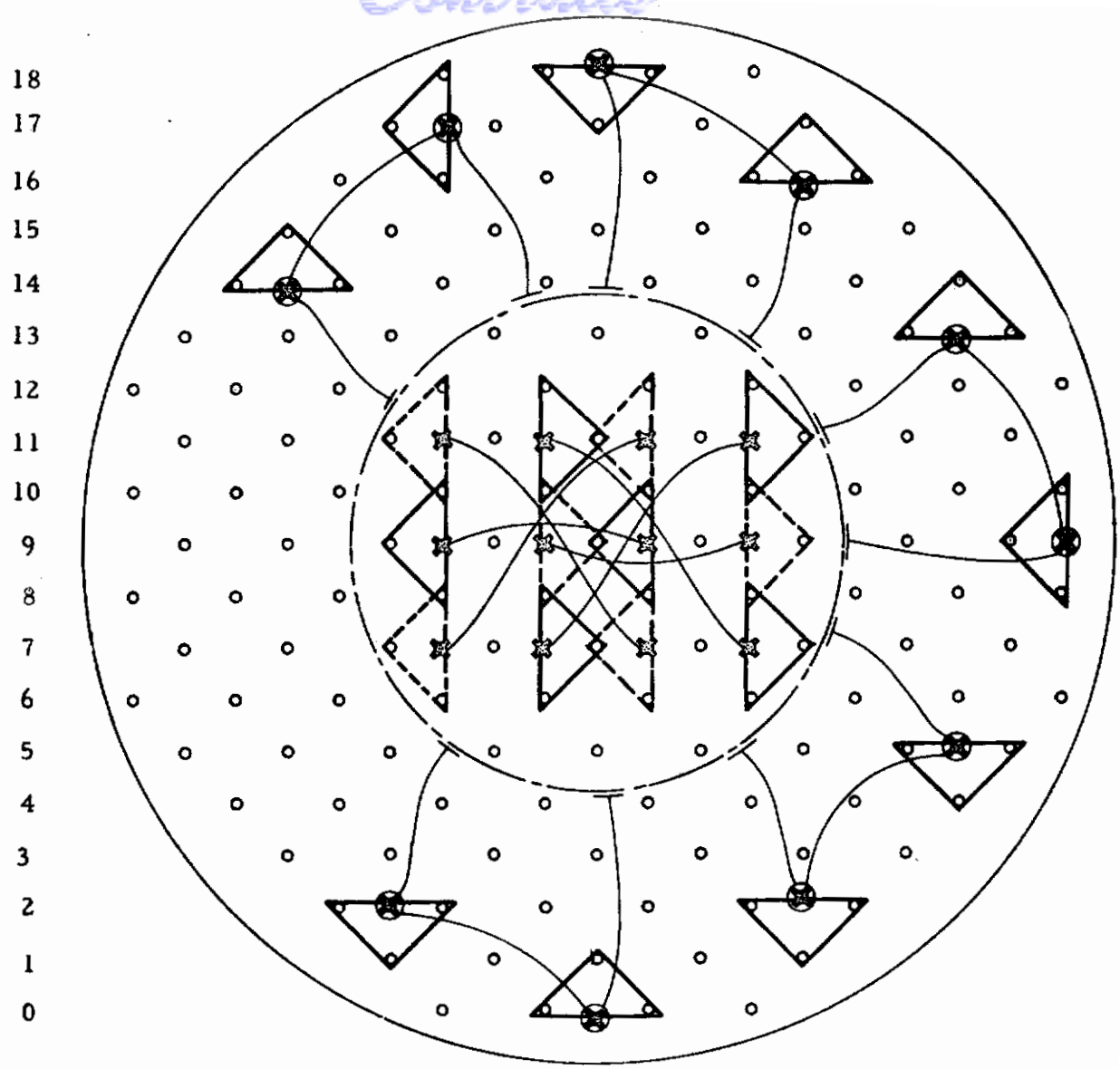
The film stimuli and required responses for this detector are as follows:

Stimulus	Response
Diffuse Light	No
Small Light Spots	Slight
Small Dark Spots	Slight
Moving Dark Spot (180°)	Yes
Moving Dark Spot (180°) – Above Center	Yes
Moving Dark Spot (180°) – Below Center	Yes
Moving Dark Spot (0°)	No
Simultaneous Spots	No
Moving Light Spot (180°)	Yes
Moving Light Spot (150°)	No
Moving Light Spot (0°)	No
Moving Dark Tongue (180°; 90°)	Maximal
Moving Dark Tongue (150°; 60°)	No
Moving Dark Tongue (0°; 90°)	No
Moving Light Tongue (150°; 60°)	No
Moving Light Tongue (0°; 90°)	No
Moving Light Tongue (180°; 90°)	Yes

As illustrated by figure 22, this ganglion receives excitatory inputs from 12 central contrast bipolars and inhibitory inputs from 10 surrounding contrast amacrines. No ganglion response occurs for diffuse light since all inputs to the ganglion originate from contrast neurons.

A light or dark spot causes one or more of the central bipolars to fire. This will cause a ganglion response provided the spot is not so large as to extend simultaneously into the surrounds and the central region. This detector is required to respond for a light or dark spot or tongue when moved from left to right. This is accomplished by providing inhibition from all direction except the exclusive direction. When a spot or tongue enters from any direction other than the exclusive direction inhibition always precedes excitation. In the exclusive direction excitation precedes inhibition. To model this detector, the surrounding amacrine circuitry is modified to have a one second inhibitory pulse width. The long pulse width of these surrounding amacrines may be thought of as the sequential firing of a large group of amacrines.

This ganglion does not respond to simultaneous spots, one from the exclusive and one from the non-exclusive direction. When the non-exclusive spot is in the extreme surrounds (18, 11), amacrine $GA_{18,9}$ fires and inhibits the ganglion. This inhibition remains for one second. As the



See Contrast Bipolars at J10, J11, J12,
and Contrast Amacrines at J35, J36, J37,
and Ganglion at J46,

Note: All Amacrines have a 1 second pulse duration

Figure 22. Directional Detector 1

two spots enter the central region a large amount of central excitation occurs. To overcome this excitatory volley the surrounding amacrine inhibition is weighted stronger than the central bipolars excitation (approximately 3:1). (Note: If a spot enters from the non-exclusive direction the ganglion will fire if the spot is moved slow enough to allow the amacrine inhibition to cease.)

This detector has a minimal response to a stationary spot in the central area due to the self-adaptation of the bipolars.

g. Directional Detector No. 2

This ganglion is modeled using the same general approach as the directional detector described above. The desired responses are listed below. The distinguishing property of this ganglion is that its exclusive direction is from 90 degrees while the previously described directional ganglion has its exclusive direction from 180 degrees.

Stimulus	Response
Diffuse Light	No
Small Light Spots	Slight
Small Dark Spots	Slight
Moving Dark Spot (90°)	Yes
Moving Dark Spot (120°)	No
Moving Dark Spot (270°)	No
Moving Light Spot (270°)	No
Moving Light Spot (120°)	No
Moving Light Spot (90°)	Yes

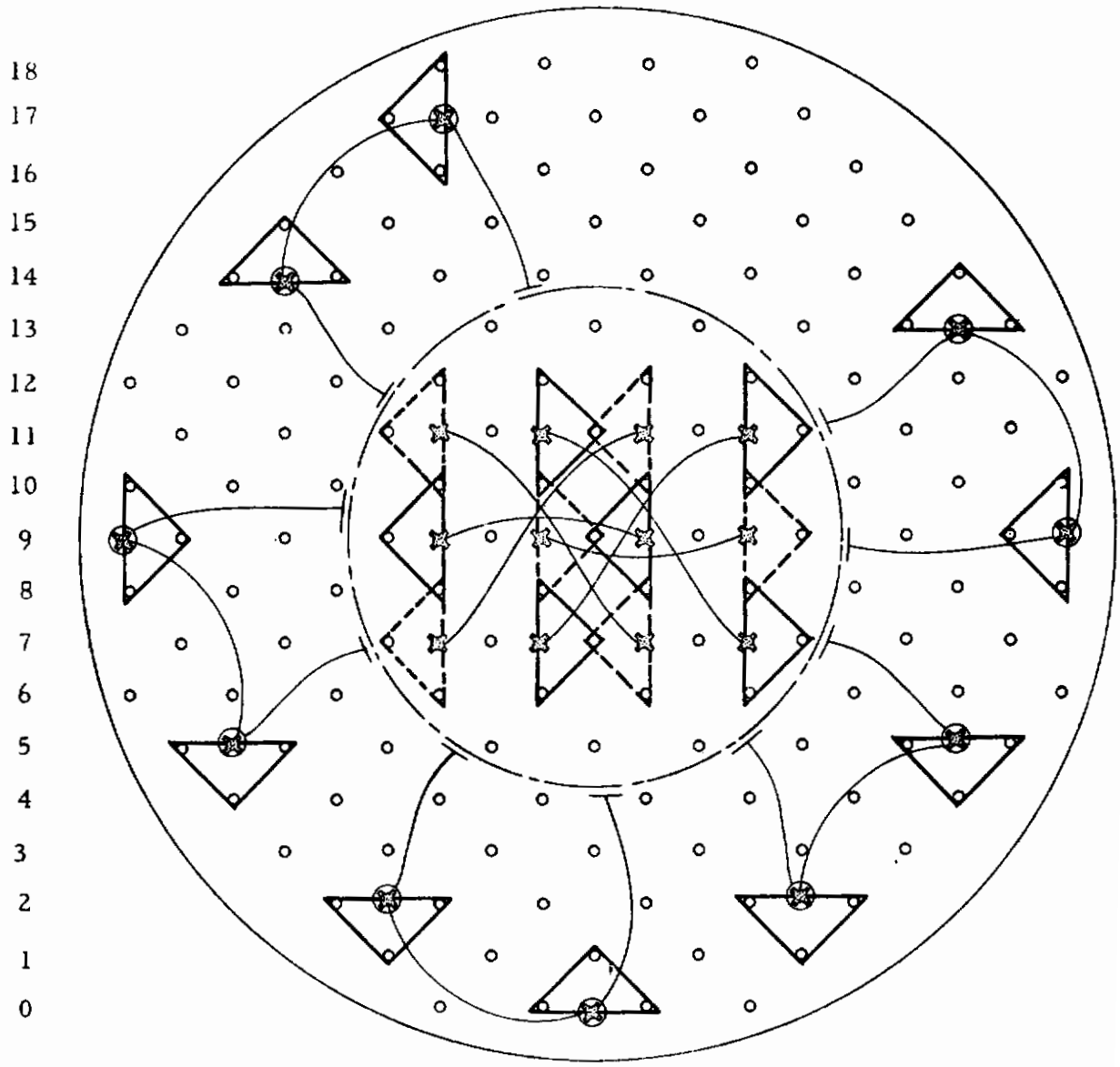
Figure 23 shows the connection arrangement of the neurons used to model this ganglion. As can be seen the difference between this detector and Directional Detector No. 1 is the removal of contrast amacrines $GA_{9,18}$, $GA_{13,16}$ and the addition of contrast amacrines $GA_{0,9}$ and $GA_{2,5}$.

h. Directional Detector No. 3 (Velocity Detector)

This directional detector has its exclusive direction for a spot or an edge moving from a 45 degree angle. The method employed for implementing this detector is different from that employed for the previous two directional detectors described.

The principal aim in the method for constructing this detector is to illustrate how the neural circuitry of the model may be interconnected to achieve a one directional movement detector which is responsive to the velocity as well as the direction of a moving spot or edge.

The stimuli and the corresponding required response for this detector are:



See Contrast Bipolars at J10, J11, J12
and Contrast Amacrines at J35, J36, J37
and Ganglion at J47
Note: All amacrines have a 1 second pulse duration.

Figure 23. Directional Detector 2

Stimulus	Response
Moving Dark Spot (75°)	No
Moving Dark Spot (225°)	No
Moving Dark Spot (45°) Fast	No
Moving Dark Spot (45°) Normal	Yes
Moving Dark Spot (45°) Slow	No
Moving Dark Tongue (45°; 135°)	Yes

The interconnection arrangement and associated neural analogs of this detector are shown in figure 24.

The operation of this detector is most readily described for a dark spot which enters upon the sensory array from a 45° angle. When the spot covers all of the receptors of $H_{15,14}$ then within 110 milliseconds $SB_{15,8}$ fires. This bipolar has a pulse width of approximately 130 milliseconds. Following this 240 msec, $SA_{15,8}$ fires for a period of 100 msec. When $SA_{15,8}$ fires, $AXX_{8,7}$ is inhibited. Only $BXX_{8,7}$, $AXX_{8,7}$, $B_{11,10}$ and $A_{11,10}$ input to the ganglion of this detector. If the firing of $BXX_{8,7}$ is coincident with the inhibition of $AXX_{8,7}$, then the ganglion will receive only bipolar excitation.

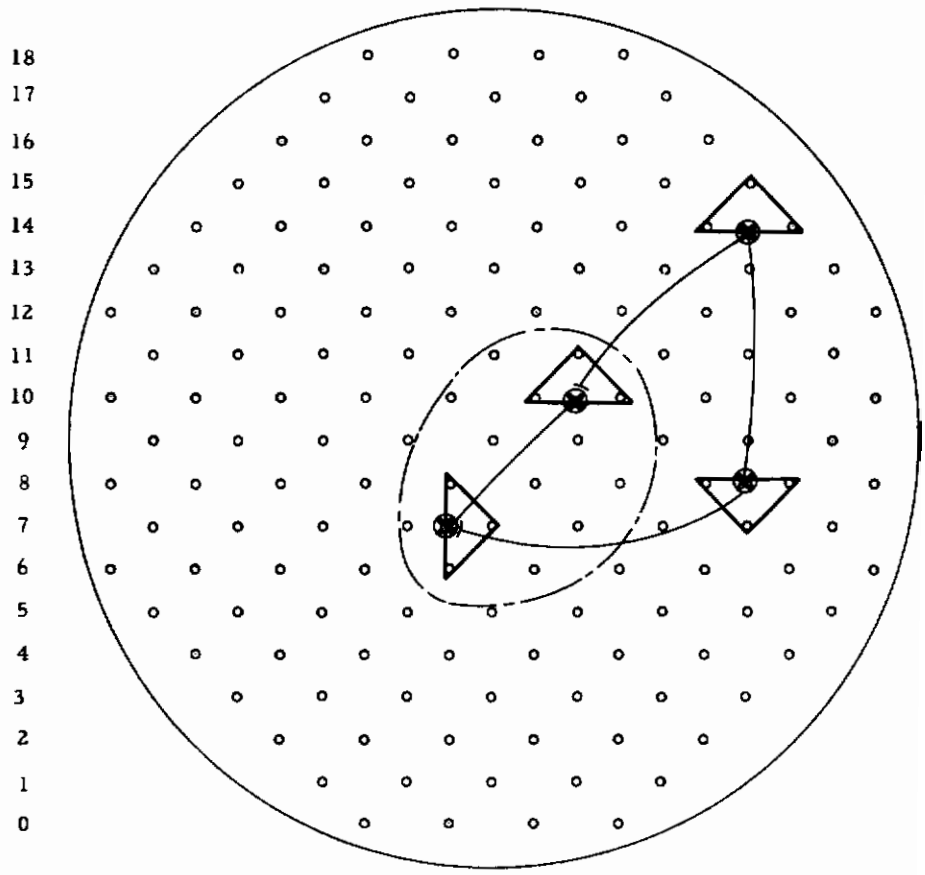
If the dark spot moves too rapidly, even though it enters from the exclusive direction, $AXX_{8,7}$ will not be inhibited since $SB_{15,8}$ will not have made a transition from +12 volts to ground and $SA_{15,8}$ will not have fired. In this event when the dark spot covers the area associated with $H_{11,10}$ both $BXX_{8,7}$ and $AXX_{8,7}$ will respond. The integrated sum as seen by the ganglion, therefore, is unchanged since the excitation of bipolar $BXX_{8,7}$ is cancelled by the inhibition of $AXX_{8,7}$.

If on the other hand, the directional dark spot moves too slowly, then the inhibition of $AXX_{8,7}$ by $SA_{15,8}$ will have ceased prior to the spots arrival at $H_{11,10}$. The effect is the same as for the fast spot and the integrated sum as seen by the ganglion again remains unchanged.

Thus, the ganglion will respond to a dark spot of a given velocity only. The correct velocity is then that which causes $AXX_{8,7}$ to be inhibited in coincidence with the excitation of $BXX_{8,7}$. The required velocity is greater than 16 cm/sec. but less than 40 cm/sec.

For a light spot, the operation of this ganglion is similar except that $SA_{15,14}$, $A_{11,10}$ and $B_{11,10}$ are the neurons which control the firing of the ganglion.

For any angle from approximately 60 degrees to 330 degrees this ganglion will not respond to a moving spot or edge since the inhibition of $AXX_{8,7}$ and $A_{11,10}$ will not be released. The use of contrast bipolars again prevents this detector from firing to diffuse changes of illumination.



See Contrast Bipolars and Amacrines at J38
and Ganglion at J48

Note: This detector employs special bipolars having a pulse width as listed: $SB_{15,8}$ = 130 msec, $SB_{15,14}$ = 130 msec. The corresponding special amacrines have a pulse width as follows: $SA_{15,8}$ = 100 msec, $SA_{15,14}$ = 100 msec.

Figure 24. Directional Detector 3 (Velocity Detector)

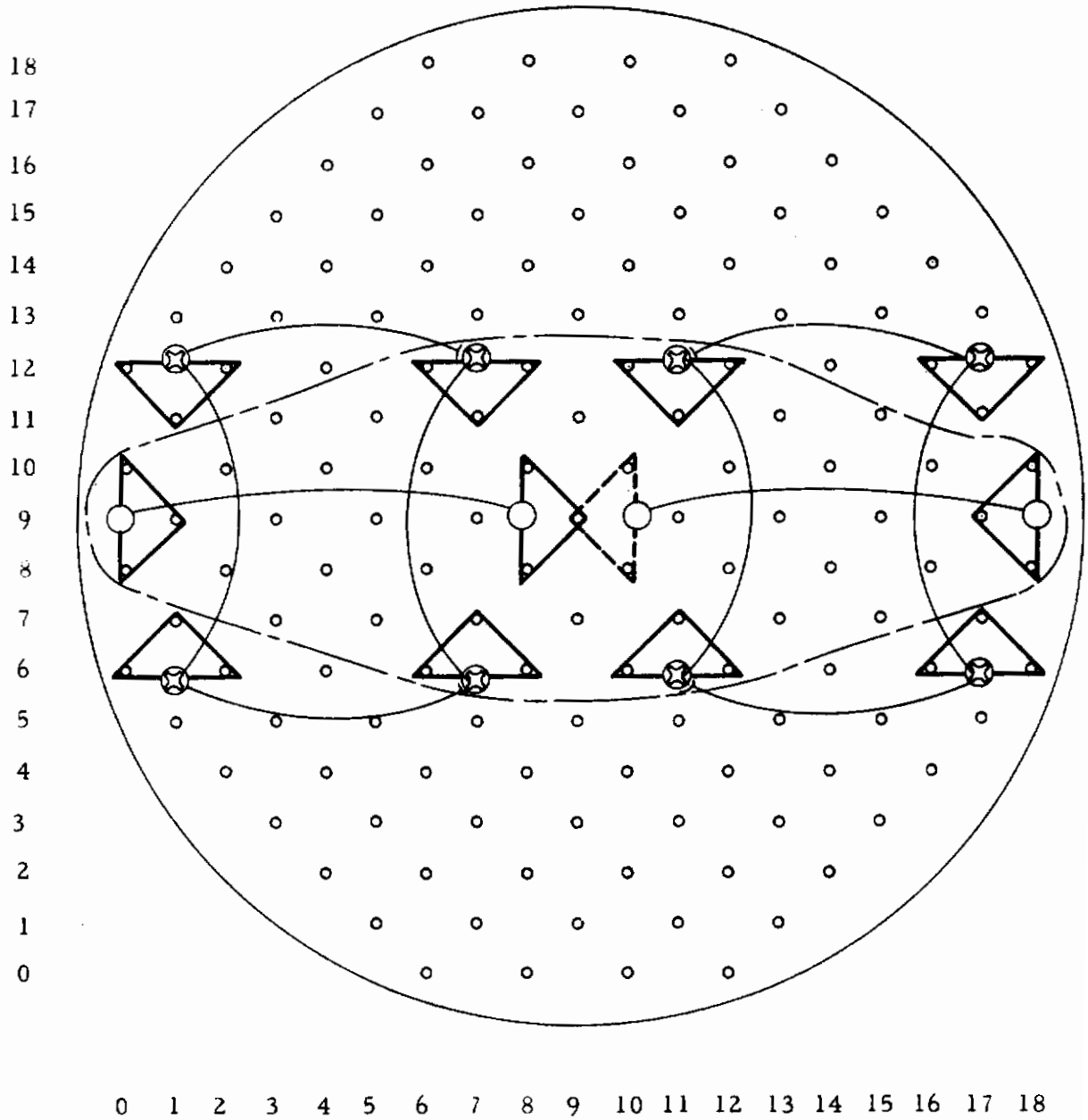
The allowable velocity range of the actual retinal ganglions is not as restricted as this neural network would demonstrate. In the ground squirrel, which possesses directionally selective ganglions of functional performance similar to that of the pigeon, the allowable velocity range is 0.1 to 20 visual degrees/sec.[17] Since 1 centimeter in the model is equivalent to 15 microns and 1 visual degree of the ground squirrel is equal to approximately 120 microns then the actual velocity range for which a response is elicited in the exclusive direction would be equivalent to 0.8 to 160 cm/sec. The data of the ground squirrel is used to define the actual velocity range of directional detectors since Maturana has not reported this type of quantitative information for the pigeon retina. The general performance of the directional detectors of the ground squirrel and the pigeon are in close agreement. In addition, both contain predominantly cone eyes with equal visual fields of view having approximately equal linear distance on the retina.[11, 2, 17]

i. Horizontal Edge Detector

The stimuli and corresponding response for this detector are:

Stimulus	Response
Diffuse Light	No
Small Light Spots	No
Small Dark Spots	No
Moving Dark Spot (90°)	No
Moving Light Spot (90°)	No
Moving Dark Spot (270°)	No
Moving Light Spot (270°)	No
Moving Dark Edge (90°; 180°)	Yes
Moving Dark Edge (270°; 180°)	Yes
Moving Light Edge (90°; 180°)	Yes
Moving Light Edge (270°; 180°)	Yes
Moving Tongue (excludes surroundings)	No
Moving Corner (less than 1/2 receptive field)	No
Moving Corner	Yes
Moving Dark Edge (120°; 30°)	No
Moving Corner	Yes

The neurons employed by this ganglion and their interconnection scheme is shown in figure 25. All bipolars and amacrines of this detector are the contrast type hence no response occurs for diffuse changes of illumination. When a dark horizontal edge enters slightly beyond row 12 then contrast bipolars $B_{1,6}$, $B_{7,6}$, $B_{11,6}$ and $B_{17,6}$ are activated. The firing of $A_{1,6}$ and $A_{17,6}$ inhibits the activity of $A_{7,6}$ and $A_{11,6}$. For this stimulus, therefore, the ganglion is activated since it is supplied entirely by excitatory inputs. For a light horizontal edge entering upon row 12 firing of $A_{1,12}$, $B_{7,12}$, $B_{11,12}$ and $A_{17,12}$ occurs, however amacrines $A_{7,12}$ and $A_{11,12}$ are inhibited. Again the ganglion is supplied only with excitatory inputs and a response occurs. $B_{1,6}$, $B_{1,12}$, $B_{17,6}$ and $B_{17,12}$ are not adaptable,



Scale: 0.3"/cm

See Contrast Bipolars and Amacrine of J44 and Contrast Amacrines at J42, J43 and Ganglion at J49

Note: The adaptation is removed from J43 so that these amacrines under contrast strongly inhibit the amacrines of J44.

Figure 25. Horizontal Edge Detector

therefore under contrast the associated amacrines provide strong inhibition of the column 7 and 11 bipolars.

Amacrines $AX_{0,9}$, $AXX_{8,9}$, $AXX_{10,9}$ and $AX_{18,9}$ are used to prevent ganglion excitation when an edge is inclined at angles greater than ± 30 degrees with respect to the horizontal axis.

If a dark vertical edge is positioned slightly past column 2, $A_{1,6}$ and $A_{1,12}$ will be off since no contrast is detected by their corresponding bipolars. However, $AX_{8,9}$ will fire causing inhibition of the ganglion. This example is sighted to show the opposing results of a horizontal and vertical edge.

If a horizontal edge enters only the surrounds (bipolars of column 1 and/or 17) only inhibition results at the ganglion. If a horizontal edge enters only the central region, again the net result appearing at the integrated ganglion sum is inhibition. This is accomplished by column 7 and 11 bipolars combining at the ganglion to yield an unchanged ganglion sum while $AXX_{8,9}$ and $AXX_{10,9}$, or $AX_{0,9}$ and $AX_{18,9}$ provide inhibition. The light horizontal tongue causes $AXX_{8,9}$ and $AXX_{10,9}$ to inhibit the ganglion, if the tongue is dark then $AX_{0,9}$ and $AX_{18,9}$ cause the inhibition.

Only if a horizontal edge is presented to both the surrounds and the central region can a response occur. This is in precise agreement with physiological data. The detector does not respond to spots in the central region since bipolar excitation is negated by amacrine inhibition. A stationary response does not occur due to the strong self adaptation of the ganglion.

j. Object Detector

This ganglion demonstrates one method for detecting objects using a network of analog nerve cells. It does not form a part of the pigeon's retinal ganglions, as reported by Maturana.

Stimulus	Response
Diffuse Light	No
Small Light Spots	No
Small Dark Spots	No
Ellipse (translated & rotated)	No
Bug (translated & rotated)	Yes
Star (translated & rotated)	No

A block diagram of this network is shown in figure 26. The input to the comparators is equal to the algebraic sum of the output voltage of each receptor in the sensor array (except $R_{9,9}$) divided by a constant, 144, the average output of the entire sensory array.

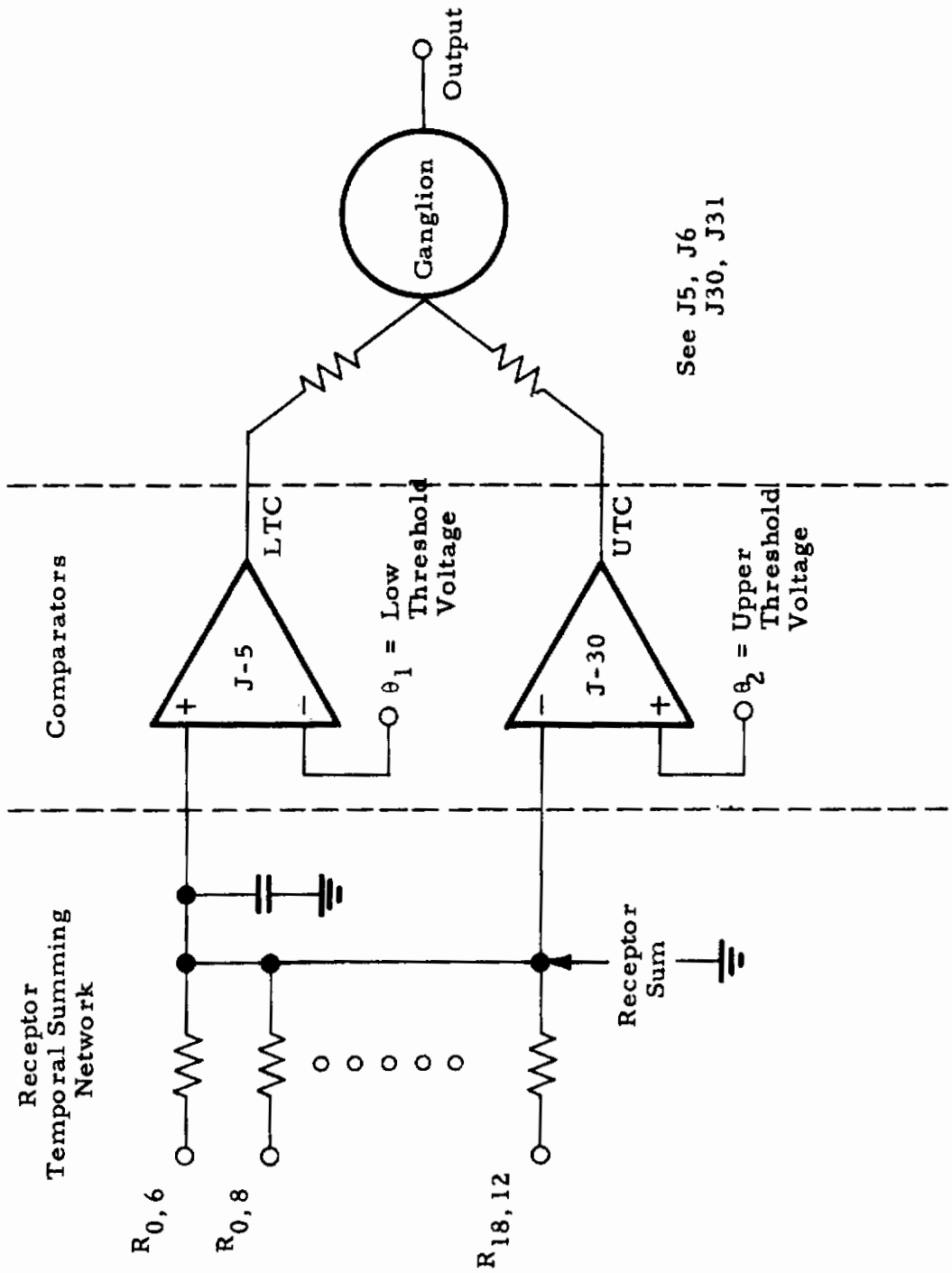


Figure 26. Object Detector Block Diagram

Let S_E = receptor sum for an ellipse

S_B = receptor sum for a bug

S_S = receptor sum for a star

For the objects as defined by the film stimulus

$$\overline{S}_E > \overline{S}_B > \overline{S}_S$$

where the bar denotes the average value of the receptor sum for the subscripted stimuli. This implies that the silhouette of the star is larger than that of the bug and more receptors are activated. The projection of the ellipse causes the activation of the least number of receptors.

For a star the output of the low threshold comparator (LTC) is -12 volts with +12 volts occurring for a bug or an ellipse if the threshold, θ_1, is properly adjusted. For an ellipse the upper threshold comparator (UTC) has an output of -12 volts with +12 volts occurring for a bug or a star if θ_2 is property adjusted. For a ganglion response to occur both LTC and UTC must be at +12 volts. This occurs only for a bug.

SECTION V

NEURAL CIRCUITRY

1. RECEPTORS

Figure 27 is a schematic of the receptor circuitry. The circuit is a simple emitter follower. The emitter follower is required since the receptor outputs to as many as ten other neurons. Each receptor card contains 20 of these circuits. The output of the receptor is an analog voltage approximately proportional to the logarithm of light flux density incident upon the associated sensor. The maximum output from this circuit is approximately +11 volts corresponding to an intense illumination. The minimum output is zero which corresponds to a dark array.

Since the sensors used by the model are cadmium sulfide, care should be taken not to subject the model to a temperature environment approaching 75°C.

2. HORIZONTALS

Figure 28 is a schematic of the horizontal circuit. This circuit is a simple operational amplifier. The horizontal circuit receives inputs from receptors and outputs only to bipolars. The output voltage from this circuit is a voltage equal to the sum of the three receptor inputs divided by three (average receptor voltage) but opposite in polarity to the receptor voltage. In addition, the output is provided with a small positive bias. The bias is set by R_4. The amount of bias is equal to twice the voltage appearing at the base of Q_2. With R_4 at 2.4K the output bias voltage is approximately +.56 volts, approximately the horizontal output voltage with the array dark. Under maximum illumination of the receptors the horizontal output will be approximately -10 volts. The receptors inputting to a horizontal are adjacent to the location defined by the horizontal subscript.

3. BIPOLAR/AMACRINE

The bipolar/amacrine is shown in figure 29. The threshold of the bipolar may be adjusted by varying R_T. The allowable threshold range is zero to six volts. The relationship between the typical input sum required to fire the bipolar and the threshold resistor R_T is plotted in figure 30. The value of R_T used by the model is 39K which yields a typical bipolar threshold of .29 volts. The graph is obtained by connecting e_2 through e_5 together and attaching a power supply to the common point. The value of R_T is then fixed and the equivalent input voltage increased until the neuron fires.

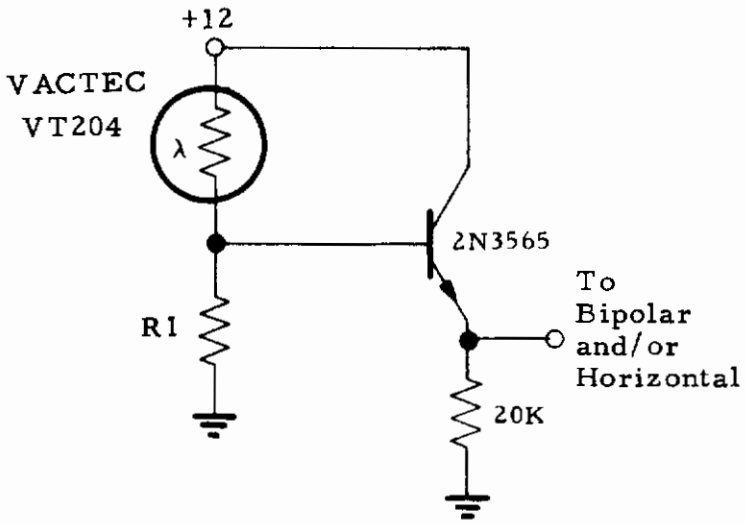


Figure 27. Receptor Schematic

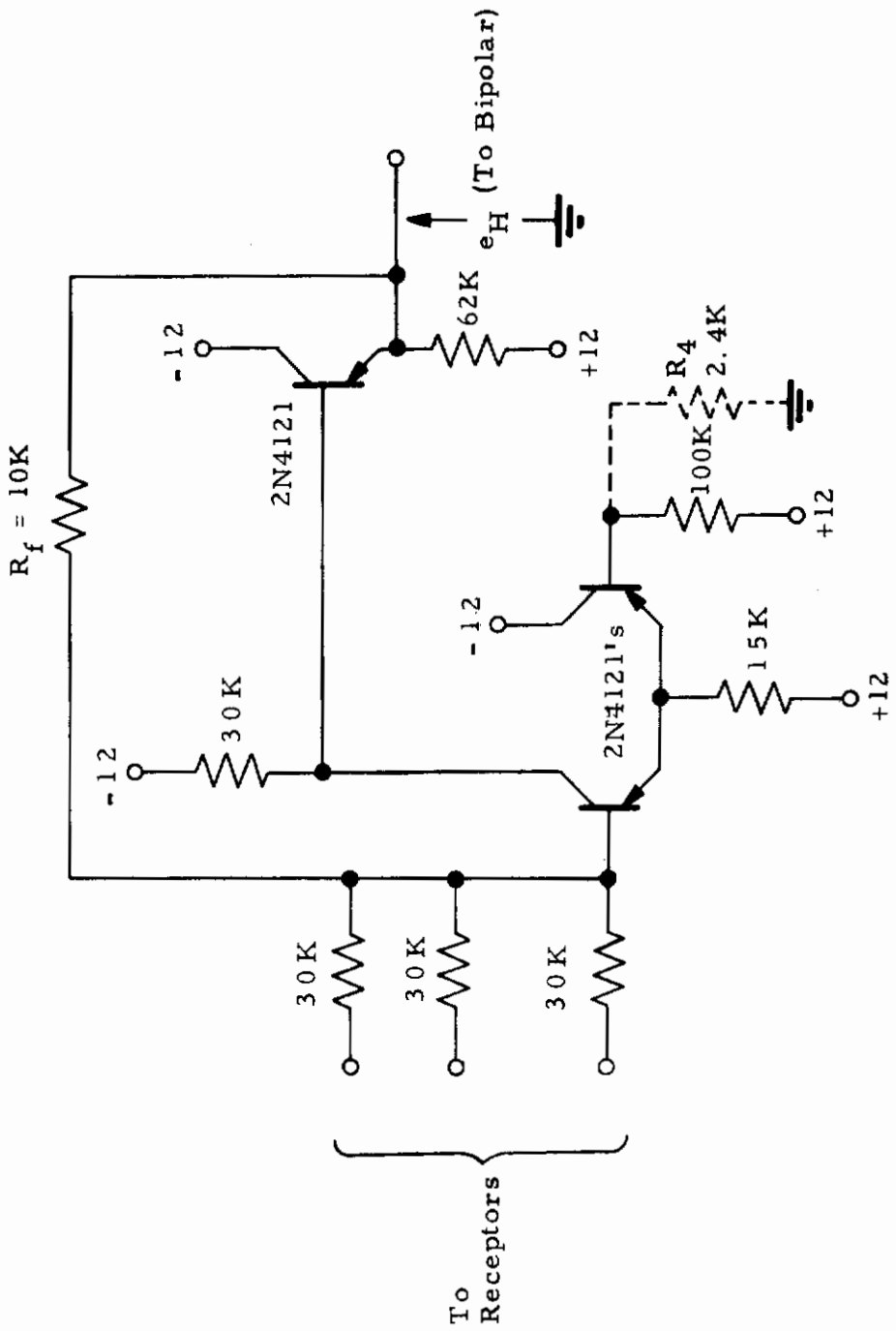


Figure 28. Schematic of Horizontal Circuit

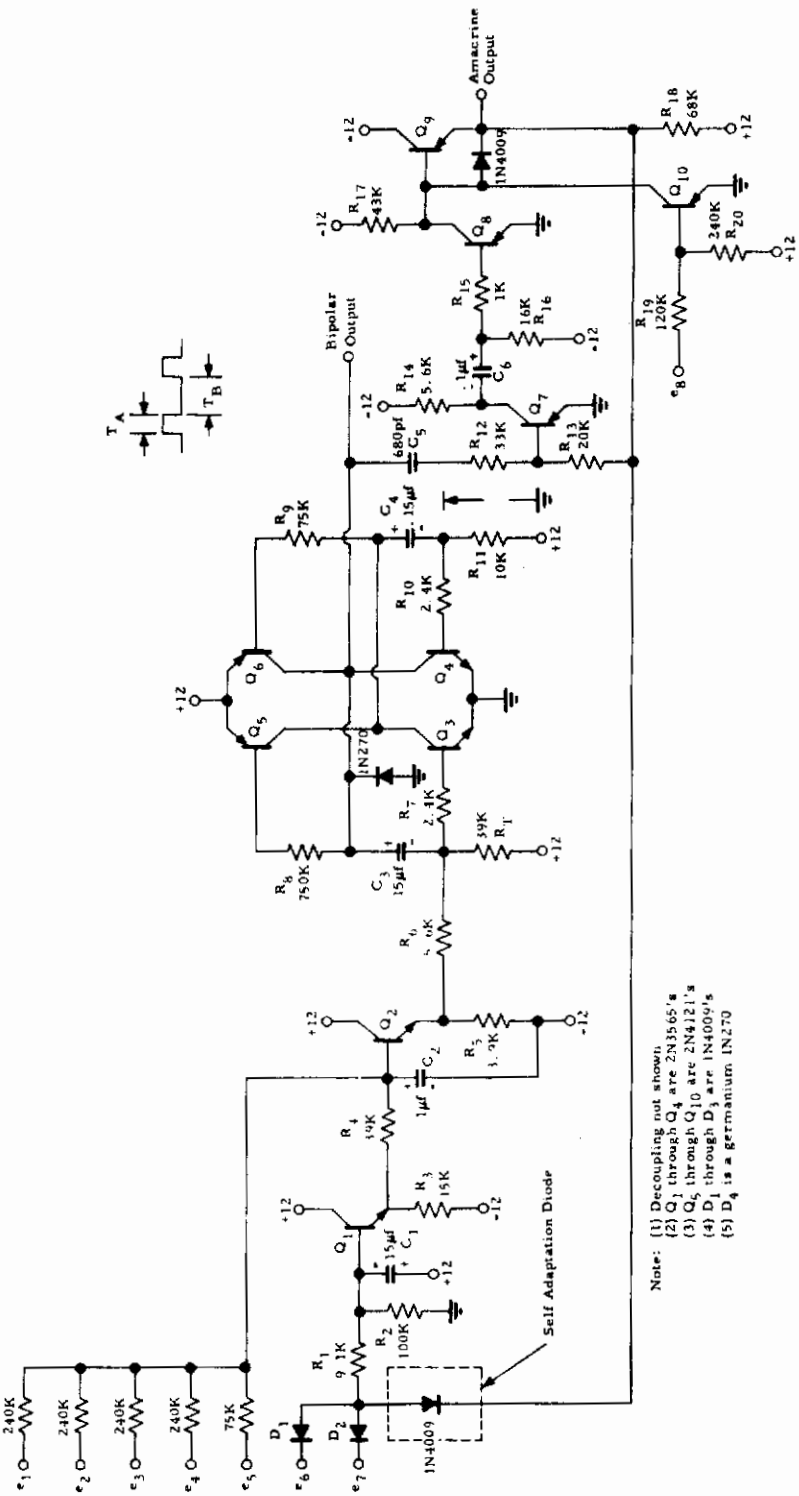


Figure 29. Bipolar/Amacrine Schematic

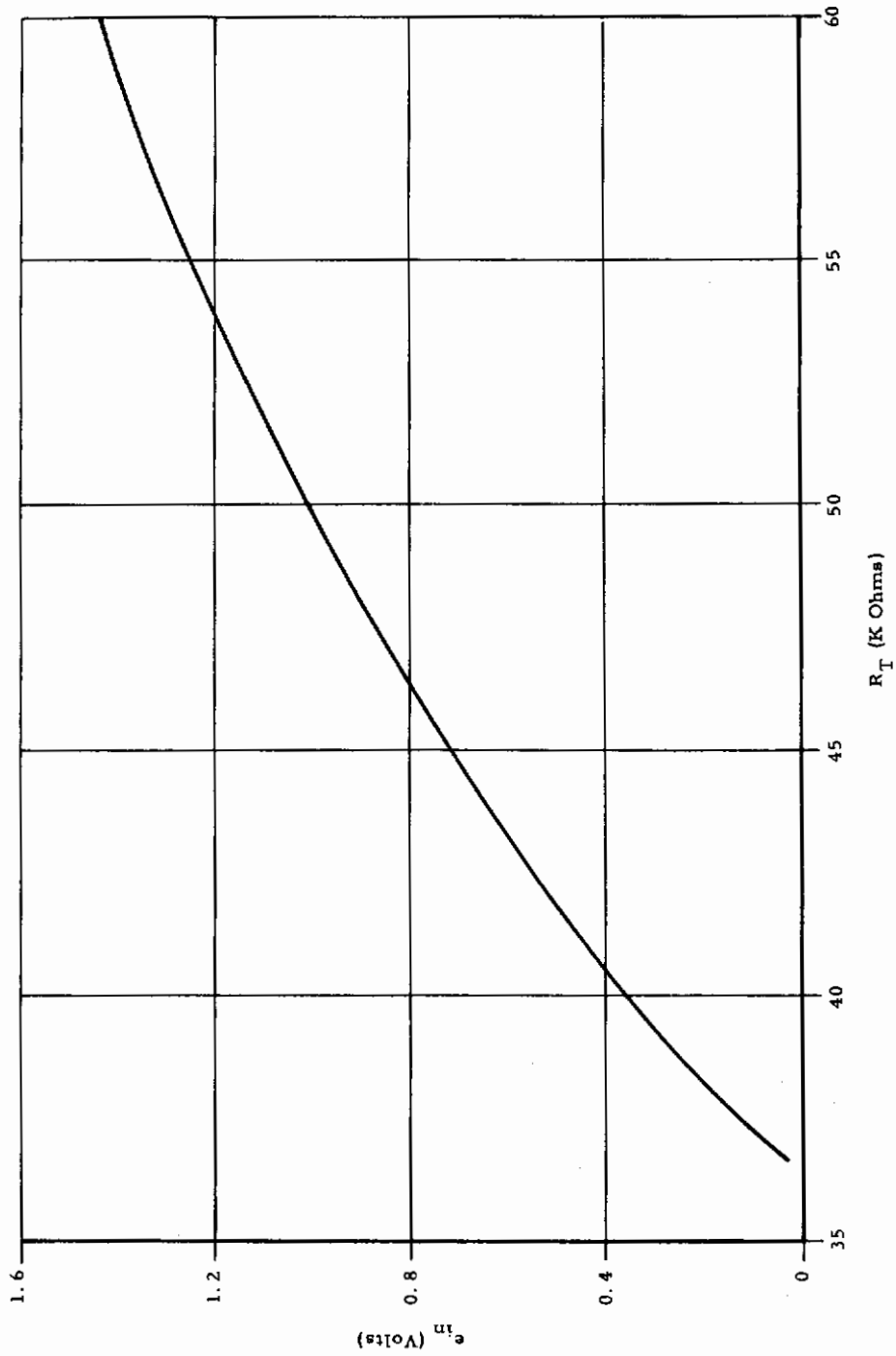


Figure 30. Bipolar Threshold Resistor vs. Firing Voltage (Typical)

Figure 31 shows a plot of the delay time of the bipolar, t_d, as a function of the amount of excitation when the excitation is applied as a step function. Note that the delay time decreases as the excitation increases.

The output of the bipolar is a train of one millisecond pulses. The pulse rises from ground to plus 12 volts. The repetition rate of the pulses is dependent on the amount that the input sum exceeds threshold. Figure 32 is a plot of the bipolar repetition rate as function of the input sum. If the bipolar has not fired for some period of time and then is suddenly excited the repetition rate will be that of the unadapted bipolar. If the excitation remains the bipolar will adapt to the lower value indicated by the graph. Note that, except under very large stimuli, it must traverse a large repetition range to move from the non-adapted to the adapted state.

The output of the bipolar is connected, on the bipolar/amacrine printed circuit board, to the input of the amacrine in the corresponding spatial position. This reduces the number of interconnections which would otherwise be made on the taper connectors and provides efficient utilization of the available space in the model. The output of the amacrine is a pulse going from ground potential to minus 12 volts. The duration of this pulse is set to one millisecond; however, longer inhibitory pulses may be obtained by increasing R_{16} and C_6. The amacrine pulse is delayed by the pulse duration of the bipolar. The inputs controlling the bipolar are designated as e_1 through e_7. The inputs e_1 through e_5 originate from either receptors or horizontals. All receptor input terminals are weighted equally and have input resistances of 240K. Only three of the four receptor terminals are used for contrast bipolars. The 75K Ω resistor provides the termination for the horizontals of the contrast bipolars. In the contrast bipolars one of the 240K resistors is left open. In the intensity bipolars the 75K resistor input terminal is left open and all of the 240K inputs are supplied by receptors. Temporal summing is provided by C_2 in combination with the input resistors associated with e_1 through e_5 and R_4.

The terminals e_6 and e_7 provide a means of inhibiting the bipolar and amacrine with an amacrine. The terminal e_8 allows inhibition of the amacrine by means of another amacrine.

When diode D_3 is mounted on the bipolar circuit board, the bipolar neuron is self adapting. This capability causes the neuron to respond with a short burst of pulses for a rapid increase in the bipolar input sum. If the input sum remains unchanged, the bipolar will adapt to a steady state firing rate considerably below that occurring when the same excitatory input is initially applied as shown in Figure 32. Note that if an amacrine is inhibited; by applying -12 volts to e_8, that the self-adaptation of the corresponding bipolar is released.

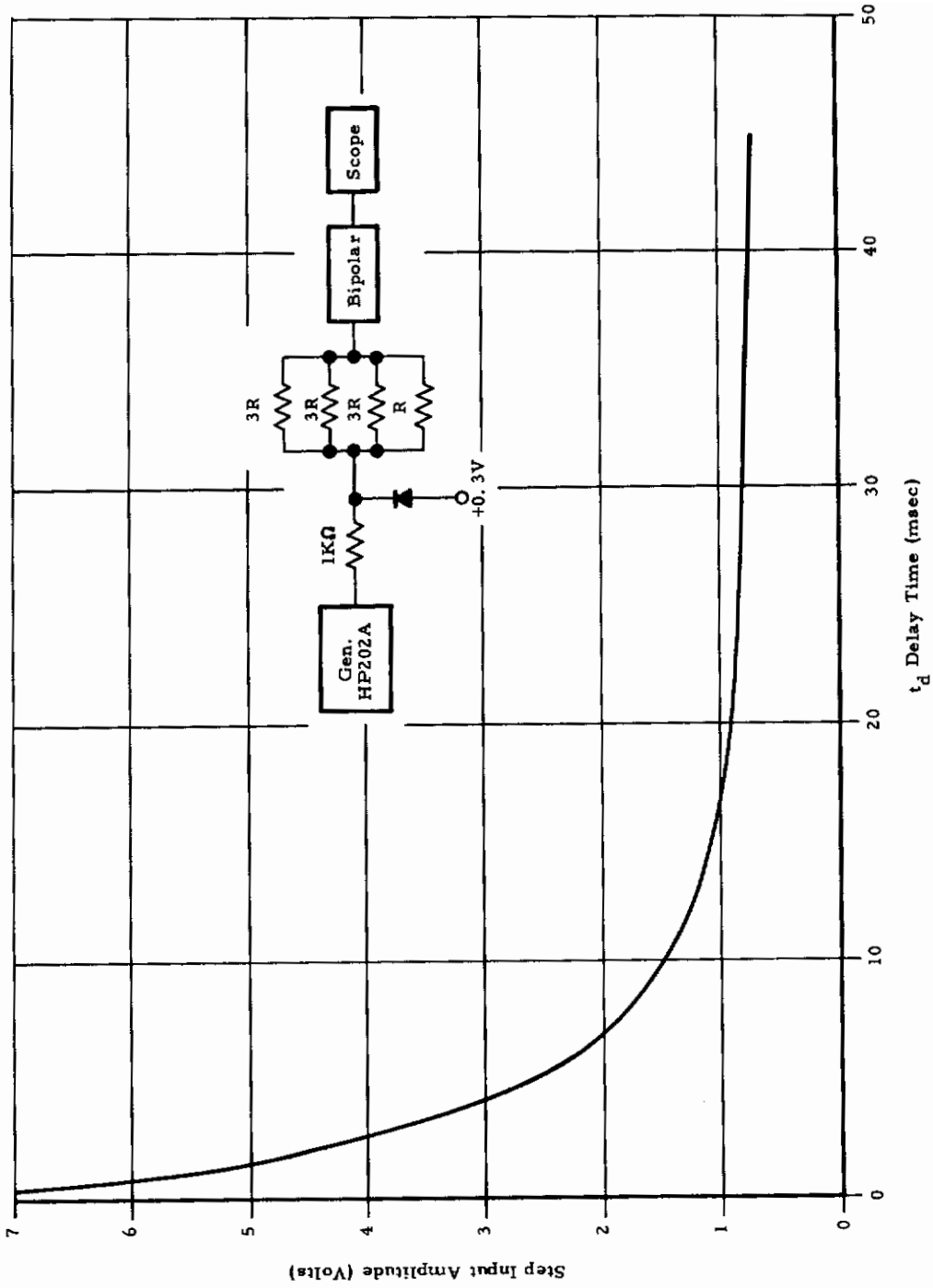


Figure 31. Bipolar Delay Time vs. Step Input Amplitude

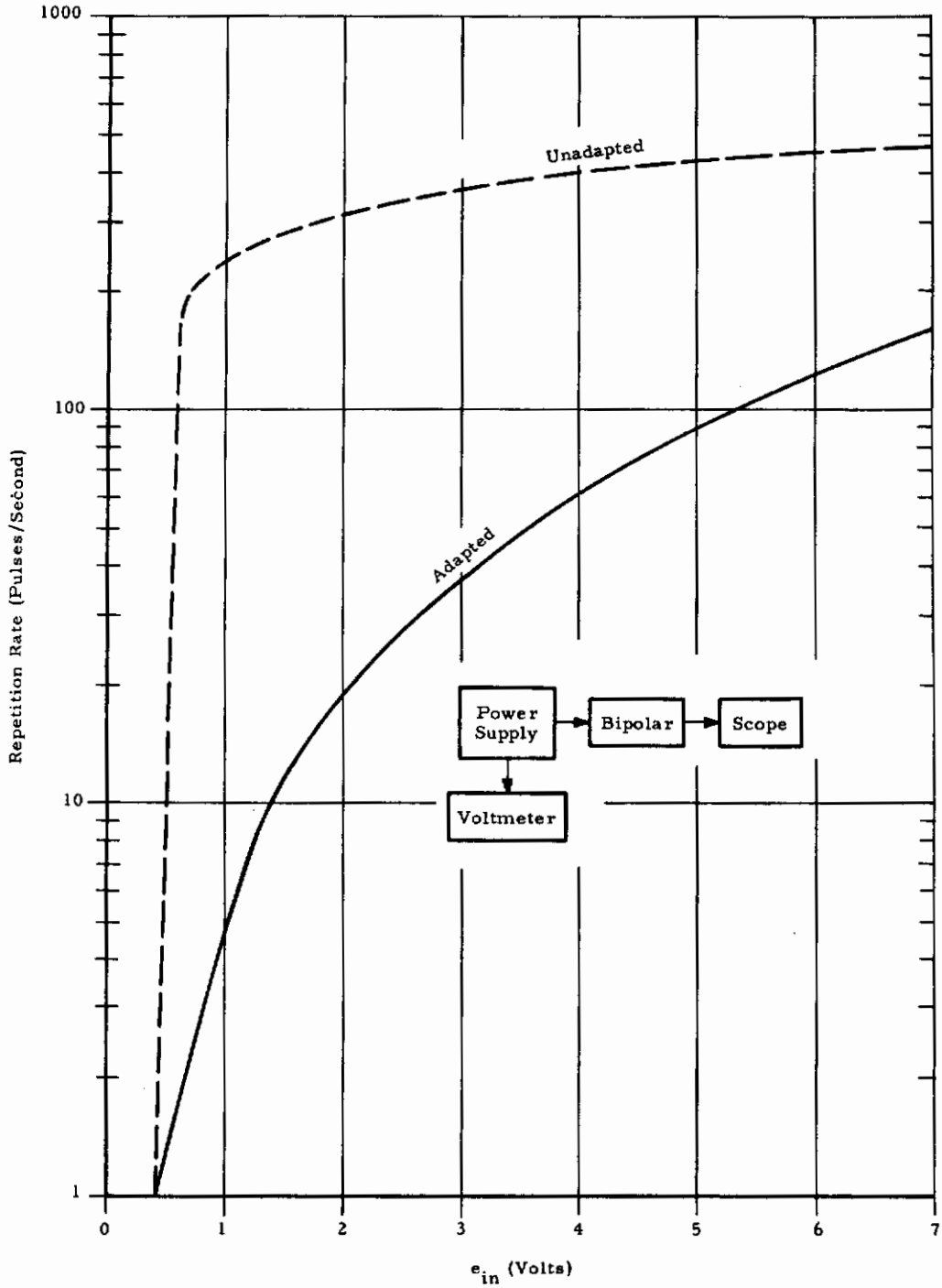


Figure 32. Bipolar Output Pulse Repetition Rate vs. Bipolar Input Sum

The temporal summation performed by the bipolar has provided a method for rejecting receptor flicker noise. The temporal summing time constant of the bipolar has proved very effective in rejecting 60 and 120 cps flicker associated with indoor lighting.

4. GROUP AMACRINE

The schematic of the amacrine circuit board is given in figure 33. This neural analog is used to inhibit other amacrines. It could be employed to directly inhibit ganglions as well. The circuit is basically a one shot multivibrator triggered by a negative going transient. When the one shot fires, the output terminal GA yields a negative 12 volt pulse. The pulse width, 200 msec, is determined by R_5 and C_2. Q_2 allows this circuit to be inhibited by another amacrine. The output $\overline{GA}$ provides a method for cascading these circuits to obtain increased delays or an inhibitory gating pulse. The diode output GA' allows sets of these neurons to jointly inhibit the same amacrine. The inhibitory pulse of this amacrine is likened to the firing of a group of amacrines, hence its title. If R_5 is set equal to 360K a one-second inhibitory pulse results.

5. GANGLION

The schematic of the ganglion is given by figure 34. The various bipolars and amacrines are summed by resistors R_1 through R_{36}. This sum is then amplified by the factor $1+\frac{R_{44}}{\frac{(R_{41})(R_{43})}{R_{41}+R_{43}}}$ The output voltage of the emitter follower, Q_1, is used to control the ganglion threshold.

The emitter follower output voltage is varied by resistor R_{38}. The network formed by R_{51} and C_5 is used to integrate the resultant sum. This sum is then supplied to a voltage controlled oscillator to generate the required pulse frequency modulated output. The oscillator circuitry is identical to that employed by the bipolar.

The final ganglion output is applied to a transistor switch that drives the monitoring speaker. The ganglion output may also be applied to diode D_1 by means of the connector to provide self-adaptation.

6. COMPARATOR AMPLIFIERS AND RECEPTOR SUMMATION

Figure 35 is a schematic of the lower threshold comparator used in the object detector. The comparators are constructed by deleting all components of the ganglion circuit board except the amplifier, threshold adjustment circuitry and resistor summing network. Notice that all feedback is removed from the amplifier so that the circuit operates as a high gain differential amplifier. Since each ganglion board provides for the summation of only 36 inputs and it is required to sum all 144 receptor outputs, modification of the ganglion board was necessary.

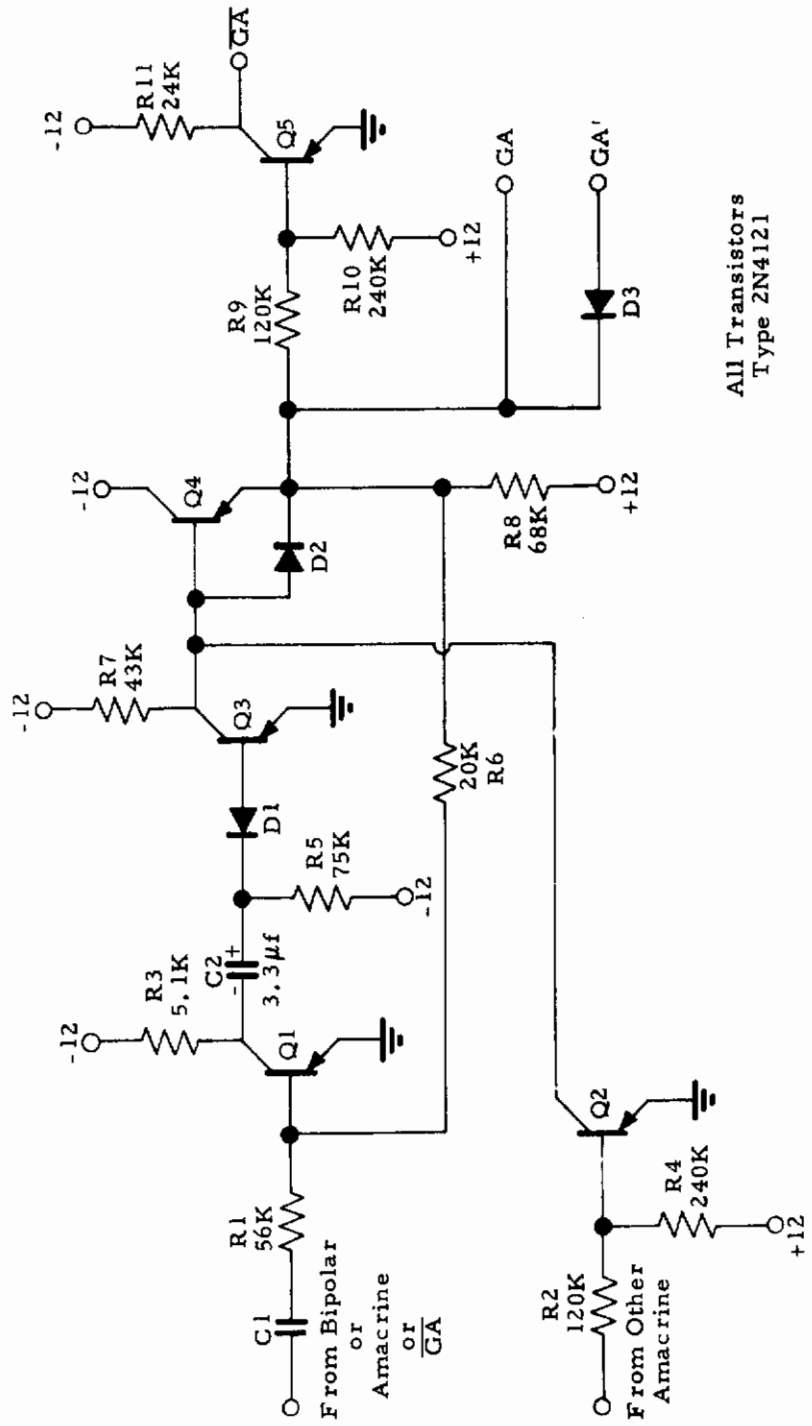


Figure 33. Group Amacrine Schematic

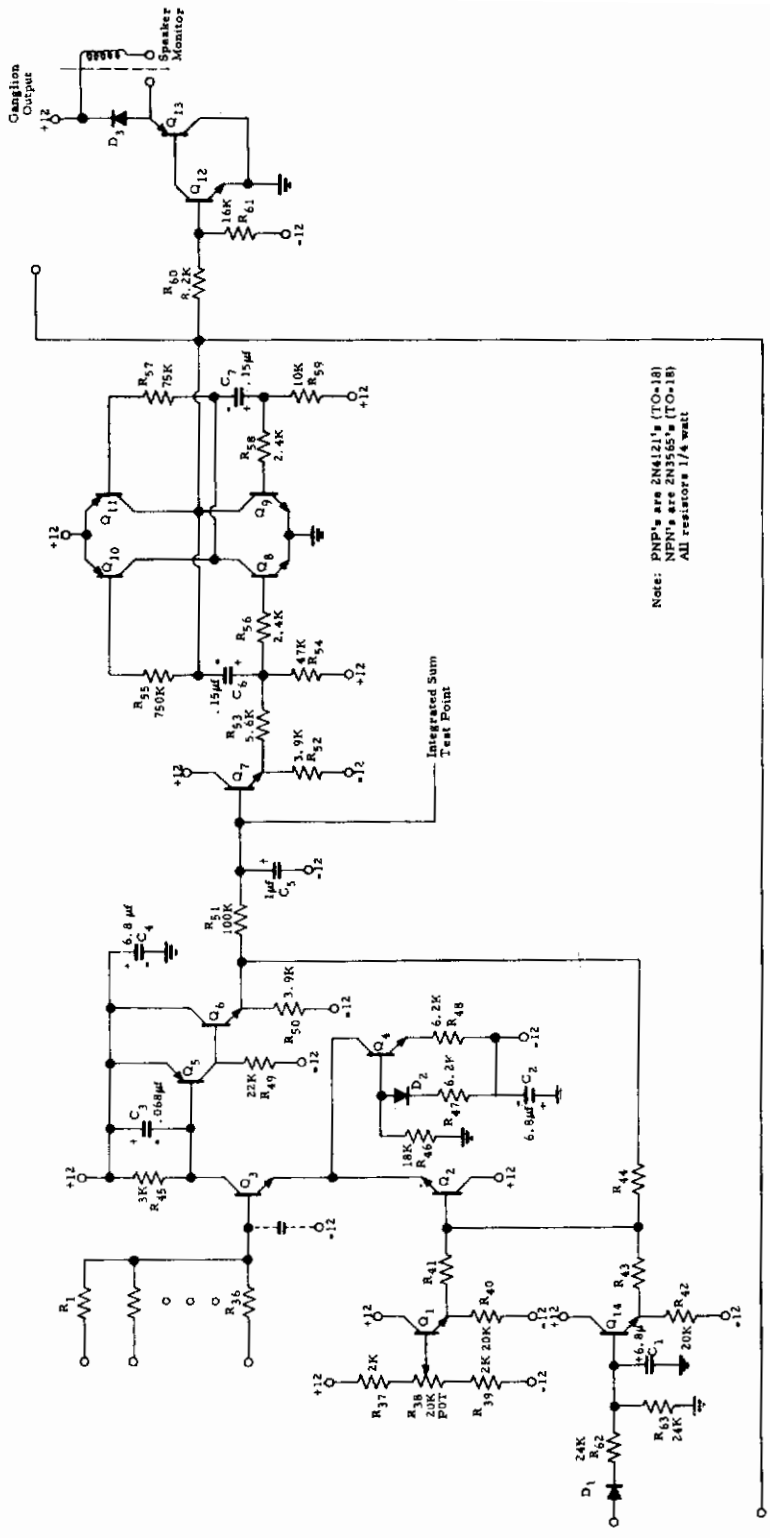


Figure 34. Ganglion Schematic

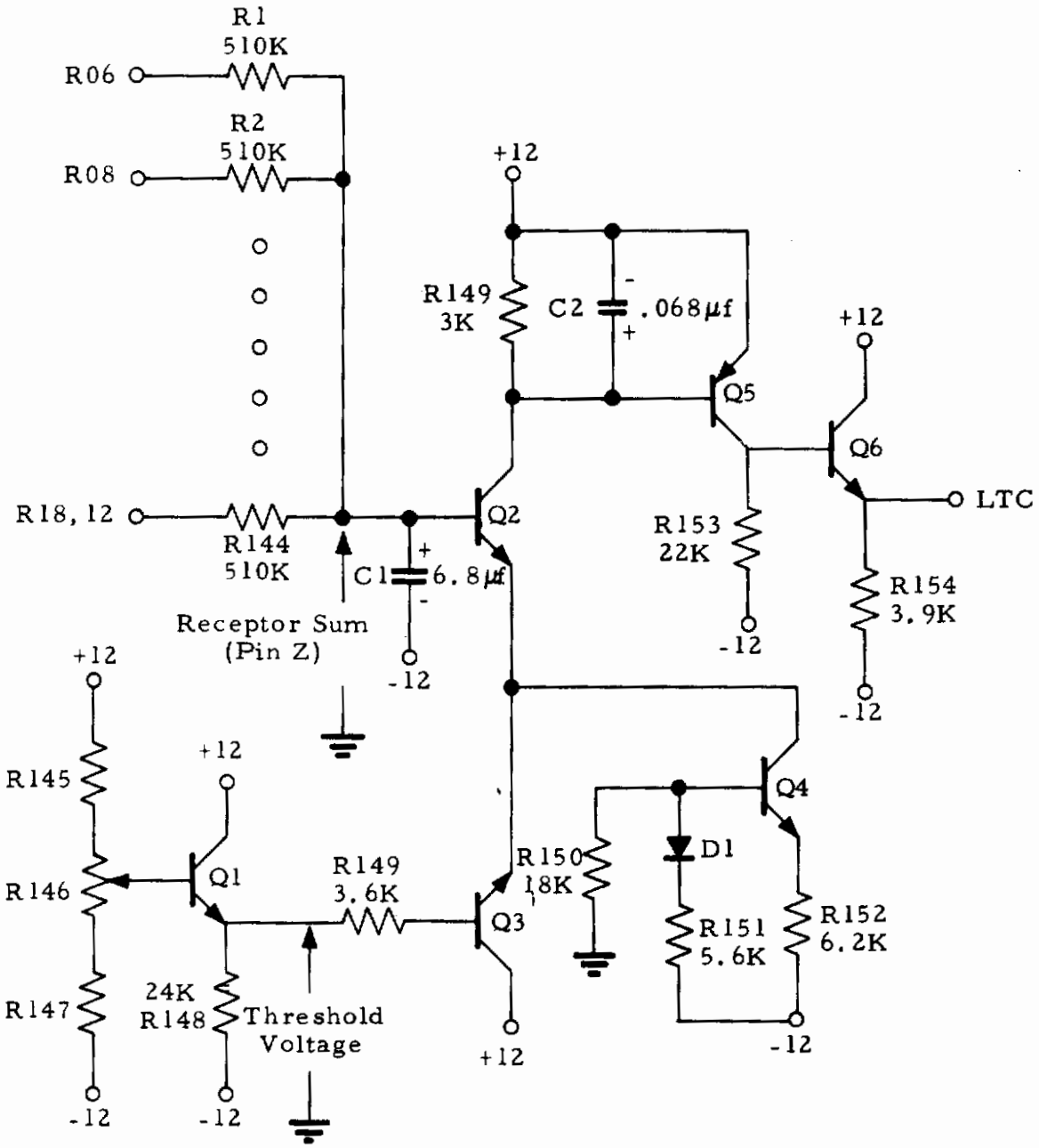


Figure 35. Threshold Comparator

SECTION VI

ACCESSORY EQUIPMENT

1. POWER SUPPLIES

The model uses two power supplies, one positive and one negative. The plus and minus supplies should be initially set to +12 ± .1 volts for best operation. The typical current demand of the supplies is:

Voltage	Current
+12	620-900 ma
-12	600-650 ma

The smaller current values correspond to an ambient indoor environment of approximately 100 footcandles falling on the horizontal plane. The larger current values listed occur when the projector is stimulating a specific ganglion response and this detector is responding with its highest pulse repetition rate. With the +12 volt supply operating at 900 ma and the -12 volt supply operating at 600 ma the respective power dissipated by these supplies is approximately 31 and 20 watts. The power supplied to the model by the +12 volt supply is 10.8 watts and by the -12 volt supply 7.8 watts.

2. BELL & HOWELL "SPECIALIST" SOUND PROJECTOR

The model 552 B&H Specialist is a 16mm sound projector featuring automatic threading. The projector is used in conjunction with the animated film to provide the stimuli for functional testing of the ganglion detectors.

3. ANIMATED FILM

To assure full and factual test of each of the ganglion detectors a special animated film is provided. This film, when run at normal speed to test the system performance, takes about 10 minutes of running time. The functional tests accomplished by this film are discussed in detail in Section IV.

SECTION VII

CONCLUSIONS

The model demonstrates that the processing of visual data by individual ganglions of the pigeon retina can be duplicated electronically. The availability of an operational and factual replica of the avian retina may provide some insight into the function and typical response of the individual cells. It is hoped that this model will prompt, and in fact point the way, to a detailed specification of the response at each neural layer. Further, as suggested earlier, an array of ganglion detectors as exemplified by this model may well provide a unique and practical input device as a part of an adaptive recognition system for processing visual inputs.

APPENDIX

AVIAN RETINA PHOTOGRAPHS

The following photographs were obtained at the Medical School of the University of Southern California under the direction of Dr. R. L. Binggeli. They are included to support the physiological and anatomical discussions of previous sections, to provide the reader with a graphic description of the system being modeled and to make the report a more complete documentation on the research performed.

Figure 36. Whole Eye of a Pigeon Showing Dimension from the Front

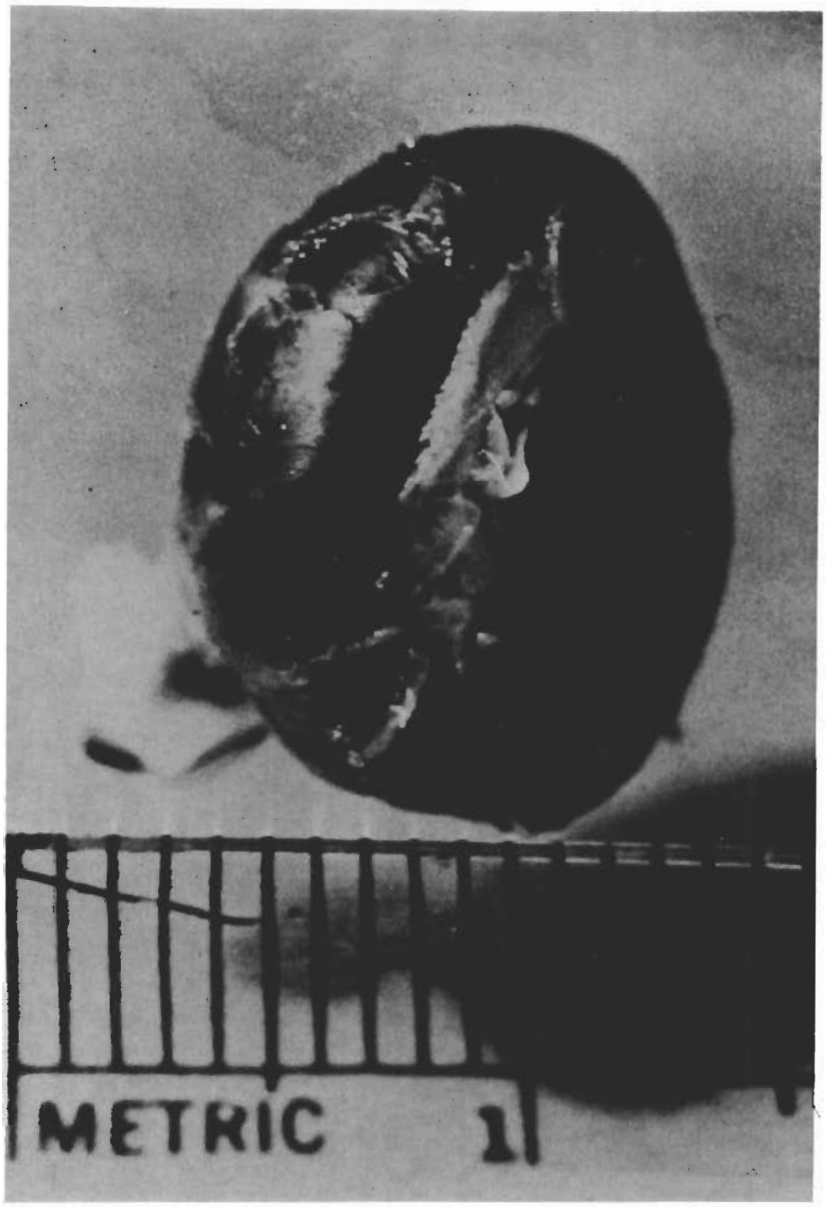


Figure 37. Whole Eye of the Pigeon Showing the Optic Nerve Bundle

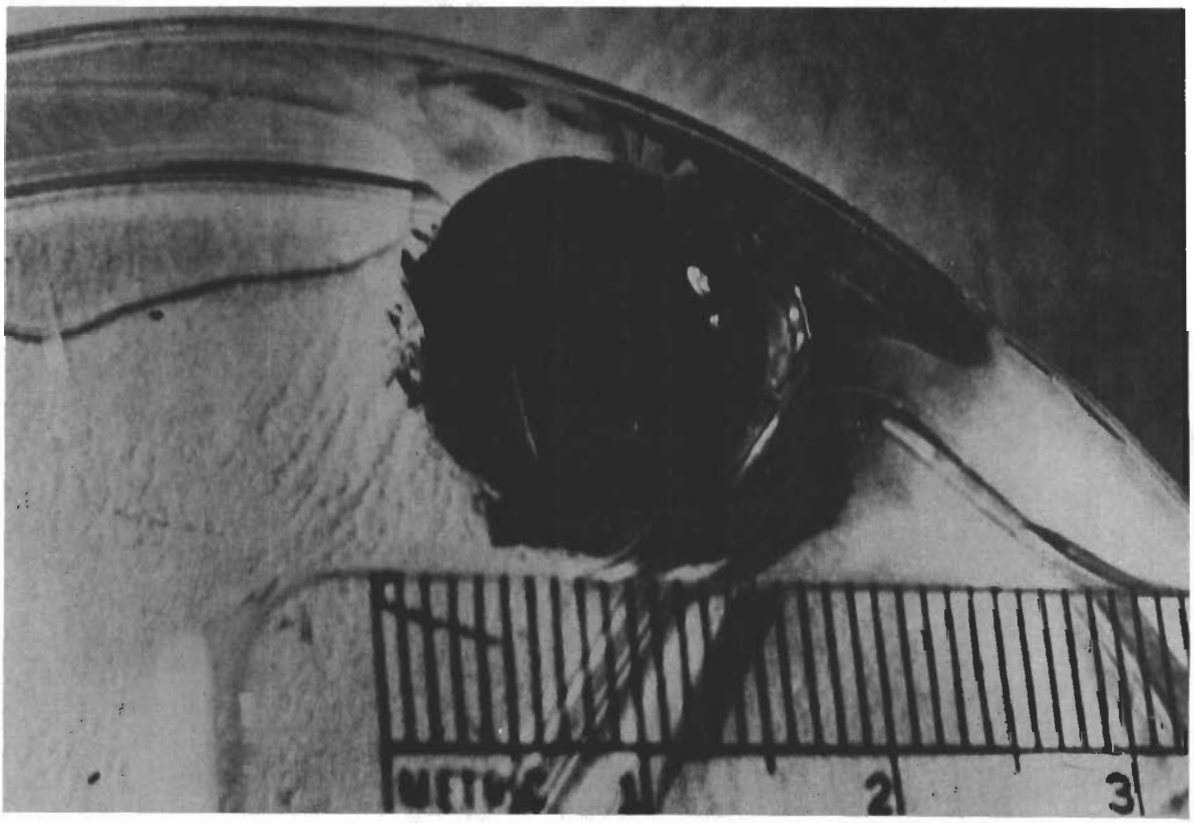


Figure 38. Whole Retina Showing the Fovea and Pecten

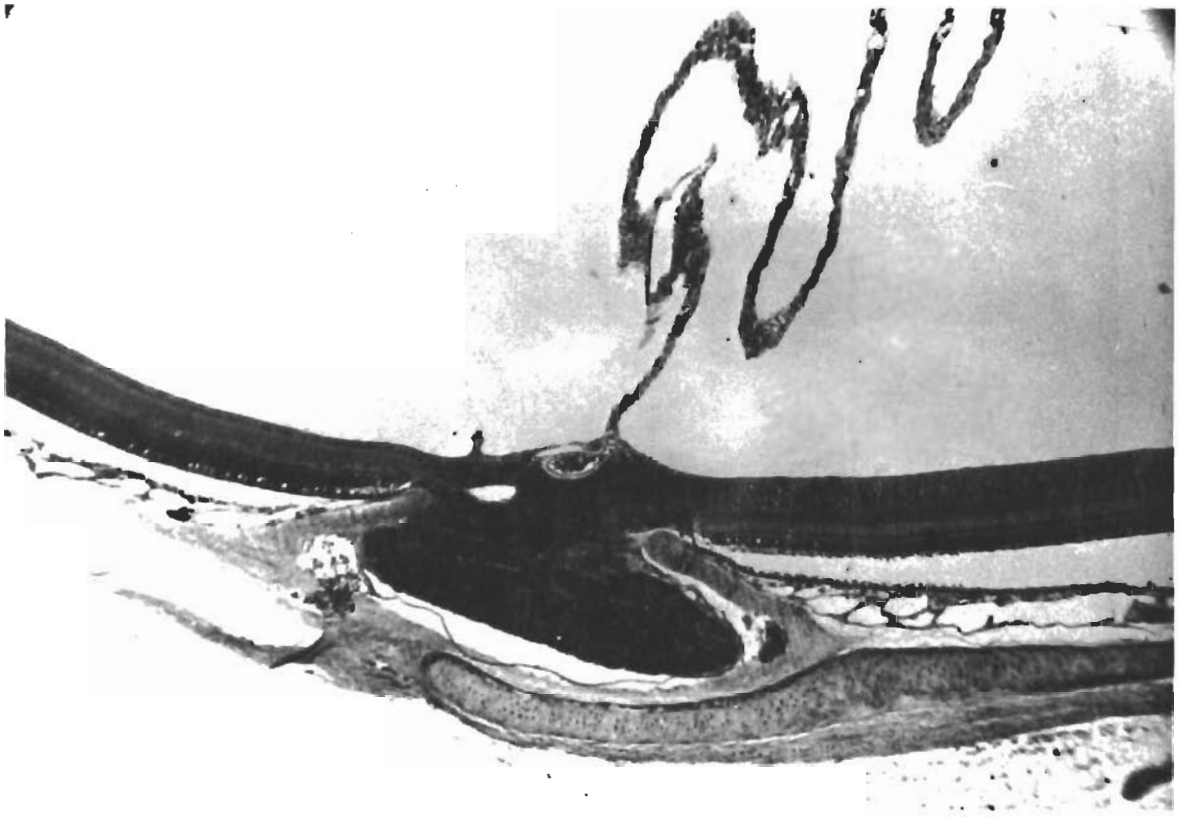


Figure 39. Stain of a Cross Section of the Retina Containing the Pecten and Optic Nerve. The retina (top) is detached from the sclera and choroid coat (bottom). 35X.

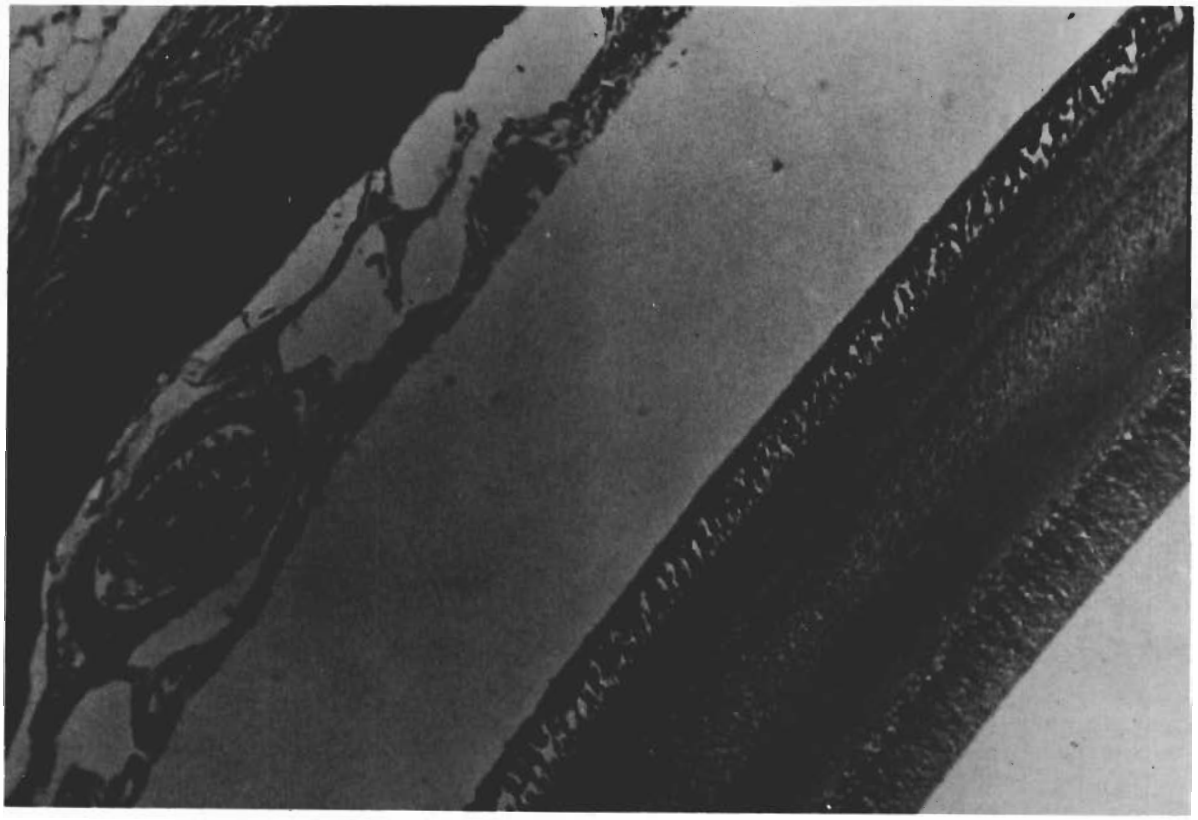


Figure 40. Cross Section of the Pigeon Retina Showing the Layered Structure of the Retina. Stained with silver-pyradine and viewed at 100X. The distance from the outer limiting membrane to the beginning of the optic nerve bundle was measured as 129 microns. The inner plexiform layer measured 53 microns while the outer plexiform was only 3 to 4 microns. The outer nuclear layer was 20 microns, the inner nuclear layer 46 microns, and the ganglion layer 7 microns.

Figure 41. Silver Stain of an Ordinary Amacrine and the Stratifications of the Inner-plexiform Layer 450X

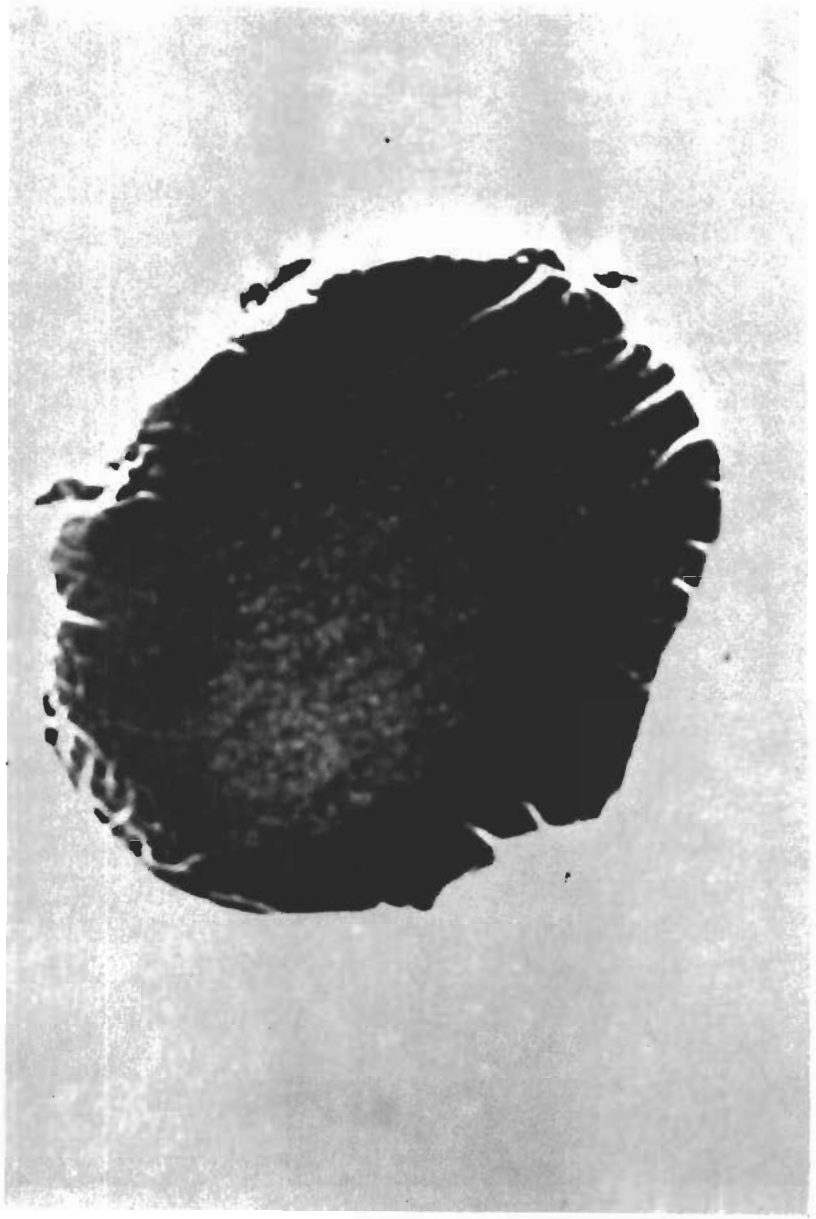


Figure 42. Whole Optic Nerve Fiber Cross Section of a Pigeon at Low Power. 35X The long dimension of the fiber bundle measures 1.62 mm. The stain is osmic acid.

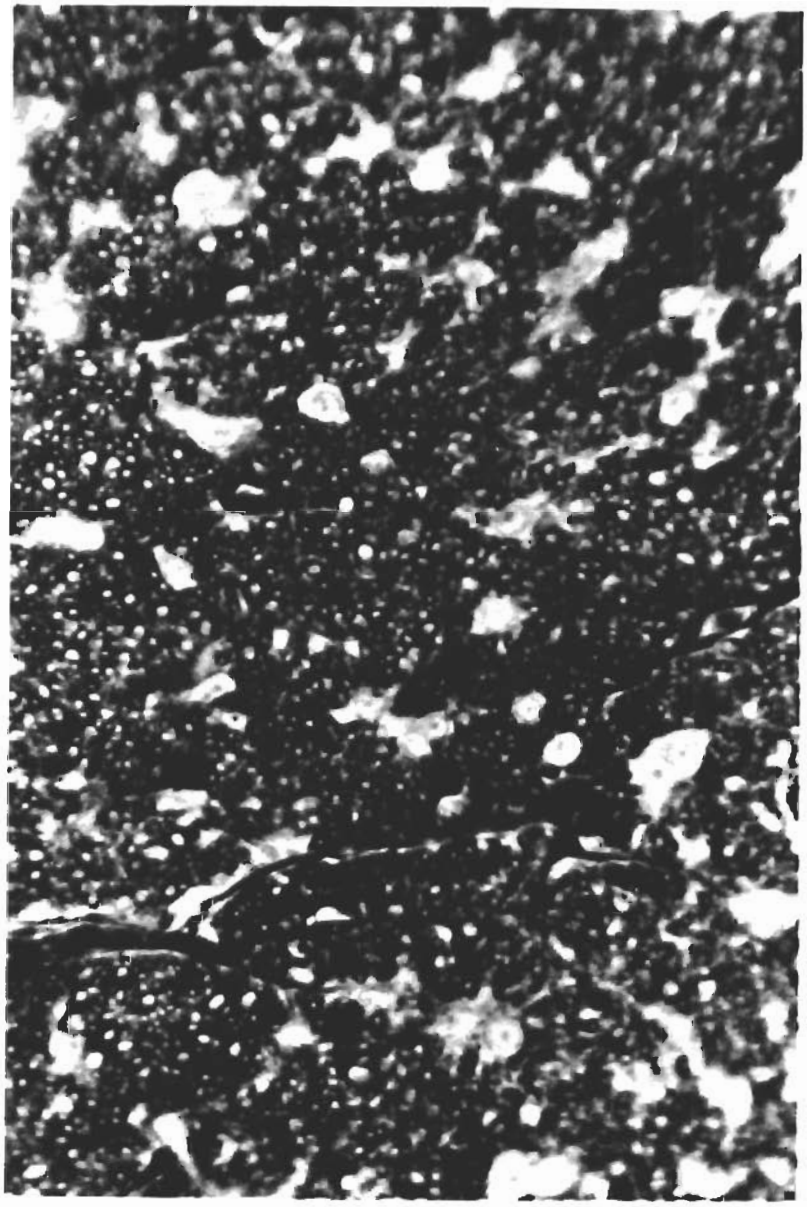


Figure 43. Optic Nerve Cross Section of a Pigeon Stained with Osmic Acid and Viewed Through a Light Microscope at 450X

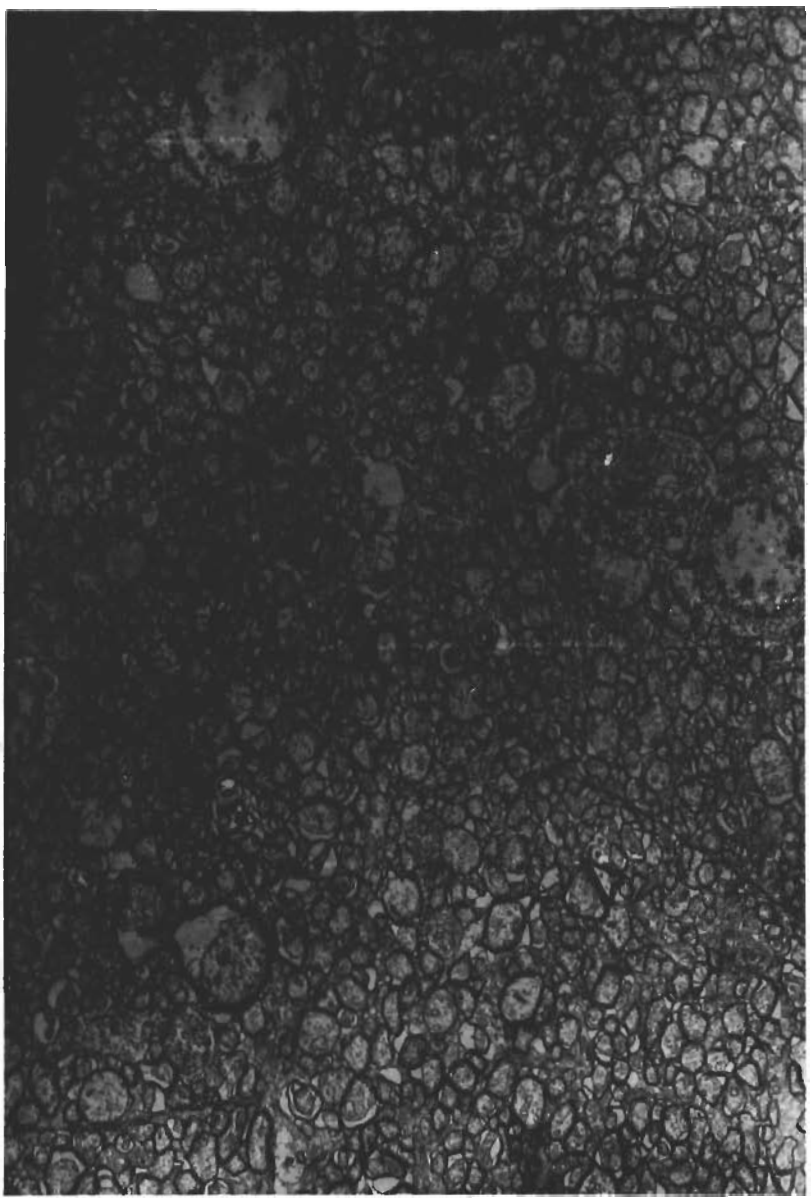


Figure 44. Low Power Electron Micrograph of a Pigeon Optic Nerve Cross Section Showing Myelinated and Unmyelinated Neurons Along with Glial Cell Processes

REFERENCES

1. H. R. Maturana and S. Frenk, "Directional Movement and Horizontal Edge Detection in the Pigeon Retina," Science, Vol. 142, pp. 977-979, 15 November 1963.

2. H. R. Maturana, "Functional Organization of the Pigeon Retina," Symposium of Information Processing in the Nervous System, Vol. III, 22nd International Congress of Physiological Science, pp. 170-178, 1962.

3. Stephen W. Kuffler, "Discharge Patterns and Functional Organization of Mammalian Retina," Journal of Neurophysiology, Vol. 16, 1953, pp. 37-38.

4. R. L. Binggeli, Anatomical Investigation of the Pigeon Retina, Progress Report, August 1966, University of Southern California School of Medicine.

5. W. H. Atwood, A Concise Comparative Anatomy, C. V. Mosley Co., St. Louis, 1947.

6. J. H. Chievitz, "Untersuchengen uber die Area centralis retinae," Arch. Anat. Entwicklungsgesch, Supple. 139, pp. 139-199, 1889.

7. S. R. Cajal, Histologie du Systeme Nerveux, Chapter XVI, pp. 326-367, Paris A. Maloine, 1909-1911.

8. W. M. Cowan and T. P. S. Powell, "Centrifugal Fibers in the Avian Visual System," Royal Society Proceeding, Series B, Vol. 158, pp. 232-252, 1963.

9. H. R. Maturana and S. Frenk, "Synaptic Connections of the Centrifugal Fibers in the Pigeon Retina," Science, Vol. 150, pp. 359-361, 15 October 1963.

10. S. R. Bruesch and L. B. Arey, "The Number of Myelinated and Unmyelinated Fibers in the Optic Nerve of Vertebrates," Journal of Comp. Neurol. 77, 631-665, 1942.

11. J. E. Dowling and Brian B, Boycott, "Neural Connections in the Retina," Cold Springs Harbor Symposium of Quantitative Biology, Vol. 30, pp. 393-402, 1966.

12. J. E. Dowling, J. E. Brown, and D. Major, "Synapse of Horizontal Cells in the Rabbit and Cat Retina," Science, Vol. 153, pp. 1639-1641, September 30, 1966.

13. M. Kidd, "Electron Microscopy of the Inner Plexiform Layer of the Cta and the Pigeon," Journal of Anatomy (London), 1962, Vol. 96, No. 2, pp. 178-187.

14. Handbook of Physiology, Section 1: "Neurophysiology," John Field, Editor, American Physiological Society, Waverly Press Inc., Baltimore 2, Maryland.

15. J. C. Eccles, The Physiology of Synapses, Academic Press, New York, New York, 1964.

16. J. E. Dowling, "The Site of Visual Adaptation," Science, Vol. 155, 20 January 1967, pp. 273-279.

17. Charles R. Michael, "Receptive Fields of Directionally Selective Units in the Optic Nerve of the Ground Squirrel," Science, Vol. 152, 20 May 1966, pp. 1092-1095.

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13. ABSTRACT

The specific objective of this contract was to construct an electronic model of the avian retina based upon reported physiological and anatomical findings and capable of replicating the specific ganglion functional responses. A critical review of the pertinent physiological and anatomical literature relating to the retina was performed. The electronic model of the pigeon retina containing the six functional classes of ganglion detectors reported in the literature was constructed. In addition the model incorporates two hypothetical detectors to demonstrate the selective performance that can be achieved with artificial neuron networks. The development of the model has shown that the complex data processing of the retina can be functionally duplicated. The results of this work could lead to the design of an effective visual data preprocessor which would operate into a self-organizing decision network to yield a multilayer optical pattern recognition system.

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	ROLE	WT	ROLE	WT	ROLE	WT
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