1-1-1976

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MORPHOLOGICAL STUDIES OF DEEP AND SHALLOW AVIAN FOVEAS: A QUANTITATIVE ANALYSIS

A Dissertation Presented

By

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Submitted to the Graduate School of the
University of Massachusetts in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 1976

Psychology

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ACKNOWLEDGEMENTS

I would like to thank the members of my dissertation committee, Drs. Kay Fite, Steve George, Arnie Well and Nico Spinelli for their helpful comments and suggestions during all phases of this research. Russ Carey's enthusiastic and critical advice also contributed substantially to the project. Friends like Mike Wessells, Sheila Rosenfield-Wessells and Elaine Reid provided much needed moral support. Kate Moran, who typed the final copy of the dissertation, was both patient and painstaking. Finally, special thanks to Jon Carr--Jon's efforts and encouragement made the final months of writing and rewriting this dissertation a truly productive and enjoyable experience.

ABSTRACT

Morphological Studies of Deep and Shallow Avian Foveas: A Quantitative Analysis

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Electrophysiological and behavioral evidence indicates that avian species are highly visual, processing complex information at the retinal level. Yet the retinal anatomy of birds has not been systematically investigated since Cajal's (1892) early description. Recently developed Golgi techniques now permit quantitative morphological analyses. Consequently, two foveate birds were chosen for detailed light microscope study; the blue jay, with a deep fovea, and the pigeon, with a shallow fovea. The pigeon also exhibits an area of increased cell density in the dorso-temporal retina, called the area dorsalis.

Tissue was processed using the Stell and Colonnier modifications of the Golgi rapid stain. Cells were drawn or photographed, then assigned to categories on the basis of morphological features. Measurements of

cell-body and process-field diameters and axonal length were compared for fovea, dorso-temporal quadrant and periphery in each species.

Morphologically, the avian cells closely resembled cells found in other vertebrate retinas, particularly those of reptiles and mammals. Single and double cone and rod photoreceptor outer segments were observed, and four distinct receptor base configurations, differing with respect to the length of lateral processes, were present. No clear correspondence was observed between outer segment configuration and receptor base structure. Two types of horizontal cell were present: The smaller exhibited a fine axon which terminated in an elaborate arborization, while the larger cell had no axon. Bipolars ending at single or multiple strata within the inner plexiform layer were found. Three varieties of monostratified amacrine cells were described, as well as diffuse and multistratified varieties. The elaboration of the dendritic processes of ganglion cells differed, so the cells were divided into two classes on that basis. Also, displaced amacrine and ganglion cells were observed.

The blue jay (deep fovea) possesses a highly differentiated retina: Cells are small in the fovea and much larger in the periphery. Cells with intermediate dimensions were found in the dorso-temporal area, suggesting

an orderly increase in cell size from central to peripheral retina, as found in many vertebrates. The pigeon retina (shallow fovea) was more homogeneous with respect to cell size. Outer plexiform processes of the fovea and the red field were similar in size, being somewhat smaller than those of the periphery. In the inner plexiform layer, ganglion cells and one bipolar type showed a similar relationship. The remaining amacrine and bipolar processes were larger in the dorso-temporal retina than in the fovea.

Evidence of a midget system similar to that found in primates was evaluated. "Midget" bipolars with dendritic fields similar to those of invaginating midget bipolars were observed in the fovea, but cells were up to 500 μ long from dendrite to axon. Small avian ganglion cells could contact a single midget bipolar. However, the cells differed from primate midget ganglion cells in that they were larger, less numerous, multidendritic and exhibited many dendritic varicosities. The absence of a true "midget ganglion cell" is related to Sjöstrand's (1976) hypothesis concerning visual processing in the outer plexiform layer.

Intracellular recordings suggest that the small ganglion cells could be the color units of Pearlman and Hughes (1976) or the convex edge detectors of Maturana (1962). The possible functional significance of the avian fovea in mediating fine spatial resolution or serving as

a visual tracking mechanism is considered. The pigeon's value as a model for studying avian foveal vision is significantly enhanced by the observation of foveal cells resembling those of deep fovead avian species. Similar cell dimensions, as well as "midget" bipolars and small ganglion cells, in the pigeon's red field and fovea suggest that the former area may be similar to the second temporal fovea found in many birds.

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> The retina has been the subject of many investigations and a bibliography of these would fill many pages. The preference that the best known anatomists and histologists have given to this area is easily understood, since knowledge of the arrangement of retinal cells is essential for a full understanding of vision and the many problems associated with it. (Cajal, 1892, translated by Mcguire and Rodieck, 1973, p. 781.)

Historically, comparative studies of visual processing, such as those of Cajal (1892), Polyak (1941; 1957) and Walls (1942), have emphasized the anatomical or structural aspects of vision. With the advent of animal psychophysics and modern electrophysiological techniques, a wealth of new information relating to the behavioral aspects of vision in non-human organisms has become available. Subsequent attempts to correlate behavioral and electrophysiological evidence with early anatomical data have indicated several gaps in the latter, particularly with respect to quantitative details, however. Consequently, recent authors have developed new anatomical techniques which can provide more precise descriptions of quantitative morphology and fine retinal structure.

The present study comprises a detailed quantitative analysis of the retinal structure of two birds, using recently developed modifications of the Golgi technique. The Golgi technique is unusual in that it stains only a small portion of the cells present in a piece of tissue,

but stains those cells completely. Data presented here provide a basis for evaluating structural and functional relationships in these highly visual avian species. Further, this description of the retinas of two closely related vertebrates provides additional evidence bearing upon the functional significance of the fovea.

The Morphology of the Retina

The first lucid description of the basic structure of the vertebrate retina was provided by Cajal (1892), who, with the Golgi rapid-method of silver impregnation, proceeded beyond Schultze's (1866) classic description of the rods and cones and delineated neural paths of contact in the retina. Polyak (1941) extended this method to primates, presenting detailed descriptions of retinal structure of monkeys, apes and humans. In an attempt to quantify these early results, a number of authors have re-examined and reinterpreted the classical descriptions of retinal morphology using more recently developed histological techniques. Golgi impregnated cells are identified with the light microscope in 80 to 120 μ transverse sections or in flatmount preparations; measurements of cell body size and field diameter are made; thin sections are cut; and finally these sections are viewed with the electron microscope to determine synaptic contacts (e.g., Kolb, 1970; Stell and Witkovsky, 1973a). The silver

that is deposited in the impregnated cell appears black in electron micrographs, and the difficulty of establishing cellular synaptic relations common to other methods is, consequently, eliminated. The following summary of the data obtained from light and electron microscope studies is organized by cell type and with reference to the species studied.

Photoreceptors. Two types of specialized photoreceptors were first described by Schultze (1866), who distinguished between rods, which have cylindrical outer segments and thin inner segments, and cones, which have tapered outer segments and thicker inner segments. Although the classical structural criteria for distinguishing the two types of cell is the outer-segment configuration (Cajal, 1892; Walls, 1942; Duke-Elder, 1958), individual receptors also differ with respect to (1) visual photopigment (Rodieck, 1973), (2) lamellar structure and outer-segment renewal capacity (Young, 1969a, 1969b; 1971), and (3) the details of synaptic contact (Dowling, 1965; Pedler, 1965a, 1965b; Missotten, 1965; Evans, 1966; Stell, 1967; Dowling and Werblin, 1969; Kolb, 1970). The retinas of diurnal species tend to be dominated by cones, while those of nocturnal and deep-sea species usually show a preponderance of rods (Walls, 1942; Duke-Elder, 1958; Tansley, 1965).

The dual classification of receptors has not been universally accepted, however. Pedler has pointed out:

> . . . the rod and cone have acquired a number of separate identities: they are morphological entities in the light and electron microscopes, they have a photochemical set of references, they are defined electrophysiological, their presence or absence is predicted by animal behavior and habit and their nature is assumed from the type of retina in which they are found . . . there is catagorization without cross-reference showing a bias towards the division of all phenomena into two classes to fit a concept of receptor varieties. (1965a, p. 55)

On the basis of electron microscope studies of the retinas of twenty-four vertebrate species, Pedler (1965a, 1965b) has suggested a three-fold classification of receptors according to threshold sensitivity and complexity of synaptic contact. Sensitive and insensitive multi-channel cells, as well as sensitive single-channel cells are described, with sensitivity being inferred from the fine structure of the receptor outer segment. Underwood (1968) has reassessed this scheme and expanded it to include the numerous varieties of receptors found in cross-species comparisons. However, since neither author's convention has been widely adopted, photoreceptors will be referred to as rods and cones in this paper.

Rods and cones have been reported in the retinas of representatives of each vertebrate class. Most elasmo-

branchs (sharks, skates and rays) are reported to have predominantly rod retinas (Walls, 1942; Duke-Elder, 1958; Dowling, 1970) though cones are found in at least some species, including Mustelus (dogfish) (Stell and Witkovsky, 1973b). Cajal (1892) reported only rods and single cones in the teleost (bony fish) retinas he examined, but later workers found double (Walls, 1942), twin (Wunder, 1925) and multiple cones (Lyall, 1957) in some species. Amphibians probably show the widest variety of receptor types. Cajal's report (1892) of red and green rods and single cones was later expanded to include double and triple cones as well (Walls, 1942; Duke-Elder, 1958), and Carey (1975) recently reported an additional type of cone in frog and toad retinas. Traditionally, diurnal reptiles (e.g., Lacerta) have been thought to lack rods. Cajal's description of straight and oblique single cones and double cones has been simplified by later authors as single and double cones in diurnal forms. Nocturnal reptiles show single and double rods (Detwiler, 1923; Walls, 1942; Duke-Elder, 1958). Cajal (1892) also distinguished between oblique and straight cones in the avian retina, which, in addition, was found to contain rods and double cones. Again, the straight-oblique distinction was dropped by later authors (Walls, 1941; Duke-Elder, 1958; Villegas, 1960; Cohen, 1963). In mammals, Cajal (1892) and others (Polyak, 1941; Walls, 1942; Duke-

Elder, 1958; Ogden, 1974; West and Dowling, 1975) have simply confirmed the existence of rods and cones, as reported by Schultze (1866).

Horizontal Cells. The defining characteristic of horizontal cells is the termination of all cell processes in or about the outer plexiform layer in proximity to the synaptic pedicles of the receptors (Polyak, 1957; Rodieck, 1973). Some of these cells may possess an axon, as revealed by the Golgi and methylene blue stains. Recent electron-microscope evidence has raised questions as to whether or not horizontal cells are neurons in the traditional sense, since they do not always show clearly differentiated dendritic and axonal terminations.

In most species, two or more layers of distinctive cell structures are present. Stell and Witkovsky (1973b) reported three rows of horizontal cells, all lacking axons, in the elasmobranch Mustelus canis. Rod spherules were believed to contact the cells of the two outermost layers, while cone pedicles occurred in close proximity to those of the inner layer. In the teleost species studied, the number of horizontal cell rows varied as a function of species and relative rod dominance, ranging from two to four layers (Cajal, 1892; Stell, 1965b, 1967, 1975; Selvin de Testa, 1966; Parthe, 1972; Stell and Lightfoot, 1975). Again, different rows were associated with input

from only one receptor type. Suprisingly, cones usually account for the input to extra cell layers even in rod dominated retinas. Pattern of receptor input to particular rows of horizontal cells is by no means consistent across species, however. Cajal (1892) reported two types of horizontal cells in frogs (Rana Temporaria), lizards (Lacerta viridis and L. muralis, and Chamaeleon vulgaris), turtles (Emys europeae), and chickens (Gallus domesticus).

On the basis of light microscope studies, several authors distinguished between two layers of horizontal cells in some mammals (Cajal, 1892--dog, cat, pig, mouse, sheep, horse, ox; Marenghi, 1901--calf; Gallego, 1971a, 1971b--cat, dog, rabbit, rat, guinea pig). Leure du Pree (1974) reported only one type of horizontal cell in the albino rat. In the primate, Polyak (1941) described a single type of horizontal cell. This finding has been confirmed in the nocturnal owl monkey Aotes (Ogden, 1974), but in a light microscope study of the Rhesus monkey retina, Boycott and Dowling (1969) distinguished two types of horizontal cells on the basis of structural configuration. Each cell type was thought to be post-synaptic to only a single class of photoreceptors.

Electron microscope studies have delineated horizontal cell synaptic connections in several species. The penetration of fine processes of horizontal cells into

regions associated with receptor terminals has led authors to postulate synaptic interaction there (Stell, 1965a; Yamada and Ishakawa, 1965; Fisher and Boycott, 1974; Stell and Lightfoot, 1975). Typically a given type of horizontal cell (identified by structural characteristics or location) is seen as receiving input from only a single receptor cell type, although some exceptions occur (Lasansky, 1972). In primates, cats and turtle, despite some differences in configuration, all horizontal cell dendritic endings have been shown with electron microscopy to envaginate into cone pedicles (Kolb, 1970, 1974; Lansansky, 1971; Boycott and Kolb, 1973b; Ogden, 1974). While some authors find that horizontal cells are synaptically related only to receptors, feeding back on rods (cat, Kolb, 1974) or cones (turtle, Lasansky, 1971), others have found morphological evidence for additional synaptic contacts of horizontal cells with other horizontal and bipolar cells in cat and rabbit (Dowling, Brown and Major, 1966; Fisher and Boycott, 1974). Electrophysiological evidence consistent with each post-synaptic termination pattern has been reported: The photoreceptor feedback loop has been demonstrated by Baylor, Fuortes and O'Bryan (1971) in turtle, and the horizontal-horizontal interactions have been confirmed by Kaneko (1971) in dogfish.

Horizontal cells have been implicated as the origin of S-potentials. L-potentials (luminosity), which

occur as hyperpolarization to all visual stimuli, have been found in all species studies. C-potentials (chromatic), which exhibit wavelength-specific responses have been reported in fish, amphibians and reptiles (e.g., Naka and Rushton, 1966; Werblin and Dowling, 1969; Saito et al, 1974). Both form and size of horizontal-cell receptive fields are similar for all species studied. Consequently, most attempts to correlate electrophysiological differences with structural dissimilarities (where these exist) have been unsuccessful to date (in fish: Svaetichin and MacNichol, 1958; Orlov and Maksimova, 1965; Naka and Rushton, 1967; Kaneko, 1970; Naka and Nye, 1971; in amphibians: Toyoda et al, 1969; Werblin and Dowling, 1969; Werblin, 1970; Norton et al, 1970; in reptiles: Saito et al, 1974; in cats: Brown and Murakami, 1968; Steinberg, 1969; Steinberg and Schmidt, 1970). However, Stell and Lightfoot (1975) have described color-specific interconnections of each of three horizontal-cell types in the goldfish. Having determined patterns of direct cone inputs to horizontal cells, those authors present a model of horizontal cell interaction which is consistent with current electrophysiological data in that species.

Bipolar Cells. The dendritic processes of bipolar cells terminate in or about the outer plexiform layer, where they are thought to contact photoreceptors

and horizontal cells; and the axons terminate in or about the inner plexiform layer where they may contact amacrine or ganglion cells. Cajal's (1892) description of two main types of bipolar cells (giant or outer and small or inner) in fish, amphibians and reptiles has been verified by recent workers (Stell, 1965, 1967; Hendrickson, 1966; Locket, 1970; Wong-Riley, 1974), although his hypothesis that giant bipolars contact only rods and that small bipolars contact only cones has been questioned by Stell (1967) who found large "rod" bipolar cells in contact with both rods and (a few) cones in fish.

Cajal also described small and large bipolar types in birds, speculating that the former contacted cones in the outer plexiform layer. Cajal noted further that the dendritic spread of these inner bipolars decreased as the fovea was approached. Since bipolar terminal arborizations were stained only rarely, Cajal declined to speculate as to bipolar synaptic relations in the inner plexiform layer. These observations of Golgi-processed bird retinas have not been repeated by current workers, although Yazulla (1974) reports differences in the location of synaptic contact for two types of bipolar cells, based on electron microscope studies. The two classes of bipolars show different termination patterns within the inner plexiform layer. If the inner plexiform layer is divided

into ten equal-sized bins (boundaries of which are parallel to the vitreal surface of the retina), for one group of bipolars, synaptic contact occurs in two areas: in the very scleral portion (bin 1) and in the vitreal layers (bins 6-8); for other cells, contacts occur in the scleral to central portions (bins 2-5) of the inner plexiform layer. Whether these two cell groups correspond to Cajal's large and small bipolars cannot be determined by Yazulla's procedures.

In mammals, the situation is somewhat more complicated: Cajal (1892), who studied only non-primates, described three types of bipolars which differed in height and form of dendritic field as well as presumed synaptic contact. The flat bipolar and the giant bipolar were thought to receive input from several cones, while the rod bipolar received input only from rods. Kolb and Famigletti's (1974) study of the cat retina suggests that rod bipolars are typically presynaptic only to amacrine cells, but cone bipolars synapse directly on ganglion cells, as well as on amacrines.

Polyak's (1941) work on primates produced the most important modification of Cajal's scheme, the addition of the midget bipolar cell. The midget bipolar can occur as either the invaginating or flat variety, which differ with respect to the form of the apical

dendrite and the depth of the cell body in the inner nuclear layer (Polyak, 1941; Kolb, Boycott and Dowling, 1969; Kolb, 1970). Polyak hypothesized that midget bipolars, which are thought to be post-synaptic to a single cone provide the structural basis for the high visual acuity associated with private focal vision. The midget bipolar is essentially an individual or "private" line from receptor to midget ganglion cell which permits an individual stimulus to be conveyed to the brain via a "private" optic nerve fiber. Midget bipolars have recently been described in diurnal squirrels (West and Dowling, 1975), but have not been reported in other mammalian species investigated by authors subsequent to Cajal (cat: Boycott and Kolb, 1973a; rabbit: Raviola and Raviola, 1967; rat: Leure du Pree, 1974).

Electrophysiological recording from bipolars has been confined to fish (Kaneko, 1970; Naka and Ohtsuka, 1975; Naka et al, 1975) and amphibians (Werblin and Dowling, 1969). Output in the form of graded potential is correlated with receptive field subdivisions involving a center-surround organization. Individual cells may hyperpolarize or depolarize to light focused on the central area, but species differ with respect to the antagonistic properties of the surround (Werblin, 1972). Werblin and Dowling (1969) and Werblin (1970) have suggested that activity associated with

the central area of the bipolar receptive field is a function of photoreceptor input, while surround characteristics are mediated by horizontal cell connections. As noted above, while conventional horizontal-bipolar contacts have been demonstrated using electron microscopy in cats and rabbits (Dowling et al, 1966), they have not been observed in comparable studies of primate retina (Dowling and Boycott, 1966; Boycott and Kolb, 1973b; Ogden, 1974). To account for the hypothesized horizontal cell influence on the bipolar surround in species such as primates, the invaginating pit of the photoreceptor synaptic terminal has been suggested as a potential site of horizontal-bipolar contact, since both cell types are normally present in the post-synaptic triads (Rodieck, 1973).

Amacrine Cells. These retinal elements have no axons--their processes are located in or about the inner plexiform layer. Numerous varieties of amacrine cells have been classified and reclassified since Cajal's description in 1892. Cajal differentiated two fundamental types of amacrine cells (diffuse and stratified) on the basis of level and extent of termination within the inner plexiform layer. Further distinctions were made on the basis of such cell body and process characteristics as size, position and orientation. Authors who investigated primate retinas (Polyak, 1941; Boycott and Dowling, 1969; Ogden, 1974)

have also opted for two major classes of amacrines in those species, but emphasized slightly different defining characteristics. Polyak described the shape of arborizations as knotted or tasseled, although later authors, following Cajal's model, focused on the spatial distribution of processes.

While all vertebrates appear to possess amacrines of each major class (regardless of criteria chosen), birds were also found to have a third type of amacrine-- called "amacrine of association" by Cajal --believed to receive input from centrifugal fibers (Cajal, 1892; Maturana and Frenk, 1965; Dowling and Cowan, 1966). Maturana and Frenk (1965) also report centrifugal contacts with other amacrine types, as well as with displaced ganglion cells. Cells similar to avian "association amacrines" have been described in primates (Polyak, 1941) and dolphins (Dawson and Perez, 1972), although their function has not been delineated. Since differences in amacrine cell structure have yet to be directly related to functional differences, and classification schemes vary from author to author, minor variations from one species to another are difficult to evaluate.

One major characteristic of amacrine cells does seem to be related to phylogenetic differences in processing, however: Several authors have shown that while the number of ribbon synapses between bipolar and amacrine cells is fairly constant across species, the number of

postsynaptic conventional amacrine-to-bipolar, -amacrine and -ganglion contacts varies and is apparently related to complexities of ganglion cell receptive fields across species. In such species as frog and pigeon, with "complex" receptive fields, the number of conventional synapses may be as much as eight times that of cat or primate, which have "simple" ganglion-cell receptive fields (Dowling, 1968, 1970; Dubin, 1970). Electrophysiological recording from individual amacrine cells has been confined to fish and amphibians where amacrines are found to produce a transient depolarization to light flashes or moving spots (Kaneko and Hashimoto, 1969; Werblin and Dowling, 1969; Kaneko, 1970; Norton et al, 1970).

Ganglion Cells. Ganglion cells are normally described as having perikarya situated in the most vitreal or proximal nuclear layer of the retina and contributing axons to the optic nerve, although exceptions do occur. Occasionally ganglion cell bodies are displaced to the inner nuclear layer (Cajal, 1892; Polyak, 1941; Boycott and Dowling, 1969), and a class of "association ganglions", the axons of which do not join the optic nerve, has been described by Gallego and Cruz (1965).

As was the case with amacrine cells, Cajal's multidimensional classification system has been reorganized, first by Polyak (1941) and again by Boycott and Dowling

(1969) in primates, and by Boycott and Wassle (1974) in cats. The only addition to Cajal's general description made by later authors was that of the midget ganglion cell, which is found in primates and diurnal squirrels and is thought to be synaptically related to a single midget bipolar cell (Polyak, 1941; Boycott and Dowling, 1969; West and Dowling, 1972). This inference is based on a correlation between the diameter of the axonal terminations of midget bipolar cells and the dendritic spread of the midget ganglion cells.

Cajal (1892) reported examples of at least some sub-classes of his diffuse and stratified ganglion cells in all vertebrates, noting that reptiles exhibited the greatest variety of these cells. While different authors have yet to agree on a single nomenclature for ganglion cells, the most important advance in recent schemes has been the addition of quantitative descriptions of various cell types, which has been accomplished in primates (Boycott and Dowling, 1969; Ogden, 1974), cats (Brown and Major, 1966; Leicester and Stone, 1967; Boycott and Wassle, 1974), rats (Brown, 1965; Leure du Pree, 1974), amphibians (Maturana et al, 1960) and fish (Stell and Witkovsky, 1973a). Such quantification provides a potential basis for correlating morphologically dissimilar ganglion-cell types with differences in synaptic contacts and receptive-field

properties.

Much current research focuses on ganglion cell receptive field characteristics, and comparative results have been summarized as follows: In some species (e.g., fish, cats, some rodents and primates) the majority of ganglion cells are found to have "simple" (i.e. center/antagonistic surround) receptive field organization, while in other species (e.g., frog, pigeon) more "complex" aspects of stimuli (edges, movement or convexity, for example) are coded at the level of the ganglion cells. Species such as rabbit, ground squirrel and mudpuppy exhibit a number of cells of each type and their retinas are termed "intermediate." (Dowling, 1970, reviews these data.)

Papers by Stone and Hoffman (1972) and Cleland and Levick (1974) underscore the point that the terms "simple", "intermediate" and "complex" probably define a continuum rather than signifying discrete groups. Those authors have demonstrated "complex" ganglion cells in a large sample of cells investigated in the cat's "simple" retina. The "complex" cells typically constitute only a small portion of the cells monitored. Consequently, such cells have been observed only infrequently by authors working with smaller samples of ganglion cells (e.g., Stone and Fabian, 1966; Spinelli, 1966, 1967; Rodieck,

1967). Currently cat retinal ganglion cells are categorized as: (1) W-units, which have complex receptive fields; (2) X-units which have center/surround receptive fields that are insensitive to alterations in luminance pattern; and (3) Y-units, again with center/surround organization, but showing changes in output in response to changes in luminance pattern within the receptive field (Enroth-Cugell and Robson, 1966; Stone and Hoffman, 1972). The cell types described differ with respect to such fundamental aspects as conduction velocity, as well as locus of termination within the central nervous system (Rodieck, 1973; Cleland and Levick, 1974).

Lettvin et al (1961), West and Dowling (1972) and Kalinina (1974) have tried to correlate receptive field properties with morphologically different types of ganglion cells as a function of anatomical size and complexity of dendritic synaptic connections. The lack of detailed quantitative data concerning both the relative frequency of each cell type and horizontal and vertical range of dendritic spread has seriously weakened their analyses. On the basis of more complete anatomical data, Boycott and Wassle (1974) have convincingly argued for a correspondence between morphologically described α, β, and γ ganglion cells and electrophysiologically distinct

Y, X and W Units in the cat retina.

This summary of research on the morphology of the retina clearly indicates several gaps. First, while Cajal provided elegant verbal and graphic and descriptions of the gross morphology of the retina, he provided no quantitative analysis as to the size, structure or location of differentiable cell types. More recently, several authors have been increasingly concerned with the problem of quantification of cell size and dendritic and axonal fields in the retina (e.g., Boycott and Dowling, 1969; Stell and Witkovsky, 1973a). However, modern authors have, for the most part, neglected avian species in their comparative studies of the retinal anatomy despite the growing body of research concerning both behavioral and physiological correlates of vision in birds.

Since Cajal's early description of chicken and sparrow retinas (1889; 1892), analyses of neural elements in Golgi-processed bird retinas have been fragmentary, typically representing an author's secondary interest. For example, in a study concerned with acetylcholinesterase localization, Shen et al, (1956) illustrated various cells of the inner plexiform layer of the developing chick retina. Brief descriptions of amacrine cells in chick and pigeon were provided by de Oliveira Castro (1966), and Boycott and Dowling (1969), respectively. In the Japanese

quail, Hazlett et al (1975) have described both gross and fine structure of the Landolt club, a specialized appendage of the bipolar cell. However, none of these studies purported to provide an exhaustive survey of avian retinal elements, nor did they present any complete quantitative data concerning the dimensions or location of the cells described.

The sole exception to this rather haphazard pattern of investigation involves studies of avian photoreceptors. Walls (1942) described the gross morphology of several varieties of receptor and subsequent authors have adopted his classification of single and double cones and rods. The spatial distribution of photoreceptors has been determined in a number of avian species (Oehme, 1961, 1962; Galifret, 1968; Fite, 1973a; Fite and Rosenfield-Wessels, 1975). Furthermore, some general analysis of the ultrastructure of the retinal cells of vertebrates have included retinas of such birds as chicken and pigeon among the material examined (Villegas, 1960; Pedler, 1965). To date, electron microscope studies of avian photoreceptors have considered the weaver-finch (Yasuzumi et al, 1958), pigeon (Cohen, 1963) and chicken (Morris and Shorey, 1967). Of particular interest in those reports is the configuration of the receptor bases. Both Morris and Shorey (1967) and Cohen (1963) have confirmed Cajal's drawings of long

processes extending both laterally and deep into the outer plexiform layer from the bases of photoreceptors. Cohen (1963) has suggested that these processes may be involved in inter-receptor synapses. However, the depth to which some processes penetrate in the outer plexiform layer may provide the potential for additional connections with bipolar or horizontal cells there.

The Structure and Function of the Fovea

The area centralis (which has been called area retinalis by Walls (1942) and Carey (1975) who noted that the position isn't always central) is a circumscribed area within which the retina is thickened and so constructed as to produce a marked local increase in resolving power (Walls, 1942). Polyak (1941,1957) and others (Slonaker, 1897; Duke-Elder, 1958) described a further specialization of the area centralis, the fovea or fovea centralis. The fovea is a small, pit-shaped depression or excavation on the inner or vitreal surface of the retina in which the inner layers of the retina are displaced centrifugally from its center, and larger local increases in receptor (foveal) and ganglion cell (parafoveal) density typically occur in primates. The fovea occurs in two general forms: shallow, or concaviclivate, found in some fish, turtles, ground-feeding and nocturnal birds, and primates; and deep, pit-shaped or convexiclivate, found in most birds,

some fish and many diurnal lizards (Slonaker, 1897; Walls, 1937, 1942; Underwood, 1951; Duke-Elder, 1958). Unfortunately the distinction between concaviclivate and convexiclivate is not clear-cut. Recently some investigators have questioned whether shallow foveas found in birds are in fact concavicivate in structure (Fite, personal communication).

Studies which have examined the effects of foveal lesions in primates indicate that these procedures produce significant decrements in visual acuity (Weisenkrantz and Cowey, 1963; Yarczower et al, 1966; Cowey and Ellis, 1967; Rolls and Cowey, 1970). Presumably the high visual acuity associated with primate foveal vision depends on the increased receptor cell density in that area. Polyak (1941) first delineated a structural mechanism which could maintain the fine resolution generated by the increased density of receptor cells in the area centralis and in the foveal region. Midget bipolar cells, which are presumably postsynaptic to only a single receptor and presynaptic to midget ganglion cells provide direct-line connections between foveal receptors and the central nervous system.

Several theoretical treatments predict additional enhancement of spatial resolution in the foveal area, although these have yet to be confirmed by experimental

evidence. For example, Walls (1942) notes that differences in refractive indices of retinal tissue and vitreous as measured by Valentin (1879) produce an enlarged retinal image when light intersects the foveal slope. A corresponding decrease in image size would occur for images falling on the bulge associated with the area centralis, hence mitigating the effect of increased receptor density in this area. Consequently, Walls argues, the foveal depression is necessary to cancel the effect of the convex surface of the area centralis, if maximal resolving power is to be obtained. The deeper the foveal depression, the greater that magnification produced. In an alternative analysis, Weale (1966) suggested that the fovea, being free of retinal blood vessels, prevents the scattering or absorbtion of light by those structures.

As Pumphrey (1961) pointed out, however, the avian retina contains no blood vessels, hence Weale's argument as to the function of the fovea is not relevant to those species. Furthermore, Pumphrey discounted Walls' model of foveal image enlargement since it did not consider aberration effects which would be particularly large in those species which possess convexiclivate foveas. Pumphrey (1948; 1961) sees the convexiclivate fovea as a structure specifically designed for aiding the exact alignment and fixation of the eye for purposes of detecting

angular movement. Presumably an image focused in the pit of the fovea would become asymmetrical as it moved onto the sloped side of the fovea. A structural mechanism which could process resultant irregularities in retinal image was not presented by Pumphrey.

Despite the fact that most psychophysical studies measure foveal vision, there has been little direct experimental evidence bearing on the function of this area in non-primates. Nye (1973) has recently compared retinal areas in the pigeon with respect to performance of pecking behavior occuring in response to color, pattern luminance and movement. Performance associated with the red field of the superior temporal retina was significantly better than that for the yellow field which contains the central fovea. Romeskie and Yager (1976) have also reported data which, in conjunction with D. Blough's (1957) work, suggests that spectral sensitivity varies as a function of retinal locus in the pigeon.

Visual acuity for the red field and foveal regions of the pigeon have also been examined by P. Blough (1971), and Nye (1968), but lesion studies suggest that the pigeon fovea is not critically involved in the resolution of fine spatial detail, since little change in acuity is associated with foveal lesioning in that species (Yarczower, 1964; Blough, 1973). Fite and her colleagues (1973b) are

currently involved in determining foveal contributions to visual acuity in the blue jay as measured by both traditional psychophysical methods (P. Blough, 1971; Fite, 1973a) and optokinesis (Fite, 1968).

Information concerning the structural basis of species differences in foveal vision could be provided from either electrophysiological or morphological data. Electrophysiological studies might reveal differences in receptive field porperties in foveal and peripheral regions. Although this problem has not been the primary focus of recent work, some data are available. Gouras (1968; 1969) reported that tonic and phasic characteristics of ganglion cells in the primate retina differed in foveal and peripheral regions. Maintained responses to a steady stimulus were common in the fovea, while transient responses occurred more commonly in the periphery. These differences may be related to the differential distribution of morphologically described cell types (Bunt et al, 1975).

Pearlman and Hughes (1976) found no consistent qualitative differences in electrophysiological response characteristics as a function of retinal locus in the pigeon, but those authors sampled only small numbers of cells from the fovea and extreme peripheral areas. Even within "simple" retinas, such as that of the cat and monkey, the center of the receptive field of ganglion cells

becomes smaller as the fovea or area centralis is approached (Hubel and Weisel, 1960; Weisel, 1960; Gouras, 1968), possibly as a result of the reduced extent of terminal arborizations of bipolar cells and the increase in parafoveal cell density (Boycott and Dowling, 1969).

Thus, while receptive field properties of ganglion cells in species with a well-defined fovea have been described (Hubel and Weisel, 1960; Maturana, 1962; Maturana and Frenk, 1963; Dejours, 1965; Gouras, 1967, 1969), the relative complexity of receptive fields has not yet been determined for foveal and peripheral regions. In this regard, a review of the synaptology of various retinal areas is particularly interesting: Dubin (1970) found a somewhat lower ratio of conventional to ribbon synapses in the foveal and parafoveal region of the monkey than that found in the periphery. This ratio is usually taken as being directly correlated with the response complexity of the corresponding ganglion cell receptive fields. Yazulla (1974) reported a similar relationship in the pigeon. The shallow foveal region was less "complex" with respect to synaptic-contact structure than either the red or yellow field. Thus, on the basis of synaptic interactions, one might expect that the receptive-field properties of foveal ganglion

cells would be less complex than those of the peripheral retina. Whether, in addition, the shape of the fovea (concaviclivate as opposed to convexiclivate) is related to synaptic or receptive-field complexity remains an open question.

Several authors have recently attempted to quantify structural differences in foveal and peripheral regions by reporting cell-density counts for photoreceptors and ganglion cells (Oehme, 1961, 1962; Galifret, 1968; Binggeli and Paule, 1969; Fite, 1973a; Fite and Rosenfield-Wessels, 1975) in avian species. However, a complete understanding of the mechanisms by which structural differences (i.e., variations in foveal shape) produce functional differences requires more than a numerical correlation between, for example, the number of receptors or ganglion cells and maximum acuity. Further, convergence or "coincidence" ratios can be interpreted only in the context of a complete description of intervening interactions mediated by cells of the inner nuclear layer. At the retinal level, the variety of structures present in foveal and nonfoveal regions must be determined and quantified with respect to synaptic interactions and electrophysiological response properties.

Cajal (1889, 1892) presented some descriptive evidence related to this question, mainly noting that

cell in the foveal region are somewhat smaller with respect to dendritic spread and number of presumed synaptic contacts, but he made no effort to quantify his findings. Unfortunately, little recent effort has been devoted to a quantitative reexamination of Cajal's early observations of foveal morphology, although the fovea reaches a high degree of differentiation in birds which feed on live prey. As noted above, Polyak (1957) ascribed the high visual acuity associated with primate focal vision to the fine resolution provided by the midget system (bipolar and ganglion cells) which is prominent in the area centralis and fovea. Visual acuity is quite good in diurnal birds (Fite et al, 1975; Hodos et al, 1976; Fox et al, 1976), although a midget system has not yet been demonstrated in avian species.

The paucity of quantitative evidence concerning the morphological structure and location of retinal elements in the bird retina suggested the present research. The work reported here involved a light microscope analysis of cellular relationships in the avian retina and supplements the growing body of behavioral and electrophysiological data related to visual processing in birds. Golgi-stained preparations of retinal tissue from two species, pigeon (Columba livia) and blue jay (Cyanocitta cristata), provided

data which verified and augmented Cajal's classical description of the avian retina, while permitting quantitative anatomical comparisons with species of other vertebrate classes.

Both species investigated in this study possess a central fovea: The blue jay has a well-developed convexiclivate fovea (Slonaker, 1897; Fite and Rosenfield-Wessels, 1975), while the pigeon has a shallow fovea (Slonaker, 1897; Galifret, 1968; P. Blough, 1971). In addition, the pigeon is reported to have a second area of increased cell density in the red field of the dorso-temporal retina. Quantitative comparisons of cellular dimensions in foveal, dorso-temporal and peripheral retina provided information bearing on the functional significance of those areas. Furthermore, the evidence for the existence of an avian "midget system," often postulated to account for the high visual acuity found in birds, was evaluated.

METHODS

Subjects

Two species of bird, White Carneaux Pigeon (Columba livia) and Northern Blue Jay (Cyanocitta cristata) were chosen for use in the present study. The pigeon is reported to possess a shallow and somewhat variable central fovea (Slonaker, 1897; Chard and Gundlach, 1938; Galifret, 1968; P. Blough, 1971), while the blue jay possesses a well-developed convexiclivate central fovea (Slonaker, 1897; Fite and Rosenfield-Wessels, 1975).

Blue jays were obtained as fledglings in the surrounding areas of Amherst, Massachusetts, and, following hand-rearing, were maintained on a twelve-hour light/dark cycle.[1]

In all, seventeen pigeons and thirteen blue jays were used as subjects. Tissue processing procedures were initially developed using pigeon retinas. A total of nineteen pigeon and nineteen blue jay retinas were sufficiently impregnated for microscopic examination.

Procedure

Region Investigated:

For purposes of comparison, the areas of interest considered here were as follows: the fovea, periphery

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[1] In addition, Drs. Alan Kamil and John Donahoe supplied some of the birds used in this study.

and the red field in the pigeon; and the fovea, periphery and an area corresponding in location and extent to the pigeon red field in the blue jay.

The red field in the pigeon was identified chiefly on the basis of color, as its name suggests. The red field is a relatively large area of the dorso-temporal retina which is characterized by a predominance of red oil droplets in the inner segments of the cones (Wealchli, 1883; Galifret, 1968; Yazulla, 1974). The remaining retina comprises the yellow field. (See Figure 1) Relative to the yellow field, the red field shows an overall thickening of both the inner nuclear and ganglion cell layers, as well as an increase in synaptic complexity (Galifret, 1968; Binggeli and Paule, 1969; Yazulla, 1974). In a small, central portion of the red field, cell densities of both the inner nuclear layer and the ganglion cell layer are comparable to those of the area centralis (Galifret, 1968; Binggeli and Paule, 1969). This dorso-temporal area of highest cell density has been referred to as the "area dorsalis" by Galifret (1968).

Clearly, comparison of foveal and peripheral cell types and structures depends on the experimenter's ability to discriminate the foveal region in Golgi-strained material. Cajal (1892) reported no difficulty in locating the foveal region in thick transverse sections of sparrow

and chameleon retinas. As his drawings indicate, the foveal depression and the almost total absence of ganglion cells in this area served as a marker. Similar morphological features were observed in the blue jay. In the pigeon, the foveal depression was shallower but clearly distinguishable, despite the fact that ganglion cells were present even in the very center of the fovea (Slonaker, 1897; Chard and Gundlach, 1938; Galifret, 1968; Binggeli and Paule, 1969; P. Blough, 1971).

Ogden (1974) identified the location of the central area in the owl monkey Aotes in the fresh retinal whole-mounts on the basis of blood vessel pattern, since retinal blood vessels are excluded from the fovea in primates. Boycott and Kolb (1973b) suggested an alternative method for determining the approximate position of cells with respect to the fovea in whole-mounted tissue. By moving immediately to one side of the cell under study, with suitable manipulation of the condenser and iris diaphragm, it was possible for those authors to count the number of cones adjacent to the cell in question. In this way, a particular cell could be related to the number of cones in a standard unit of area, which correlated with retinal location.

Since birds possess no retinal blood vessels (Pumphrey, 1961), and relative rod/cone densities have not been determined for various retinal areas in birds,

a more satisfactory method for locating the fovea in the avian retinas studied here was developed. Based on the distinctive configuration of retinal elements in the foveal region of birds, this method will be described in detail in the results section.

For purposes of this investigation, the fovea was defined as encompassing a circular area of 1.5 mm diameter, the center of which coincided with the center of the foveal pit, and the periphery included all portions of the retina which fell within 2 mm of the ora serrata. Although the latter definition is arbitrary, the former value was derived as follows: Yazulla (1974) estimated the width of the foveal clivus to be approximately 0.5 mm in the Pigeon, while Fite and Rosenfield-Wessels (1975) reported that the width of the foveal clivus was 0.72 mm in the blue jay. Furthermore, my data indicated that the lateral displacement of bipolar cells in the foveal region frequently exceeded 0.3 mm. Additional lateral displacement of information originally derived from foveal receptors which is less easily quantified may occur via horizontal or amacrine cells. It was therefore concluded that cells, particularly amacrines and ganglions, from a region of up to 0.75 mm from the foveal center might be legitimately considered forveal cells.

Tissue Preparation:

A light microscope study of retinal tissue stained with modifications of the Golgi procedure was carried out in order to compare cell types present in the foveal and peripheral areas of the retinas of pigeons and blue jays. Several alternative staining procedures were considered for use in this study but eliminated. From the earliest work of Cajal (1892) authors have consistently reported poor results with both the Golgi-Cox method applied to the retina (Cajal, 1892; Boycott and Kolb, 1973a; 1973b; Kolb, 1974) and with the Kopsch modification of the Golgi stain (Kolb, 1974). While some recent authors have reported data obtained from tissue stained with methylene blue (Maturana and Frenk, 1965; Witkovsky and Stell, 1973), Cajal's (1892) criticism of the stain as lacking clarity and failing to stain some cell types while incompletely impregnating others has been substantiated by Stell and Witkovsky (1973b), who reported that receptors and horizontal cells were not stained vitally with methylene blue.

In both light and electron microscope studies, a number of authors have reported results based on Stell (1965) and Colonnier (1964) modifications of the Golgi-rapid procedure (e.g. Boycott and Dowling, 1969; Kolb, 1970; Stell and Witkovsky, 1973; Ogden, 1974). The

staining procedure developed by Stell and his colleagues (Stell, 1965; 1967; Stell and Witkovsky, 1973a, 1973b; Witkovsky and Stell, 1973) was employed on some tissue for this study. The Stell procedure fixed flat-mounted tissue in an ice-cold solution of glutaraldehyde (2.25%), paraformaldehyde (0.9%), osmium tetroxide (0.4%) and sodium chloride (1.35%) buffered with 0.1M sodium cacodylate. The tissue was then washed in 3% potassium dichromate at room temperature for 30 to 60 minutes and fixed for two days in 0.2% osmium tetroxide in 3% potassium dichromate. Following rinsing in distilled water, tissue was transferred through several changes of 0.75% silver nitrate and left for two days. At this point, the tissue was examined to evaluate staining, then either reimpregnated or embedded and sectioned (Stell and Witkovsky, 1973a). Despite the use of a double impregnation procedure, my data and those of R.G. Carey (personal communication) suggest that oil droplets found in the outer segments of pigeon and frog photoreceptors may have an unusual affinity for the silver stain in the Stell procedure. The opaque background thus produced by the oil droplets precluded a light microscrope analysis of flat-mounted preparations processed by the Stell method.

Several variations of the Colonnier (1964) procedure were also used to process retinal tissue for this study. A composite of the Colonnier and Stell techniques was

found to provide optimal staining and separation of individual retinal cells. Both whole eyes and flat-mounted retinas were stained following the same basic method.

Eyes were removed under chloroform anesthesia and opened by removing the cornea and lens. To prepare flat-mounts, the retina was then dissected from the eye cup. The isolated retina was mounted on a coverslip, which served as a base. Due to the thickness of the inner nuclear layer in birds, cells in the other plexiform layer were most clearly visible if the scleral surface of the retina was mounted toward the coverslip and, conversely, cells of the inner plexiform layer were more easily distinguished if the vitreal surface was mounted toward the coverslip. The exposed surface of the retina was covered with one or more layers of porous paper through which the fixative could penetrate. Flexible lens paper, which was easily peeled off the retinal surface after processing, was used as the first layer, and was covered with one or two strips of filter paper, which remained through dehydration and were removed prior to embedding (Stell and Witkovsky, 1973a).

The whole eye or sandwiched retina was placed in an aqueous solution of one part 25% glutaraldehyde and four parts 2.5% potassium dichromate for two or three days. The specimen was washed briefly in distilled water, then

transferred to a 0.75% silver nitrate solution for one to two days (Colonnier, 1964). Double impregnation (i.e. repeating the cycle of glutaraldehyde-potassium dichromate and silver nitrate) was typically sufficient for both flat-mounted and whole eye preparations, although additional repetitions of the staining sequence are theoretically possible (Cajal, 1892; Stell and Witkovsky, 1973a; Raviola, personal communication).

Following staining, some flat-mounted retinas were dehydrated through several baths of 95% and 100% alcohol and isopropyl alcohol. The retinas were then mounted in Permount on glass slides and examined under a light microscope as described below. Additional flat-mounted retinas and whole eyes were embedded in celloidin and sectioned transversely for light microscope analysis. The embedding procedure involved rapid dehydration through several baths of ethyl alcohol (95% and 100%) and ether alcohol. Tissue was then processed through increasing concentrations of celloidin (4,6, and 12%) and embedded in 12% celloidin following the procedure described by Fite (1973) for LVN, substituting 12% celloidin for thick LVN. Tissue shrinkage for this procedure is approximately 20-23% (Fite, personal communication). Sections of 100 μ were cut on a standard sliding microtome, with careful attention paid to the maintenance of retinal orientation and the order of sections.

Sampling Procedure:

In an effort to eliminate possible experimenter bias, a systematic procedure to assure random sampling of those cells which were adequately stained and well-isolated was adopted. Flat-mounted retinas were repeatedly scanned in a horizontal pattern. That is, a starting point was randomly chosen, and the horizontal and vertical coordinates indicated on the stage micrometer were noted. The vertical coordinate was held constant while the tissue was scanned along its entire horizontal extent. Following each horizontal scan the vertical coordinate was increased by 2 mm until the entire retina had been scanned. This procedure is illustrated schematically in Figure 2A. As seen in Figure 2B, smaller grids were used to sample foveal areas. Data was recorded for all cells of a particular catagory (i.e. horizontal, amacrine or ganglion cells) which were sufficiently isolated to allow clear resolution of process extent and orientation. Representative cells of each class were drawn and/or photographed as well.

A slightly modified procedure was used for observing photoreceptors in flat-mounted preparations. Receptor cells were examined at 1 mm intervals along the horizontal axes previously established. The cell to be investigated at each point on the grid was that closest to the center of

the viewing field. Linear distance from the center of the viewing field to the center of the receptor cell base was determined by using a concentric-ring eyepiece micrometer. The modified procedure was justified by arguing that well-isolated receptors were more numerous in Golgi-stained material than were the other cell types investigated. First, it was assumed that approximately equal proportions of each class of retinal cells was impregnated by the Golgi stain. Secondly, the receptor bases were generally considerably smaller than the fields of other retinal cells, so photoreceptors were more likely to be well-isolated in a given retinal area than were other larger retinal cells. Thus, a sufficiently large sample of receptor cells was obtained to produce reliable quantitative comparisons using the modified sampling procedure.

In addition to the exhaustive scans, which were carried out on at least two retinas of each species, comparable sampling procedures were used to provide supplemental data for areas of particular interest in several additional retinas. Also, measurements obtained from horizontally oriented, transverse sections of whole eyes were used to verify information derived from flat-mounted tissue.

Structures of Interest:

Photoreceptors. Since the fine structure of avian

photoreceptors has been widely studied (e.g. Cohen, 1963; Morris and Shorey, 1967), this investigation was primarily concerned with determining the potential range of receptor interaction with cells which terminate in the outer plexiform layer. In both flat-mounted retinas and transverse sections, the dimensions of the receptor synaptic bases were determined according to the procedures described below. Also, the number of processes radiating from the receptor base was counted in flat-mounted preparations. The radial extent of these processes was measured by determining the length and breadth of the field containing the terminal processes.

Horizontal, Amacrine and Ganglion Cells. For each of these cell types, the following information was obtained from flat-mounted tissue: (1) cell-body dimensions; (2) process dimensions or field diameters; (3) "axonal" length and direction; and (4) symmetry. In the case of exceptionally large elements (i.e. greater than 50 μ diameter), additional data were collected from partially obscured cells in order to supplement and confirm findings derived from the fewer perfectly isolated instances (see Stell and Witkovsky, 1973). In addition, verification of cell-body and field dimensions of horizontal and amacrine cells was obtained from transverse sections.

Bipolar Cells. Bipolar cells were investigated in both flat-mounted retinas and transverse sections.

Bipolar cells were frequently stained in large groups, and because the processes of foveal cells are comparatively long with respect to the thickness of the transverse sections, instances of completely stained, well-isolated cells were rare. Consequently, additional data was obtained from well-isolated portions of cells. For example, distal process dimensions could be determined from a cell for which the proximal protion was obscured. Even such partial cells are clearly discriminable from horizontal or amacrine cells on the basis of size and location. Information concerning distal and proximal process dimensions and displacement was collected according to the procedures described below.

Measurement Procedure:

Measurements were made of the characteristics described above for each cell sample in the flat-mounted retinas. With a Bausch and Lonb light microscope, under either "high dry" or oil immersion objectives (which produced magnifications and X400 and X1000, respectively) size estimates were obtained using square or concentric-ring eyepiece micrometers. Cell location was determined with a stage micrometer.

Cell Dimensions. Measurement of cell bodies, pedicles and process extent in flat-mounted retinas always involved determining the length of the longest diameter (a) of the

structure in question and then measuring the length of a second diameter (b), perpendicular to the first, and passing through the center of the first. This procedure is illustrated in Figures 3A and B. If an "axon" was present, its length was measured by centering a concentric-ring eyepiece micrometer on the center of the cell body if, indeed, the cell possessed a clearly defined cell body (Figure 3C). Some structures, as described below, did not exhibit a clearly defined cell body, but rather, radiated from a thickened central trunk. For these structures, "axonal" length was determined as the distance from the point at which the "axon" left the thickened central trunk. (See Figure 3D.)

In transverse sections, width and depth of cell bodies or fields were defined respectively as the longest diameter parallel to the outer limiting membrane and the longest diameter perpendicular to the outer limiting membrane, as shown in Figure 4. An additional characteristic measured in transverse sections was the displacement of bipolar cells. Displacement is defined as the horizontal distance between the center of the distal or "dentritic" process and the center of the proximal or "axonal" process at the point where the latter enters the inner nuclear layer. This dimension is also illustrated in Figure 4. Since transverse sectioning obscured morphological details

critical to cell classification and probably led to an underestimation of the size of larger cell fields (which were not completely confined within a single 100 μ section), measurements obtained from such sections were used primarily to confirm or verify those obtained from flat-mounted cells.

Measurement error of cell characteristics described in this section was estimated to be about 3 μ for small cells ($< 100\,\mu$) and about 10 μ for larger cells.

Location. In flat-mount preparations, the location of the cell under investigation was determined by centering the cell on the middle point of the eyepiece micrometer and reading the position from the rectangular coordinates of the stage micrometer. The entire flat-mounted retina was drawn on graph paper, using coordinates of corners and edges to reproduce the appropriate orientation. Each cell could then be located with respect to this diagram of the retina, and assigned to appropriate regional catagories described above.

Cells observed in transverse sections were localized by noting section number (serial sections had been saved through the retina) and distance from the fovea, as measured using an eyepiece micrometer. The error in measurement for location was approximately 100 μ (or less than 1 visual degree), both for cells in transverse sections and for

those in flat-mounted whole retinas.

Classification:

On the basis of drawings, photographs and cellular dimensions detailed above, cells of each major retinal class (i.e. receptors, horizontals, bipolars, amacrines and ganglions) were further divided into anatomically distinct varieties. First, drawings were grouped according to gross qualitative characteristics such as field organization, then cells within each group were compared with respect to quantitative characteristics. Since the drawings constituted the primary basis for classification, Figure 5 shows a drawing of a retinal structure which may be compared with a photograph of the same structure, found in Figure 19.

The final criteria established for assigning a particular cell to each major class (receptor, horizontal, bipolar, amacrine and ganglion), as well as to its appropriate subclass, are discussed fully in the results section. In order to establish the reliability of the classification schemes developed, the process was repeated for horizontal cells by an independent observer familiar with general retinal structure.[2] Discrepancies were discussed where they occurred, and the classification of individual cells was modified accordingly.

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[2] Russell G. Carey, who has studied avian retinas extensively, very generously offered to evaluate the classification scheme developed.

RESULTS

General organization of the retina

Examination of transverse horizontal sections of the retinas of both blue jay and pigeon indicated the existence of central foveas in both species. Foveal configuration was clearly deep and convexiclivate in the blue jay, as shown in Figure 6A. In pigeon, the fovea was shallower (Figure 6B), and the distinction between convexiclivate and concaviclivate more difficult to discriminate. Since the terms convexiclivate and concaviclivate were not operationally defined by authors such as Walls (1942), blue jay and pigeon foveas will be distinguished simply as deep and shallow, respectively.

Close examination of transverse sections through the foveal regions of both species revealed a very distinctive lateral displacement of bipolar cell processes which was not observed in any other retinal area (Figure 7). Inner-plexiform-layer terminals of the foveal bipolar cells were displaced by approximately 300 μ from corresponding outer-plexiform processes. This phenomenon permits the accurate localization of the fovea in flat-mounted retinas, since bipolars appear to radiate symmetrically from the center of the foveal pit (Figure 8).

A red field was clearly visible in the dorso-temporal portion of the freshly excised pigeon retina. The field

was similar in location and extent to that described by Galifret (1968) and by Binggeli and Paule (1969), encompassing about 1/4 to 1/3 of the retinal surface. A very slight pink tint was observed in a corresponding area of the blue jay retina. However, the pinkened area was visible only in flatmounted, detached retina, and was not seen in all blue jay specimens. A small increase in red oil droplets may occur in blue jay dorso-temporal retina, but vertification of such an increase would require more detailed examination of that area, including quantitative comparisons of red-oil-droplet density.

Using a procedure described by Fite and Rosenfield-Wessells (1975), estimates were obtained of retinal length, visual field and average number of microns per visual degree for three Golgi-impregnated, celloidin-embedded retinas of each species (Table 1). Data essentially confirmed Fite's observation that blue jay and pigeon retinas are comparable in those dimensions (personal communication), and are consistent with Nye's (1968) estimate of μ/visual degree in the pigeon.

Classification of cell types

Cells occuring in flat-mounted retinas and transverse retinal sections were classified into seven broad catagories, including two catagories of glial cells. These catagories were defined primarily in terms of soma and process

location within the retina. In both flat-mounted and transversely sectioned retinas it was possible to discriminate three cell layers and three intervening fiber layers. When the orientation of flat-mount tissue was known, the layers could be labeled readily as outer nuclear layer, outer plexiform layer, inner nuclear layer, inner plexiform layer, ganglion cell layer and optic fiber layer (from scleral to vitreal surface of the retina).

Receptor cells have cell bodies in the scleral-most cell layer (outer nuclear layer) with inner and outer segments extending toward the pigment epithelium. Receptor bases are attached to nuclei by a descending process and lie on the outer border of the outer plexiform layer. Basal processes extend laterally and proximally from the receptor base. Horizontal cells have cell bodies which lie in the outer portion of the inner nuclear layer, and processes which terminate in the outer plexiform layer. Bipolar cells also have cell bodies in the inner nuclear layer, but distal (and presumably dendritic) processes terminate in the outer plexiform layer, while proximal ("axonal") processes end in the inner plexiform layer. Cell soma of amacrine cells typically occur in the viteral half of the inner nuclear layer, and all processes terminate in the inner plexiform layer. Only amacrines of association exhibit an axonal process. Ganglion cell bodies usually lie in the ganglion

cell layer, with dendritic processes extending into the inner plexiform layer and an axon following a course through the optic fiber layer, usually joining the optic nerve. Muller cells are large glial cells which extend vertically throughout the entire extent of the neural retina. Cell bodies of Muller cells are found in the inner nuclear layer. An additional class of cells was observed interspersed throughout the ganglion cell and fiber layers. Processes typically ran parallel to ganglion cell axons. In some instances both the cell bodies and processes of these cells were contained within the optic fiber layer. Some cells exhibited thickened and irregular processes. Axons were never observed to emanate from either conventional or thickened cells. These cells resemble glial cells described by Cajal (1892) and Stell and Witkovsky (1973), and may correspond to glial cells found in the pigeon ganglion cell layer by Binggeli and Paule (1969).

Clear-cut examples of well-isolated cells within the five non-glial catagories were further subdivided according to structural criteria, as described below. Once criteria had been established, additional partially obscured, incompletely impregnated or displaced cells could be assigned to categories on the basis of observable characteristics. For example, displaced amacrine cells were

occasionally observed with cell bodies in the ganglion cell layer. Such cells were assigned to the amacrine cell category only after many similar cells were observed in the inner nuclear layer with processes terminating in the inner plexiform layer. Since these cells more closely resembled a distinct amacrine class with respect to cell-body size, process-field distribution and dimensions than they resembled any category of ganglion cells, and since, furthermore, they never exhibited an axon, they were classified as displaced amacrine cells. (Stell and Witkovsky (1973) followed a similar procedure for extablishing the identity of displaced ganglion cells.) Following classification, quantitative information as to cell body and process-field dimensions was obtained for three retinal areas: the central fovea; the dorso-temporal retina; and the peripheral retina.

Photoreceptors. Despite the fact that subjects were dark adapted prior to enucleation and tissue fixation, photoreceptor outer segements were rarely completely impregnated. Receptor cells were therefore classified according to synaptic base configuration, and subsequent attempts were made to correlate base configurations with inner (and occasionally observed outer) segment characteristics.

Four receptor-base configurations were observed in both species studied. These have been arbitrarily labeled R1, R2, R3, and R4, and are illustrated in Figure 9. R1 is

a small (3-5 μ diameter), round spherule attached to the receptor cell nucleus by a thin descendant process. A tight cluster of short processes (2-3 μ) emanate toward the inner nuclear layer from the base. Occasionally one or two longer processes are attached to the spherule as well. The R2 base is also small in diameter, but is typically attached to the receptor cell nucleus by a thickened trunk. Several (8-20) long (10 μ or more), slender processes spread laterally from the R2 base, often ending in tiny (1 μ) bulbous terminal swellings. R3 bases are much larger, usually appearing horseshoe shaped in flat-mounted tissue. Like the R2 bases, thin fibers emerge from the base, but the fibers are typically somewhat shorter than those of R2. The R4 ending is very distinctive: the pedicle base, which resembles that of R2, is attached to the nucleus by an oblique descendant process. Thin basal filaments extend from both the descendant process and the terminal base of these cells.

Each configuration described above has been observed in each retina examined; hence these appear to represent distinct classes rather than artifacts produced by small differences in staining procedure. In flat-mounted tissue, R1 and R2 are observed most commonly, R3 is seen somewhat less frequently and R4 is encountered only rarely. All pedicle base configurations have been observed in each retinal area studied.

Although it is tempting to label R1 bases as rod spherules, and R2 and R4 as straight and oblique cone pedicles, respectively, resemblance between these structures and mammalian receptor bases cannot be considered sufficient grounds for such an assignment. Preliminary efforts were made to match available drawings of avian photoreceptors (Walls, 1942; Cohen, 1963; Morris and Shorey, 1967) with their Golgi-impregnated counterparts. Establishing a correspondence between drawings and dimensions based on light and electron microscopic examinations required the assumptions that receptor configurations were consistent across avian species and that they were not significantly modified by Golgi impregnation. Comparison of the drawings just mentioned brought to light major disparities between avian species with regard to both receptor configuration and dimensions. Furthermore, Pasternak and Woolsey (1975) reported that Golgi-Cox precedures enlarged cortical neurons significantly. Whether comparable changes occurred in retinal cells impregnated in the present study is not known. However, as Ramon-Moliner and Ferrari (1972) point out, the Golgi stain is thought to produce precipitates along membranes and would therefore be expected to increase the apparent size of impregnated cells.

Since comparisons of Golgi impregnated photoreceptors with the drawings currently available in the literature were

inconclusive, an alternative strategy was adopted. By examining the cut edge of flat-mounted retinas, it was often possible to find instances of transversely oriented, unstained photoreceptors. Manipulation of the light source and iris diaphragm brought these outer segments into clear focus. As illustrated in Figure 10, it was possible to trace these structures using the drawing attachment. Such reconstructions provided information as to the approximate size and shape of photoreceptor outer segments in the pigeon and blue jay. Opaque, Golgi-impregnated cells could then be compared with regard to outer segment configurations and tranced to receptor bases for purposes of classification. The vertical orientation of most cells was such that translation of the three-dimensional structure into a two-dimensional drawing obscured the most critical characteristics of inner and outer segment configuration. Since drawings were not particularly useful, attempts to correlate outer and inner segment configurations with receptor-base structure involved direct observation of the cells. That method enabled the experimenter to consider the depth of focus in estimating receptor outer segment length.

Several completely impregnated cells were classified as rods, cones and double cones. When the synaptic bases of such cells were compared, no consistent relationship was

found between photoreceptor base configuration and outer segment characteristics. In particular, R2 and R4 bases occurred with both rod and cone outer segments in both peripheral and central retina. Cells with R2 bases are illustrated in Figure 11, which contains drawings of rare instances in which completely impregnated cells were transversely oriented in flat-mounted tissue. R1 bases were usually attached to cone-like outer segments, but were occasionally observed with double cone or even rod outer segments. R3 bases were associated with both double and single cone outer segments. Due to the scarcity of completely impregnated cells, conclusions as to the relationship between outer segment and base configuration must remain tentative at this time. Implications of the problems associated with photoreceptor classification will be discussed more extensively below.

Horizontal cells. Three distinct horizontal cell structures were observed in both blue jay and pigeon. The photograph, Figure 12A, shows examples of the three horizontal structures occurring in close proximity in the peripheral retina of the pigeon. The first type of horizontal cell, call H1, exhibits a clearly defined cell body. (See Figure 12B.) The processes are usually deep and densely packed, hence some of the processes appear out of focus in the photograph. Field shape of these cells varies from

relatively circular in the central retina to elliptical, more peripherally. Approximately 80% of these cells possess a clearly differentiated "axon-like" process, which typically terminates with about 100 μ of the cell body. The second type of horizontal cell (H2) also has a distinct cell body, as shown in Figure 12C. Its field is typically larger, flatter and more diffusely organized than those of nearby H1 cells. The H2 cells have never been found with a clearly defined axon.

Finally, a third horizontal structure has been observed (Figure 12D). Most of its processes are thick and branching, although one is finer and resembles an "axon-like" process. Careful examination of a number of retinas produced several instances in which the first and third structures were connected by a single fiber, as shown in Figure 13. Since the latter structures possess no discriminable cell body, this observation suggested that the claw-shaped structure may correspond to an axonal-expansion or termination of the H1 cell. Thus, two morphologically distinct types of horizontal cells were observed in these bird retinas: The H1 cell, which possesses a large terminal expansion, and the apparently axon-less H2 cell.

Bipolar cells. A number of potential classification schemes were considered for the bipolar cells, based on such dimensions as outer plexiform layer (distal) process

spread or location (depth) of cell body within the inner nuclear layer. Those dimensions which defined continua, rather than separating cells observed into discrete classes, were eliminated. Ultimately, cells were classified on the basis of inner plexiform layer termination pattern, a procedure followed by Witkovsky and Stell (1975) in classifying dogfish bipolar cells. All bipolars were observed to terminate in one or more discrete layers in the inner plexiform layer. Thus cells were labeled B1, B2, B3, and B4 on the basis of the number of proximal ramifications. The predominant cell patterns, B1 and B2, are illustrated with drawings from flatmounted and transversely sectioned retinas in Figure 14. While distal processes were often very fine, proximal processes typically exhibited bulbous varicosities. B1 and B2 cells occurred commonly in all parts of the retina. B3 cells were confined primarily to the blue jay peripheral retina and B4 cells were very rare in both species.

Difficulty in determining inner plexiform layer boundaries and the changing thickness of that layer across the retina made it impossible to obtain reliable estimates of the precise level of bipolar termination within the inner plexiform layer. However, examination of transverse sections suggested the B1 proximal processes and the outer processes of multi-stratified cells may terminate in

scleral portions of the inner plexiform layer, while inner processes of multi-stratified cells may terminate in deeper (more vitreal) portions of the inner plexiform layer, as seen in Figure 15. The figure clearly illustrates and confirms Yazulla's (1974) observation that bipolar cell terminations were confined to specific levels within the inner plexiform layer.

Some authors (e.g., Witkovsky and Stell, 1973; Mariani, personal communication) have classified bipolar cells as to the presence or absence of a Landolt club. Landolt clubs did become impregnated in blue jay whole eyes later cut in transverse sections, but did not appear in blue jay flatmounts. Clearly, it is either the case that no Landolt-club bipolars stained in blue jay flatmounts, or that while the Landolt club did not stain, the corresponding bipolar was impregnated. A comparison of field dimensions of a sample of pigeon bipolars with and without Landolt clubs showed no significant difference between the samples along the dimensions measured when inner-plexiform-layer termination pattern and retinal location were held constant. Therefore, cells of both species were grouped according to termination patterns of proximal processes for purposes of quantitative inter- and intra-species comparisons.

Amacrine cells. Like bipolar cells, amacrine cells were classified on the basis of inner plexiform layer

termination pattern. The vast majority of amacrines observed in these avian retinas were monostratified. On the basis of process configuration, the monostratified amacrines could be further subdivided into three classes called, arbitrarily, A1, A2, and A3. The A1 cell was very distinctive: It was almost perfectly radially symmetrical and all processes appeared to extend from a single central trunk. The A2 cell, which was more compactly organized, showed a large number of process varicosities. The A2 cell was sometimes seen with its cell body displaced to the ganglion cell layer, but no axons were ever observed emanating from these displaced cells. The A3 cell exhibited an irregular, open and sometimes asymmetrical branching pattern. A number of extremely large A3 cells were observed (cell bodies of 25X25μ and process fields of up to 1200X1500μ). These large cells may constitute a class of "giant amacrines," or may be displaced ganglion cells with unimpregnated axons. The latter possibility is discussed in more detail in the next seciton. Monostratified amacrines are illustrated in Figure 16.

In addition to the monostratified varieties, several multistratified or diffuse amacrines were observeed. Typically, the multistratified and diffuse cells resembled A2 or A3 cells, but terminated a two or more discrete lamina within the inner plexiform layer, or spread diffusely

throughout half or more of that fiber layer. In general, multistratified cells appeared to be A3 types, while diffuse amacrines more often resembled A2. However, the distinction between multistratified and diffuse cells was difficult to make reliably in flatmounted tissue and the distinctions between A2 and A3 cells were obscured in transverse section. No multistratified or diffuse amacrines were ever observed which resembled the distinctive A1 cell. Figure 17 includes drawings of several multistratified and diffuse amacrines. For purposes of quantitative comparison, all multistratified and diffuse amacrines have been grouped together, since any attempt to further subdivide the group would have reduced cell numbers in each location to such a low level as to make quantitative comparisons meaningless.

Ganglion cells. Ganglion cells were divided into three categories. G1 cells send thin, diffuse processes deep into the inner plexiform layer in central retinal areas. More peripherally, where the inner plexiform layer is thinner, the fibers were found to have more shallow fields. G2 cells also had thin processes, but those ramified extensively at their ends forming one or more layers within the inner plexiform layer. The distinction between G1 and G2 cells is illustrated in Figure 18A, B. A third, rarely encountered, class was the displaced ganglion cells (G3), which had cell bodies in the inner nuclear

layer. Those cells had distinct axons which were traced through the inner plexiform and ganglion cell layers to the optic fiber layer.

Two qualifications must be considered with regard to the ganglion cell classification scheme. First, the distinction of G1 and G2 cells as representing qualitatively different classes may be erroneous, resulting from limitations of the staining and observation procedures. The G1 cell closely resembles a G2 cell with the final terminal layer(s) absent. It is possible that cells classified as G1 cells may be partially impregnated G2 cells. Furthermore, even in peripheral regions, dendritic fibers of both cell types are very fine (less than 1/2 μ in diameter), approaching the limits of resolution of the light microscope. In fact, in some cases fibers can be traced only by following bulbous varicosites which occurred at intervals along their extent. G1 cells typically had smaller cell bodies than G2 cells in any given retinal area (as will be seen in the quantitative analysis presented below). That finding is consistent with the notion that the terminal processes of the G1 cells had only been partially impregnated or were invisible to the light microscope. Some instances of cells intermediate between G1 and G2 cells were observed, but normally cells were readily classified as deep/diffuse (G1) or stratified (G2). Since this difficulty cannot be

resolved given the techniques available for this study, the cells have been classified on the basis of their light-microscopic appearance.

A second difficulty with the ganglion cell classification system concerns the existence of the displaced ganglion cell. Clearly, the most critical defining characteristic of the ganglion cell class is the existence of an axon which joins the optic fiber layer and in most cases presumably leaves the retina via the optic nerve to terminate in the central nervous system. Using this criterion, only two displaced ganglion cells were observed in all the tissue examined. This low frequency of occurrence may not reflect the actual prevalence of the displaced ganglion cells in the retina, or even their proportion among the cells impregnated with the Colonnier Golgi procedure, however. Only about half the G1 and G2 ganglion cells observed exhibited a well-defined axon, and that proportion varied as a function of cell size and retinal location. With normal ganglion cells, this presented no problem, since other characteristics of cells were sufficient to confidently classify them as ganglion cells. However, the situation was more complicated in the case of displaced cells, which, if axonless, could not be distinguished from amacrine cells. Even if the axon of a displaced ganglion cell was stained, the cell might be

confused with an amacrine cell. As indicated below, only the first 20 to 60 of the G1 and G2 axons were typically impregnated. Axons of a comparable length associated with displaced ganglion cells could not be distinguished from other processes which terminated within the relatively thick inner plexiform layer. In the case of the two confirmed displaced ganglion cells, the axon was traced for over 200 μ, much of which distance involved transversing the inner plexiform and ganglion cell layers.

The two displaced ganglion cells observed were similar in configuration to the A3 amacrine cells described above. Cell body and process-field diameters were only slightly larger than the mean values obtained for A3 cells in the same retinal region, and fell well within the range of values observed for those cells. The G3 and A3 cells could, therefore, represent a single class of displaced ganglion cells. The additional observation that A3 cells had cell body diameters of up to 25X25 μ (versus the 12X12 μ common to other amacrine varieties) is intriguing but inconclusive. While cell bodies of that size are not uncommon among ganglion cells, such large A3 cells could simply be giant amacrine cells.

In sum, the data clearly imply that displaced ganglion cells are present in the avian retina. However, the possibility that two similarly appearing yet distinct

groups of amacrine and ganglion cells exist cannot be eliminated. If that is the case, the similarity between G3 and A3 configurations strongly suggests that at least some of the cells classified here as A3 amacrines were displaced ganglions. This disparity is probably not critical in terms of the quantitative analysis discussed below, since inter-area and inter-species relationships were quite similar for amacrines and ganglions. At worst, grouping two potentially disparate classes together (by including unrecognized displaced ganglion cells in the A3 data analysis) would be expected to artificially inflate the variance within the A3 class, and reduce the likelihood of observing significant differences. For this reason, A3 cells have been treated as a single class, emphasizing the possibility that some or all of those cells may in fact be displaced ganglion cells.

Quantitative analysis

As described above, measurements of cell body and process dimensions for each category of retinal cells were made in each of three retinal areas: fovea, dorso-temporal retina and peripheral retina. These data are summarized below for each subvariety of cells which occurred in sufficient frequency to generate reliable estimates for each of the three areas in both species studied. The number of cells measured in each subclass and for each

retinal location is presented in Table 2.

Formal statistical tests which compare differences between group means were not used in evaluating quantitative data, since the data obtained clearly violated the assumptions required for the application of the appropriate statistical tests. In particular, the use of a t-test or an analysis of variance requires that the population from which samples were drawn be normally distributed and that population variances be homogeneous. The effect of violating the latter assumption is usually more profound, especially if the samples differ in size as they did here (Hayes, 1973).

Differences between retinal areas and between species were therefore evaluated informally. The reasoning involved was similar to that from which formal statistical tests are derived. Essentially, if the means (or medians) for two samples differ (e.g., mean A$\leq$2$\cdot$(mean B)) and if there was very little overlap in values observed in each sample, it was concluded that a substantial and significant difference existed between the populations from which the samples had been drawn. The range was used to estimate the variability in each sample, since it facilitated comparisons of sample variability by providing a direct measure of overlap between distributions. Asymmetry within the sample distributions would have made the standard deviation or variance more difficult to interpret.

Photoreceptors. Process-field diameters and base dimensions were measured for R1, R2 and R3 cells, and number of basal filaments was determined for R2 and R3 types. Basal processes of R1 cells were so small and tightly packed that good estimates of their number could not be obtained. Oblique receptors occurred only rarely in each retinal area sampled and were not, therefore, included in the comparisons described.

Table 3 summarizes mean process-field diameters and corresponding ranges for pigeon and blue jay. In pigeon, R1 and R2 dimensions were comparable in foveal and dorso-temporal areas, and, on the basis of mean values, appeared to be somewhat smaller than those of the peripheral retina. An examination of the range values suggested that the increase in the size of process-field dimensions in the peripheral retina were at best marginally significant, as there was considerable overlap in field size between areas. Surprisingly, the mean dimensions of the R3 cells were largest in the foveal region. However, the differences between foveal, dorso-temporal and peripheral values for that cell configuration were small. Range overlap indicated that the differences may simply be a sampling error.

Table 3 indicates that the differences in receptor process dimensions were more substantial in the blue jay. The most striking differences occurred in comparisons of foveal with dorso-temporal and peripheral retina. Mean

dimensions of all cell types were smaller in the foveal areas. Also, there was virtually no overlap in the range of process-field diameters for R1 and R2 cells and very little overlap among R3 cells. Taken together, these values of mean and range indicate a highly significant difference between the foveal and non-foveal areas. Note, in addition, that while pigeon foveal and dorso-temporal retina had similar values and were lower than those of the periphery, in the blue jay, where no area occurs, dorso-temporal values more closely approximate those of the peripheral regions. These general patterns were observed in evaluations of all outer plexiform layer processes investigated.

As shown in Table 4, receptor-base dimensions varied somewhat less with changes in retinal area than did process-field diameters. In pigeon there were no substantial differences as a function of retinal area, while in blue jay, peripheral diameters were clearly larger than those of the fovea. In terms of pedicle base size, dorso-temporal retina appeared to be intermediate between fovea and periphery in the blue jay, particularly with regard to R2 and R3 cells.

The data suggested that changes in receptor base size accounted for only a small portion of field increases associated with R2 and R3 cells from fovea to periphery in the blue jay. Receptor-base dimensions increased by appro-

ximately 3 to 5 μ from fovea to periphery, while mean field dimensions increased by 10 μ or more. Hence, a major portion of the increase in the size of those process fields must be derived from increases in the length of basal processes. As shown in Table 5, there was no corresponding increase in the number of basal processes for R2 and R3 cells in either species. Virtually all of the 3-4 μ increase in field size of R1 cells could be traced to corresponding increases in receptor-base diameter. This was to be expected since, by definition of R1, cell processes are short and compactly organized at the proximal portion of the receptor base.

Horizontal cells. Both horizontal cells and terminals were investigated with respect to field diameters. Cell bodies of H1 and H2 cells were also measured, as were incompletely stained axons emanating from H1 cells and separately stained H1 terminals. Substantial quantitative differences in horizontal cells seen in pigeon and blue jay retinas were associated with equally striking qualitative changes, which will be illustrated with photographs below.

Table 6 summarizes data relating to pigeon and blue jay horizontal-cell process field diameters. Considering first the pigeon data, both H1 "dendritic" and "axonal" fields reach their smallest values in the dorso-temporal retina. Differences between dorso-temporal and foveal H1 "dendritic" fields are not substantial, however. In both areas,

"dendritic" fields were slightly smaller than their peripheral counterparts, particularly with regard to the length of the longest axis. Thus, circular H1 fields observed in foveal and dorso-temporal regions tended to appear more elongated and elliptical as the periphery was approached. Foveal H1 terminals, which were observed in only two pigeon retinas, were similar in size to those of the peripheral region. However, H1 terminals in the dorso-temporal retina were significantly smaller than either foveal or peripheral terminals. As was the case with H1 "dendritic" fields, H2 field dimensions were very similar in both foveal and dorso-termporal regions and enlarged in peripheral areas.

Blue jay H1 and H2 dendritic fields were small and circular in the fovea, and occupied less than one tenth the area of their larger and more elongated counterparts in the dorso-temporal and peripheral retina. Again, lack of overlap in range values implied that these differences were highly significant. In blue jay, cells of the dorso-temporal retina had sizes and shapes intermediate between those of foveal and peripheral cells but clearly approaching the later in dimensions. As was the case with photoreceptor fields, horizontal cell "dendritic" fields covered a considerably wider range of areas in blue jay retinas than they did in pigeon retinas.

As indicated in Table 6, no H1 "axon terminals" were observed in the blue jay foveas examined in this study. In all, seven blue jay foveas were searched exhaustively for H1 terminals, including two retinas which were processed in exactly the same way as the two pigeon retinas in which foveal H1 terminals were found. Several factors must be considered in evaluating this potential species difference.

Not only did blue jay peripheral and dorso-temporal H1 cells and terminals differ significantly in size from their pigeon counterparts, the cells differed qualitatively as well. Blue jay peripheral H1 cells and terminals exhibited more extensive process branching and elaboration, while pigeon dendritic and (particularly) axonal fields were thicker, with fewer fine processes. This difference can be seen by comparing blue jay peripheral H1 cells and terminals, shown in Figure 19 with those of the pigeon previously illustrated in Figure 12B and C.

Retinal thickness in the blue jay fovea and in the pigeon central dorso-temporal retina reduces light transmission through tissue in those areas, making resolution of thin processes difficult. However, clearly impregnated H1 cells were common in blue jay fovea, and closely resembled similar cells found in the pigeon central dorso-temporal retina. H1 terminals of the pigeon central dorso-temporal retina were smaller and more difficult to see than those of

the pigeon fovea or periphery. In two instances, partially obscured processes bearing some resemblance to the H1 terminals of the pigeon dorso-temporal retina were observed in blue jay foveal areas. However, these structures, if H1 terminals, lacked clear definition.

Finally, data as to axonal length was found to have bearing on the issue of possible species differences in foveal H1 cells. Six completely impregnated and connected H1 cells were observed during the routine collection of horizontal cell data. Mean axonal length of those cells was 118 μ, with a range of from 50 to 240 μ. Due to the small number of such connections observed, additional measurements were made of axons emanating from unconnected H1 cells and terminals. Results are summarized in Table 7. Axonal length as measured from both cell bodies and from terminals did not vary significantly as a function of retinal locus in the pigeon. In the blue jay, axons appeared to be considerably shorter in the foveal region. Again, reduced microscopic resolving power in the foveal region make this difference difficult to evaluate. Blue jay foveal axons, and pigeon axons in general, are substantially thinner than blue jay peripheral axons. Hence, the seemingly shorter length may simply reflect the fact that thin axons are more difficult to impregnate completely, or, if impregnated, are more difficult to resolve.

Of particular interest with regard to the apparent absence of H1 terminals from blue jay foveal areas, is the short length of axons there. Taken in conjunction with other data, this is open to three possible interpretations: (1) H1 cell axons in the blue jay fovea show no typical terminal expansions; (2) H1 cells do have terminal expansions, but these lie outside the foveal area; or (3) H1 cells have terminal expansions in the foveal regions, but these were not impregnated or were obscured in each of the seven foveas examined. Until additional evidence, possibly from tissue impregnated with other variations of the Golgi stain or processed for electron microscopy, becomes available, these alternatives cannot be directly evaluated.

General relationships between cell body dimensions, species and retinal location, as shown in Table 8, were similar to those of process field diameters although smaller in magnitude. In pigeon, foveal and dorso-temporal horizontal cell somas were approximately the same size and only slightly smaller than peripheral cell bodies. Blue jay cell bodies of both types again seemed to define a continuum, with foveal cells being smallest, those of dorso-temporal retina intermediate and peripheral cells the largest. Clearly, increases in cell body diameter did not contribute significantly to changes in field diameters across the retina in either species.

Bipolar Cells. Only single and double layer bipolar cells (B1 and B2) were present in sufficient numbers to justify quantitative comparisons across retinal areas. In the peripheral retina, both proximal and distal processes of bipolars were visible for single cells, and measurements of cell body and process dimensions were made in tissue mounted both scleral side up and vitreal side up. Since the agreement between those two sets of data was quite good (less than 10% difference for any cell dimension in any location), data were combined in Tables 9, 10 and 11 presented below. Unfortunately, cell size, retinal thickness and density of impregnated cells made comparable measures of foveal bipolars impossible to obtain. That is, an individual bipolar could not be accurately traced from proximal to distal process. Consequently, measurements of outer plexiform layer (distal) processes were made in tissue mounted scleral side up, while inner plexiform layer (proximal) processes were measured in tissue mounted with the vitreal surface mounted toward the coverslip. It was therefore possible to classify foveal proximal processes as belonging to B1 or B2 cells, but that could not be done for distal processes. An overall mean was calculated for distal processes of cells in the foveal areas of both species.

Table 9 presents dimensions of outer-plexiform-layer processes for pigeon and blue jay bipolar cells. In

pigeon, bipolar cells of the fovea exhibited slightly smaller mean proximal process dimensions than did those of the dorso-temporal retina. While this difference between foveal and dorso-temporal retina did not appear to be significant, the increases in field size from foveal to peripheral retina may approach significance, given the minimal range overlap. In blue jay, differences in outer-plexiform process dimensions were more clearcut. Based on mean and range measures, foveal cells were significantly smaller than those of the dorso-temporal retina or the periphery. As was the case with comparisons of blue jay receptor and horizontal cell fields, dorso-temporal bipolar cells had distal dimensions intermediate between foveal and peripheral bipolar cells, approaching the latter in size. The significance of the small field bipolars will be evaluated further in the context of data relating to the possible existence of a "midget system" in birds.

As shown in Table 10, there were essentially no significant differences in cell body size as a function of either retinal area or species. Small differences in mean values were completely overshadowed by the extensive overlap in ranges across species and areas.

Dimensions of proximal terminations of bipolar cells, the first inner plexiform layer processes to be considered, are summarized in Table 11. In pigeon, B1 and B2 outer (or more scleral) terminations were smallest in

the foveal region, while larger dorso-temporal and peripheral fields were very similar to each other in size. B2 inner (more vitreal) process dimensions, on the other hand, were comparable for foveal and dorso-temporal retina. B2 inner terminations in those two areas were about half the size of those in the more peripheral portions of the retina.

Again, blue jay foveal bipolar cells were quite small. Although there was more overlap between foveal and dorso-temporal or peripheral sizes than found in previous comparisons, differences still appeared to be significant. Dorso-temporal and peripheral cells were, on the average, three to five times as large as foveal cells, in terms of inner-process areal extent.

As the mean values suggest, B2 outer terminations, which occur toward the more scleral side of the inner plexiform layer and possibly on the same level as B1 terminals, were larger than the more vitreal inner terminations. In comparisons of outer with inner proximal dimensions proximal dimensions for individual B2 cells across the entire retina, outer processes were found to be larger 82% of the time in pigeon and 66% of the time in the blue jay.

Amacrine cells. As indicated above, amacrine cells varied widely in size across the retina. The relatively large field diameters, together with the thinness of processes, made observation of the largest cells difficult,

since large cells are more likely to be partially obscured than small cells. Given the irregularity of the A2 and A3 process fields, those cells could not be reliably measured when partially obscured. As a result, process-field values obtained for amacrine cells were not only highly variable, but also severely skewed towards the right, showing a few very high values. Consequently, for purposes of intra- and inter-species comparisons, median values were used to summarize the data, since they were less likely to be affected by the few high values than were means. Note that since the largest cells were less likely to be observed, the medians, although clearly the most representative measure for the samples obtained, probably underestimated the actual population characteristics.

Table 12 summarizes the median field diameters for amacrine cells occurring in the three regions of interest in pigeon and blue jay retinas. In both species, foveal cells were substantially smaller than their more peripheral counterparts. Again, although the details varied somewhat from one cell type to another, the dorso-temporal cells were more similar to peripheral cells in terms of process dimensions. Thus, a given cell type might be larger, in terms of median value, in either the periphery or the dorso-temporal retina, but the variability within each area suggested that the differences between areas were not

significant. Even the largest difference observed (that between the blue jay A1 cells) lost its significance when ranges were considered. The presumably smaller dorso-temporal cells encompassed a wider (and higher) range than did the peripheral cells. Whether A1 cells were actually the largest amacrines was difficult to determine: The perfect symmetry of those monostratified cells permitted the confident measurement of even partially obscured cells.

The monostratified amacrines of blue jay retina differed both qualitatively and quantitatively from those of the pigeon retina. As was the case with horizontal cells, pigeon amacrines were typically thicker than similar cells from the blue jay retina. This difference is illustrated in Figure 20, which shows photographs of A1 cells from blue jay and pigeon retinas. The greater thickness of the pigeon amacrines can probably be attributed to an increase in varicosities along the processes.

Interestingly, approximately half of the A2 cells found in the pigeon fovea had cell bodies displaced to the ganglion cell layer. Whether similar proportions of foveal A1 cells also were displaced was impossible to judge, since cell bodies were often obscured. As was the case with previous cell types, differences between foveal and peripheral cell dimensions were found to be the largest in the blue jay retina, suggesting a more highly differentiated retinal structure in that species.

Cell body dimensions, shown in Table 13, varied only minimally with retinal locus and no substantial between-species variation was observed. As indicated above, some A3 cells were found to have very large cell bodies. Those cells, or some proportion of them, may be displaced ganglion cells.

Ganglion cells. As was the case with amacrine cells, distributions of ganglion-cell dimensions were found to be positively skewed, so medians rather than means were calculated to summarize the data. Note again that the difficulty of obtaining data from partially obscured, large cells, together with the choice of the median, probably served to underestimate the true ganglion cell field sizes.

Table 14 presents dendritic field diameters for pigeon and blue jay ganglion cells. In pigeon, foveal G1 cells were similar in size to those of the dorso-temporal retina, and cells from both of those regions were somewhat smaller than peripheral G1 cells. Very few G2 cells were observed in pigeon foveas, so quantitative data are presented only for dorso-temporal and peripheral G2 cells, which were found to be similar in size. In blue jay retinas, both G1 and G2 cells were significantly smaller in the fovea than in either dorso-temporal or peripheral retina. Cells of dorso-temporal retina were typically smaller than their peripheral counterparts as well. Again, in terms of range of cell dimensions encompassed, the blue jay retina was

found to be more highly differentiated than that of the pigeon.

Cell body diameters (shown in Table 15) varied less than field dimensions in both species. In the pigeon, very little change was observed as a function of retinal area, although in blue jay, foveal cell bodies were smaller than those of the dorso-temporal retina, which were in turn smaller than peripheral cell bodies.

Axonal length for ganglion cells is summarized in Table 16. Clearly, only the initial portions of ganglion cell axons were impregnated using this procedure. Although axonal length varied somewhat from area to area, the variation did not appear to be systematic. Most axons observed were between 20 and 60 μ in length, although axons could sometimes be traced for up to 400 μ. As indicated above, following preliminary classification, a number of cells were assigned to the ganglion cell category on the basis of cell body location, process configuration, and size, despite the fact that no axon was observed. The proportion of ganglion cells showing a clearly differentiated axon varied as a function of location, and possibly as a function of cell size, but was generally between 50 and 60% of the cells.

Summary. The major findings of the quantitative analysis included the following:

(1) Process-fields showed considerably greater variability as a function of species and retinal locus than did other dimensions measured (cell body diameter; axonal length; number of processes).

(2) In the blue jay, field and cell body dimensions varied systematically and significantly as a function of retinal area. Foveal cells were always smaller than dorso-temporal retinal cells, which were, in turn, smaller than peripheral cells. The magnitude of these differences was substantial, as illustrated in Figure 21. Mean areal extent of processes are represented diagramatically there. All cell types which were found in all three retinal areas were included in the figure.

(3) Pigeon field dimensions also varied systematically with retinal area, but two distinct patterns emerged. All cell-process fields terminating in the outer plexiform layer, as well as G1 ganglion cell dendritic fields and B2 inner proximal fields exhibited the following relationship: foveal dimensions were very similar to those of the red field, and both foveal and red field cell dimensions were somewhat smaller than those of the periphery. The exceptions to that rule, the amacrine and bipolar cells (B1 proximal and B2 outer proximal processes) showed a pattern similar to that observed in the blue jay. The latter group of cells were smaller in the foveal region, intermediate in the

dorso-temporal retina and largest in the periphery. The magnitude of the differences observed is illustrated schematically in Figure 22.

(4) Interpretation of differences between pigeon and blue jay retinas, to be discussed fully below, depends on the following observation: Mean and median figures obtained for the dorso-temporal retina of the pigeon may be misleading, in that they treat that area as homogeneous. In fact, the red field includes a localized area dorsalis, known to have ganglion cell densities comparable to those of the fovea (Binggeli and Paule, 1969; Galifret, 1968). Note that in cases where mean values for dorso-temporal retina and fovea are similar, a substantial portion of cells in the red field may be smaller than foveal cells. Informal observations indicated that the peripheral portions of the red field showed the largest cells for that area, so smaller cells were probably confined to the more central portions, including the area dorsalis.

(5) Concerning quantitative intra-retinal variability, the blue jay retina was found to be more highly differentiated than that of the pigeon. In particular, foveal/peripheral differences were enhanced in the blue jay. However, the quantitative analyses of this Golgi-impregnated tissue did indicate that a portion of the pigeon dorso-temporal retina resembled the fovea in terms of many cellular dimensions. This observation confirms suggestions that there

are two specialized areas in the pigeon retina.

(6) Qualitative differences were observed with regard to the structure of the two lateral elements in these retinas. Horizontal cells and amacrine cells were considerably thicker in the pigeon retina. The pigeon's horizontal cells exhibited fewer fine processes than did their blue jay counterparts; while the pigeon's amacrine cells seemed to show a greater number of varicosities along the processes.

The midget system

A bipolar- and ganglion-cell midget system was first described in the primate fovea by Polyak (1941) and later confirmed by Boycott and Dowling (1969). The foveal midget system is believed to be organized in such a way that an individual ganglion cell receives information from only one midget bipolar, which in turn is related to only one foveal photoreceptor. In this way, resolution obtained at the level of the receptor mosaic can presumably be maintained into the central nervous system. According to Polyak (1941) and Boycott and Dowling (1969), midget varieties of bipolar and ganglion cells account for the greatest proportions of those cell types in the foveal area, presumably mediating the fine spatial resolution associated with focal vision.

Currently, there is little evidence bearing upon the possible existence of a "midget system" in birds. Cajal

(1892) found small bipolars in the foveas of birds and lizards. According to Cajal, "The ascendant process (of a small bipolar) reaches the outer plexiform layer where it terminates in a tiny, flattened and quite rudimentary arborization, whose shortness allows it to connect with only one basal swelling of a cone." Although Cajal observed that ganglion cells were smaller in the fovea, he noted that the reduction in size of the dendritic arborization of ganglion cells was not as great as that observed in bipolar dendritic spread. Since Cajal did not provide quantitative information as to the spread of the inner nuclear layer processes in foveal areas, the possible existence of a one-to-one, ganglion-cell-to-bipolar-cell relationship cannot be evaluated from his data.

Both Cajal and Polyak based their descriptions of foveal structure on observations of tissue impregnated by the rapid Golgi and Golgi-Cox methods. The recently developed Colonnier modification of the Golgi-Kopsch procedure (Colonnier, 1964) has proved very successful in impregnating retinal elements in several vertebrate species; for example, Boycott and Dowling (1969) elaborated Polyak's descriptions of midget bipolars and midget ganglion cells in the primate retina. Since the Colonnier method was used to impregnate tissue evaluated in the present study, data obtained here permit a direct quantitative comparison of

avian retinal cells with those of primates, as described by Boycott and Dowling (1969).

The evaluation of a potential midget-bipolar and midget-ganglion cell system was based on several criteria. First, the distinctive morphological configuration of primate midget cells was compared with that of small bipolar and ganglion cells found in the two avian retinas studied here. Secondly, quantitative dimensions of bird and primate cells were contrasted. Finally, cellular relationships were considered. That is, the possibilities that a small bipolar might form synaptic contact with a single photoreceptor and that a small ganglion cell might form synaptic contact with a single "midget" bipolar were assessed.

Fovea: Two varieties of midget bipolar have been observed in the primate retina, the invaginating and flat midget bipolars (Boycott and Dowling, 1969; Kolb et al, 1969). As the names suggest, the flat midget bipolar has a small, flat dendritic expansion, while the invaginating midget bipolar is characterized by small but distinct apical processes at the point of dendritic termination. The small bipolars of the avian fovea resembled the latter variety, as shown in Figure 23.

Midget ganglion cells found in primate retinas usually have dendritic expansions which emanate from a

single central trunk attached to the ganglion cell body, as shown in Figure 24A. Neither G1 nor G2 ganglion cells found in the avian retinas investigated here were similar to the midget ganglion cells observed in primates. As seen in Figure 24B, the smaller of these, G1, usually had three or more branches extending from the cell body and ending in small (1 μ) terminal bulbs. The processes of the small G1 cells observed in the foveal area usually terminated in the inner half of the inner plexiform layer, often at more than one level.

An alternative approach to this question could be to compare the size of potential "midget" bipolars and "midget" ganglion cells with those observed in the primate. Boycott and Dowling (1969) described midget bipolars as having dendritic spreads ranging from 4 to 7 μ (mean = 5 μ), while midget ganglion cells had field diameters of less than 10 μ, more commonly 4-5 μ. As shown in Tables 11 and 12, both blue jay and pigeon foveas contained bipolars with dendritic spreads comparable in absolute size to those described by Boycott and Dowling. Furthermore, pigeon and blue jay cells with distal field diameters of as little as 3 μ were commonly observed. Both blue jay and pigeon ganglion cells exceeded the dimensions found for primate midget ganglion cells: The smallest blue jay ganglion cell had a dendritic field of 10 X 15 μ, while the smallest

pigeon ganglion cell field was 10 μ in diameter.

Unfortunately, a direct comparison of absolute cell dimensions fails to take into account differences in eye size and visual fields of view for the avian and primate species considered. The field diameters observed in the rhesus monkey were corrected for this discrepancy by noting that one visual degree in rhesus monkey subtends an arc of 211 μ in length (Fite and Rosenfield-Wessels, 1975), while one visual degree is equal to approximately 170 μ and 175 μ for blue jay and pigeon, respectively (Table 1). Thus, a bipolar cell with a dendritic spread of about 4 μ would correspond in size to an "average" midget bipolar for the rhesus monkey; and a ganglion cell with a 4 μ field would be comparable to an "average" primate midget ganglion cell. The upper limit of size for midget bipolar and ganglion diameters becomes, respectively, 6 and 8 μ. On the basis of the revised dimensions it again appears that the two species exhibit foveal midget bipolars, but not midget ganglion cells.

Drawings of small ganglion cells and nearby bipolars (illustrated in Figure 25) suggested that the field size of ganglion cells was comparable to that of the larger bipolar axon terminals. Such two dimensional representations were somewhat misleading, however, since G 1 processes sometimes terminated at more than one level in the inner plexiform

layer, and those levels did not always correspond to the termination levels of surrounding bipolars. (See the caption of Figure 25 for examples of the discrepancies found to occur.) As noted above and by Yazulla (1974), bipolar axonal terminations were typically found only at a few discrete levels within the inner plexiform layer.

Arguments based on numerical and pictorial comparisons such as those described above are not particularly compelling. Clearly, the critical aspects of the primate midget system depend not on the absolute diameters or configurations of bipolar and ganglion cell dendritic fields, but rather on the relative diameters of (1) bipolar dendritic fields and receptor synaptic bases; and (2) ganglion cell dendritic fields and bipolar axonal expansions. To be classified as a midget cell a bipolar must have a distal field so small that contact with more than one receptor is unlikely; and a ganglion cell field must be so small that contact with more than one midget bipolar cannot occur. Traditionally, the relationships described have been stated more directly: Midget bipolar dendritic fields must be as small as or smaller than cone pedicle bases, while ganglion cell dendritic fields must be smaller than midget bipolar axonal expansions. Frequently, light microscope photographs showing closely related bipolar axons and ganglion cell dendrites have been provided to buttress assumptions of

nearly exclusive synaptic interaction.

Figure 26 indicates the sizes of bipolar dendritic fields occurring in the blue jay fovea. Frequency of occurrence of various sized fields was plotted. The fields were approximately elliptical in shape. So field size, or areal extent, was determined by the formula $1/4\pi ab$, where a and b were the length and width of the distal field, measured through its midpoint, as described in Figure 3B. Also shown in Figure 26 is the range of base sizes found for R1, R2 and R3 receptor cells from the foveal area. Note first that most bipolars are between 6 and 20 μ^2 or above 35 μ^2 in area (that is, between 3 and 5 μ and above 7 in diameter). A bimodal distribution is consistent with the suggestion that two distinct classes of bipolars exist in the foveal area, as Cajal reported (1892).

Furthermore, a comparison of the size of bipolar fields with the size of receptor synaptic bases and process fields indicated that one-to-one contact between receptors and bipolars could occur. The "one-to-one" contact mediated by the midget system refers to the fact that a midget bipolar may contact only one receptor, but does not require that the contacts of any receptor be limited to a single bipolar. (This point has occasionally been misinterpreted, e.g., Pedler, 1965.) It would appear, then, on the basis of these light microscope observations, that a "midget" bipolar does

exist in the avian convexiclivate fovea. A similar argument can be made for the occurrence of a somewhat larger "midget" bipolar in the shallow pigeon fovea, by comparing the range of receptor-base areas, found in Figure 27 with the distribution of bipolar distal field areas. Note that the dimension of both receptor bases and bipolar distal fields were more variable in the pigeon's fovea than they were in the blue jay fovea.

The next requirement for a "midget system" is actually two-fold, involving a comparison of ganglion-cell field dimensions with those of midget bipolar proximal terminations. In order to argue that a given "midget" ganglion cell receives input from only one bipolar, it must be shown that ganglion fields are as small, or smaller than, bipolar axonal expansions. Figure 28 plots the frequency with which ganglion cell fields of various dimensions were found in the blue jay fovea. Only G1 fields were included in the figure, since they were smaller than G2 fields, and therefore the strongest candidate for "midget" ganglion cells. The distribution was unimodal and positively skewed. As data discussed earlier indicated, even the ganglion cells with the smallest fields were larger than the largest primate midget ganglions.

More significant was the comparison between ganglion cell dendritic spread and the axonal spread of

foveal bipolars. The very smallest ganglion cells correspond in size only to the very largest bipolar axonal expansions. If one assumes that the diffuse G1 cells form synaptic contacts only at the ends of their dendritic processes, it is possible that the smallest of those could contact a single bipolar. Again, a similar situation occurred in the pigeon fovea, where the smallest ganglion cells were approximately the same size, in terms of field dimensions, as the larger bipolar proximal processes. As shown in Figure 29, process fields in the fovea of the pigeon covered a wider range of areas than did those of the blue jay.

While the data summarized above indicated that a very small ganglion cell could receive input from only a single bipolar, the final aspect of the "midget system" remains to be confirmed in the avian retina. The requirement that the bipolar contacted by the small ganglion cell be a midget bipolar must be evaluated. Unfortunately, direct evidence on this point is not available in the present study. As noted above, retinal thickness, density of cells stained and the fineness of bipolar processes in the foveal area made it impossible to trace individual "midget" bipolars from their dendritic to their axonal expansions, and thereby determine the size of the latter structure.

Some indirect evidence, involving a statistical

analysis, does, however, have bearing on this issue. Essentially, the final demonstration of a "midget system" in birds revolves around the question of whether the bipolars with the smallest distal process dimensions ("midgets") also have the largest proximal processes. Given the similarity between proximal and distal bipolar fields found in the rhesus monkey fovea, one must admit that this seems unlikely; however, a more rigorous analysis is necessary.

The small ganglion cells had been found to terminate in the inner (vitreal) portion of the inner plexiform layer, which suggested that they would be most likely to make synaptic contact with either B1 terminals or B2 inner terminals. Since proximal and distal processes of individual bipolars could be observed in the more peripheral portions of the retina, the correlation between proximal and distal process dimensions was determined for those cells. The correlation between B1 distal and proximal process dimensions for the blue jay was found to be 0.49 ($N=33$; $p < .005$, one-tailed); and for B2 dendritic and inner axonal terminations, 0.48 ($N=57$; $p < .001$, one-tailed).

By assuming that comparable correlations obtained for more central, and particularly for foveal, regions, an estimate of the maximum proximal process termination size for blue jay "midget" bipolars was obtained. Referring to Figure 26, it was found that the largest "midget"

bipolar probably had a dendritic diameter of about 5 μ, or an areal extent of 20 μ^2. A regression analysis, based on the correlation coefficients obtained above, indicated that a B1 bipolar with a distal field or 20 μ^2 would be expected to have a proximal expansion of greater than 66 μ^2 less than 0.1% of the time. A comparably sized B2 cell would have a vitreal axonal termination of more than 55 μ^2 less than 0.1% of the time. The smallest ganglion cell field observed in the blue jay retina was 117 μ^2 in area, or approximately twice those values. This statistical analysis strongly suggests that even the smallest foveal ganglion cells form synaptic contacts with more than one bipolar cell, and cannot, therefore be classified as "midget" ganglion cells according to the criteria established by Polyak (1941).

As would be expected from the greater variability observed with respect to the dimensions of pigeon foveal cells, the statistical analysis was somewhat less conclusive in that species. Correlations between the size of B1 distal and proximal process fields and between the size of B2 distal and inner proximal fields were, respectively, 0.55 (n=14; $p < .025$, one-tailed) and 0.56 (N=21; $p < .005$, one tailed). From Figure 27 it was determined that the large "midget" bipolars would have an area of approximately 32 μ^2. A regression analysis indicated that B1 cells would have

proximal fields with areas greater than 87 μ^2 less than 5% of the time. B2 cells would be expected to have inner fields greater than 45 μ^2 less than 0.1% of the time. The two smallest ganglion cells observed in the pigeon fovea had areas of 75 μ^2 and 107 μ^2. On the basis of the statistical analysis, it appears extremely unlikely that such a ganglion cell could make exclusive synaptic contact with a "midget" B2 cell. One cannot, however, rule out that possibility that contact could be made with a single B1 "midget" bipolar, although that would also be a fairly unusual occurrence, given small proportions of "midget" bipolars expected to have such large distal fields and the infrequency with which ganglion cell fields of less than 100 μ^2 were observed.

In summary, comparisons of the primate midget system with avian foveal structures impregnated by the Colonnier procedure produced the following observations: First, small bipolars, comparable in absolute and relative size and configuration to primate midget bipolars were observed in both species. The relationship between the size of the distal field of the small bipolars and that of the receptor bases supported the hypothesis that a single small bipolar would typically contact only one receptor. The small bipolars were therefore believed to be "midget" bipolars, as defined by Polyak (1941). Secondly, small

field G1 ganglion cells were observed in the avian fovea, but were considerably less numerous than primate midget ganglion cells. The smallest avian ganglion cells were found to have several processes emanating into the inner plexiform layer, and were larger in both absolute and relative size than the primate midget ganglion cells. The field of the smallest ganglion cells corresponded in size to those of the largest bipolar proximal terminations. However, a statistical analysis indicated that midget bipolar fields found in the blue jay would be expected to have axonal fields about half as large as those of the smallest ganglion cells. These data suggested the conclusion that the prerequisites for a "midget" ganglion cell had not been met by the small ganglion cells observed in the fovea of the blue jay. A very small ganglion cell might possibly contact a single, large "midget" bipolar in the pigeon fovea. On the basis of the evidence obtained in this investigation, it is unlikely that the two birds studied have midget systems comparable to that found in primates, although it is marginally possible that the pigeon might have a very small number of ganglion cells which form one-to-one synaptic contacts with midget bipolars.

Red field. The work of Binggeli and Paule (1969), Galifret (1968), and Yazulla (1974), as well as the quantitative results reported above, suggested that the central

portions of the pigeon red field might have an organization similar to that observed in the fovea. Consequently, the possibility that a "midget system" might be present in that area was investigated.

According to the definition of midget bipolars (distal fields as small or smaller than receptor bases), central red field cells with dimensions of less than 6X6 μ or 5X7 μ (areal extents of approximately 28 μ^2) were considered to be "midget" bipolars. As seen from Table 3, R1 and R2 receptor pedicle bases were contained within that range, as had been the case for foveal midget bipolars. In the red field, it was possible to trace such cells to their proximal terminals. Mean dimensions of red field "midget bipolar" cells are presented in Table 24. Referring to the range of ganglion cell fields found in the red field (Table 20), it is apparent that at least some ganglion cells in that region had smaller fields than the midget bipolar axonal expansions, meeting the criteria for midget ganglion cells. Thus, using relational criteria and direct comparisons, small bipolar cells and ganglion cells were found which could provide the potential basis for a "midget system" in the central red field of the pigeon. Confirmation of this observation depends on the demonstration that the "midget" ganglion cells do, in fact, make synaptic contact with only one "midget" bipolar, and that the "midget" bipolars, in

turn, make synaptic contact with only one receptor pedicle. An electron microscopic analysis of Golgi-impregnated retinal tissue would further clarify this matter.

DISCUSSION

The quantitative morphology of two avian retinas has been described in detail. While strictly anatomical comparisons of the retinas of the blue jay and pigeon with each other and with those of other vertebrates are possible, a more productive and interesting approach would emphasize the similarities and differences which are likely to be of functional significance. On the whole, the retinas studied here show a strong resemblance to those of other vertebrates which have been studied. The differences which do exist are primarily quantitative rather than qualitative in nature: i.e., cell type X found in birds may be larger or smaller, with fewer or more branches or vericosities than its apparent homologue,[3] cell type X', in another vertebrate class. As the discussion below will indicate, the most profound differences between species undoubtedly exist at the level of synaptic interaction.

In many cases, describing a given cell type occurring in several species as representing a continuum with respect to its morphology may be more accurate than assigning the cells of different species to discrete

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[3] Cells which are anatomically similar in all five vertebrate classes may be homologous (that is, derived from the same ancestral unit). However, structural similarity alone is not sufficient to demonstrate homology.

classes.[4] However, although most vertebrate species studied exhibit an increase in average cell dimensions from the central to the peripheral retina, there is a suggestion in the present data that the structure and function of avian foveas may differ qualitatively from that of primates. Information as to the functional significance of specific neuroanatomical features will ultimately be derived from electrophysiological studies which determine the response properties of the cells in question. Species for which extensive anatomical and electrophysiological data are available will be the focus of interspecies comparisons in the discussion which follows. Where intracellular recordings are available in birds, they will be discussed with respect to quantitative information obtained.

By far the most important and provocative anatomical observations are those which can be related to larger bodies of information. Although many authors have studied various aspects of retinal circuitry using light and electron microscope techniques, information concerning some cell types is still fragmentary. Ganglion cells have been most widely studied, but a growing body of information pertaining to receptor and horizontal cell ultrastructure

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[4] Differences in qualitative, rather than quantitative, aspects should provide the basis for establishing structures which occur in different species as distinct cell types.

and electrophysiology is becoming available as detailed below. Bipolar and amacrine cells have been more difficult to evaluate with intracellular recording, although information about their synaptic relations in the inner plexiform layer has been obtained.

Limitations of the Golgi Techniques

Since all of the data described here were derived from tissue impregnated using a modification of the Golgi technique, an evaluation of the problems associated with the technique which might potentially influence conclusions is in order. The Golgi techniques, encompassing many variations, are reputed to completely impregnate between 1 and 5% of all cells in successfully processed tissue (Scheibel and Scheibel, 1970). In the field of vision, the power of the technique was most fully exploited by Cajal (1892) in his comparative studies of the vertebrate retina, and by Polyak (1941) who described cellular morphology in the retinas of primates. More recently, Stell (1965) has developed a Golgi technique suitable for electron microscopic analysis, and Kolb (1970) has adapted the Colonnier procedure for use with retinal tissue. Thus, direct assessment of synaptic relations has become possible, and the need for exhaustive serial reconstructions has been reduced. In conjunction with electrophysiological and behavioral analyses, the anatomical data provided by the light and electron

microscope studies of Golgi-impregnated tissue has provided a tremendous increase in our understanding of the functional organization of the vertebrate retina.

The data analysis presented above indicated several limitations of the Golgi method, however. First, it is commonly assumed that stained cells are "completely impregnated," yet, in several instances that did not occur. H1 axons were not always completely stained, nor were ganglion cell axons. Whether these failures to obtain complete impregnation are the fault of the staining procedure itself, or simply represent the effects of handling the tissue, which might break fine axons, cannot be determined. However, as noted above, such observations necessarily make many classifications tentative (e.g. some displaced ganglion cells may have been erroneously classified as amacrine cells; some G1 cells may be partially impregnated G2 cells; H2 cells are believed to be axonless).

A second, more difficult, aspect of the incomplete-impregnation problem relates to the staining of very fine processes. Often only varicosities along the process are visible with the light microscope. However, isolation and configuration of the varicosities provided convincing evidence that the small bulbs were in fact connected, as similar connections were visible for larger cells. Particularly in the case of small cells with very fine processes (e.g. midget

bipolars and small or "midget" ganglion cells), it was impossible to be sure that (1) all processes were impregnated and that (2) all impregnated processes were visible. Thus, for the smallest cells, measurements may underestimate the true field dimensions.

The probability that a given cell would be observed and included in the sample evaluated was not simply determined by whether or not the cell was well impregnated. Small units of any variety were more likely to be well-isolated than larger cells, possibly producing underestimations with respect to quantitative dimensions. Magnification used in scanning for a particular cell type (X400 or X1000) could bias the data toward large or small examples of a given cell type. Distinctive, and particularly symmetrical, cells (such as A1) could be traced reliably even when partially obscured. Hence, larger cells of those varieties may have been included in the quantitative analyses when large, asymmetrical cells were not.

Furthermore, the assumption that the Golgi techniques stain a fixed proportion of cells has not been demonstrated in retinal tissue. Pasternak and Woolsey (1975) found that the percentage of cortical cells stained with the Golgi-Cox procedure varied from 0.73 to 2.26% from specimen to specimen, and Valverde (1970) reported that the rapid Golgi procedure impregnates about 10% of the cells.

The demonstration that staining is random requires that one know what cells are present. Unfortunately, in most cases that is exactly what authors hope to determine with the Golgi technique. A case in point involves the observation of H1 axon terminals in the fovea of the pigeon. No terminals were observed in the first retinas examined, but in a final pair of retinas used as a check for data obtained earlier, H1 terminals were found in the foveal areas. Does one conclude that the last retinas were aberrant, or that H1 terminals were present in other foveas but did not stain?

Some authors (e.g. Boycott and Wassle, 1974) have used silver impregnated tissue as a basis for determining distributions of retinal ganglion cells. However, in the absence of evidence that the silver stains randomly impregnate cells, and given the difficulties associated with obtaining a truly unbiased sample of completely impregnated, well-isolated cells, the validity of such procedures must be questioned. A more persuasive approach would attempt to describe cells quantitatively with regard to some characteristic, such as size of cell body. If different cell groups were found to differ significantly along this dimension, cell counts and distributions could be determined in other tissue. As can be seen from the data analysis presented above, although large differences are seen in average field

diameters among different cell subclasses, cell bodies are usually similar in size from one subclass to another.

Regardless of the end point chosen by any investigator, the possibility cannot be eliminated that a cell type may be overlooked due to the vagaries of the Golgi stain. For example, the interplexiform cell was first observed by using fluorescence techniques and only later demonstrated in Golgi-impregnated material (Dowling, 1976). As noted above, Gallego et al (1975), found only one variety of horizontal cell in avian retinas, although both Mariani (personal communication) and I found two. One common procedure which has been used to reduce the possibility of missing a cell type involves using several different Golgi procedures to impregnate different specimens. That approach has several drawbacks, particularly for quantitative studies. "New" cell types may be discovered which are simply artifacts of the different procedures. Furthermore, Boycott and Wassle (1974) report that different procedures may differentially distort the size of cell bodies and process fields; often as much as 30% difference in dimensions was observed with different Golgi procedures.

In sum, the Golgi technique is a powerful tool for describing structural morphology and, if used in conjunction with the electron microscope, is capable of determining synaptic relationships. Yet the vagaries of

the method and its unknown chemical foundations combine to bias or make premature any strong conclusions as to quantitative relationships. Following a conservative approach, the present study has therefore sought to emphasize those aspects of the data which were least likely to be substantially effected by these considerations.

Interspecies Comparisons

Cellular Morphology

Receptors. On the basis of outer segment configuration, the photoreceptors of pigeons and blue jays can be classified as cones, rods and double cones. With regard to gross morphology, then, the photoreceptors observed in blue jays and pigeons were similar to those of other birds, differing primarily with respect to thickness and length of outer segment. The outer segments seen here were shorter and thicker then those described by Walls (1942) for birds, but this difference could be an artifact of the Golgi procedure, which may produce precipitates along cell membranes (Ramon-Moliner, 1970), or of dark adaptation, which can change cellular configurations (Walls, 1942). Alternately, the inconsistency could be the result of true species differences, as Walls (1942) illustrated cones from sparrow and marsh hawk. Basically, the photoreceptor cells were similar to those described by Cohen (1963), Morris and Shorey (1967) and Gallego et al (1975) in electron microscope studies of other avian retinas.

Each type of receptor base observed exhibited extensive lateral processes, although the spread of such processes was smaller in the central areas. Furthermore, some processes extended toward the inner plexiform layer, suggesting the possibility of contact with horizontal and

bipolar cells there. Cajal (1892) reported basilar processes in amphibians, reptiles and birds, and recent investigators have confirmed his observations (e.g. Pedler, 1965; Morris and Shorey, 1967). In mammals, cones show lateral processes, but rods are found to terminate in small spherules which exhibit no lateral processes (e.g. Cajal, 1892; Boycott and Dowling, 1969). Although four receptor-base structures were observed in the pigeon and blue jay, they were not reliably related to any given outer segment configuration. Authors such as Morris and Shorey (1967), Cohen (1963) and Pedler (1965) have also found rod and cone outer segments to be associated with similar base configurations in their electron microscope analyses of avian photoreceptors. Observation such as these have led to serious questioning of the concept of the duplex retina.

Schultz (1866) first proposed the concept of a duplex retina, composed of rods and cones. Subsequent authors have found numerous bases on which to group receptors dichotomously, including threshold and spectral sensitivity; pedicle base structure; outer segment configuration, photopigment and so forth. Recently, increasing concern has been expressed that these dichotomous catagories do not correlate perfectly with one another (e.g. Pedler, 1965a; 1965b; Underwood, 1968; Young, 1971). While some authors have suggested alternative classification schemes

to replace the traditional rod/cone concepts (Pedler, 1965a, 1965b; Underwood, 1968), others perfer retention and redefinition of the rod/cone concept (Young, 1971). The latter approach misses the point of the Pedler and Underwood critiques. Pedler and Underwood would probably agree that receptors fall into distinct classes on the basis of some characteristics (e.g. sensitivity or outer segment renewal capacity); they argue, however, that one cannot assume perfect correlations among the groups thus established. As Young (1971) himself notes, foveal cone outer segments look like rods, but regenerate like cones.

Essentially, both Pedler (1965) and Underwood (1968) expanded the receptor-cell classification scheme to include additional morphological dimensions beyond that of outer segment structure. Hence, Pedler (1965) spoke of sensitive (rod) single and multi-channel cells and insensitive (cone) multichannel cells, thereby adding the property of synaptic connectivity. Underwood (1968) further elaborated the scheme to include large and small single, double and twin cones. Clearly, this proliferation of "cell types" could get out of hand -- inclusion of various organelles (oil droplets, paraboloids), regenerative capacity, lamellar configuration and photopigment characteristics produces an intimidating array of "photoreceptors." It is little wonder that authors such as Boycott and Dowling

(1969) have been reluctant to replace traditional rod and cone terminology, which seems to hold well for many mammalian species, with the more precise yet unwieldy systems presented by Underwood (1968) and Pedler (1965).

Although the impetus for reevaluating the rod/cone dichotomy has come from comparative anatomists, ultimately even authors who study only a single mammalian species must recognize that the current rod/cone classification scheme requires revision. However, perhaps reorganization, while necessary, is premature at this time. Available alternatives to the rod/cone scheme are complicated, emphasizing structural, rather than functional aspects of the cells in question. Functions of outer segment shape and organelles, the significance of regenerative capacity and the role of complex synaptic interconnections are poorly understood at present and must be regarded as speculative.

Analyses such as those of Carey (1975) are suggestive in this context. In studying photoreceptors in several species of anurans, Carey (1975) found that the distributions of single and double cones and red and green rods did not vary consistently with retinal locus across species. When Carey reanalysed his data in terms of photopigment instead of outer segment configuration, a consistent pattern emerged. For example, in both bufonid

and ranid species, cells with 575 nm photopigment increased as the area centralis was approached. In bufonid species this was accomplished by an increase in double cones, while in ranid species, single cones increased. Interestingly, in Leeper's studies concerning receptor input to turtle horizontal cells, photopigment rather than morphological structure determined synaptic relations also (Leeper, personal communication). For example, the chief member of the double cone (620nm) and large single cones (620 nm) were presynaptic to one horizontal structure, while accessory members (520 nm) and smaller single cones (450 and 520 nm) were presynaptic to other horizontal cells. Thus, the spectral sensitivity of individual photoreceptors appears to be an important determinant of their retinal distribution and synpatic relations. To the extent that other functionally important "common denominators" are shown to be relevant in a variety of situations, a set of dimension useful for classifying photoreceptors could be evolved.

As was evident in the literature survey presented in the introduction to this paper, the concept of the duplex retina has been a pervasive and powerful force in the analysis of other aspects of retinal structure. Early authors observed "rod" and "cone" horizontal cells and bipolar cells, and speculated as to separate rod and cone pathways through the retina (e.g. Cajal, 1892; Polyak, 1941). Although more

detailed electron microscopic and electrophysiological observations have confirmed these ideas in some species (Stell and Lightfoot, 1975; Kolb and Famiglietti, 1974), more complex patterns of synaptic interactions are observed in other species (Stell and Witkovsky, 1973; Nelson, 1975; Leeper, personal communication). In the discussion of cellular relationships which follows, it becomes apparent that attempts to force-fit all photoreceptors into two mutually exclusive and internally consistent classes seriously distorts the picture of retinal organization which has begun to emerge.

Horizontal cells. Two distinctive types of horizontal cells were observed in both blue jay and pigeon retinas. One cell was found to exhibit an axon with an extensive terminal arborization, while the other, larger cell type was apparently axonless. Both cell types were present in all retinal areas, although the axon-less H2 type was less numerous in both species. Cajal (1892) also reported two types of horizontal cells in the retina of birds. He identified the H1 cell and illustrated instances in which it was connected with an axonal arborization. His second type horizontal cell does not seem to correspond to the H2 cell described here; it exhibits an axon and resembles the unattached H1 axon terminal. Since independent unattached H1 terminals were frequently stained in the material investigated here, it

seems possible that Cajal mistook the axonal terminal for a separate cell type. Gallego et al (1975) have advanced a similar interpretation of Cajal's second horizontal cell.

In their brief report of avian horizontal cells, Gallego et al (1975) found only one type of horizontal cell, corresponding to the H1 cell described here. As noted above, H2 cells were observed less frequently than H1 cells and, because of their larger size, instances of perfect isolation were rare. However, systematic and extensive examination of several retinas from each species, supplemented by drawings and photographs, provided convincing evidence that this cell was, indeed, a separate type of horizontal cell. H2 cells not only lacked an axon, they were also morphologically distinct from nearby H1 cells in each retinal area. In an independent investigation, Mariani (personal communication) has also reported two types of horizontal cell in the pigeon retina.

Most vertebrate species studied to date exhibit both axoned and axonless horizontal cells. A number of subvarieties within those two classes have been reported in fish (Stell and Witkovsky, 1973b; Stell and Lightfoot, 1975; Stell, 1975), although turtles, cats and rabbits appear to have just two morphologically distinct types of horizontal cells, those with and without axons (Dowling et al, 1966;

Gallego, 1965, 1971; Fisher and Boycott, 1974; Leeper, personal communication). The anatomical appearance of the two varieties of horizontal cells found in reptiles and mammals suggests that the cells are homologous to those found in birds, although H1 cells vary with regard to the extent of terminal arborizations. Polyak (1941; 1957) reported only one type of horizontal cell in primates. Later, Boycott and Dowling (1969) reported that two varieties of horizontal cell, each with an axon, could be distinguished in the Rhesus monkey retina. However, studies by Kolb (1970) and Boycott and Kolb (1973) have indicated that horizontal cells in the Rhesus monkey fall into a single class. The cells vary continuously in appearance and size as a function of retinal excentricity, but synaptic contacts appear to be similar for all horizontal cells. Ogden (1974) has also found only one type of horizontal cell in the retina of the owl monkey.

While light microscope analyses such as those presented here indicate that the structure of horizontal cells is similar for many vertebrate species, more detailed information concerning synaptic relations and electrophysiological response properties is necessary to confirm that suggestion. With the development of Golgi techniques suitable for electron microscopic examination (Stell, 1965; Kolb, 1970) and dye-injection methods for identifying cells following

intracellular recording (Kaneko, 1970), such data has begun to accumulate. As yet, electron microscopists and electrophysiologists have not investigated avian retinas, but anatomical and electrophysiological information is available for turtles and cats whose retinal cells resemble those of birds in many respects.

Intracellular recordings from horizontal cells in fish, turtles and cats indicate that those cells are the point of origin for slow (S) potentials (e.g. Kaneko, 1970; Lasansky, Niemeyer and Gouras, 1973). Some horizontal cells hyperpolarize to all wavelengths and are called luminosity (L) cells, while the polarity of the response of other cells depends on wavelength (chromaticity, or C, cells). Some authors have further distinguished subvarieties of C- and L- cells (Tomita, 1965; Norton, 1968; Simon, 1974; Saito et al, 1974; Fuortes and Simon, 1974; Yazulla, 1976).

Both electrophysiological and anatomical data suggest that the variety of L-cell which corresponds to the H1 cell body receives most of its input from cones (Nelson et al, 1975; Yazulla, 1976; Leeper, personal communication). Electron microscopic analyses indicate that the H1 terminal is postsynaptic primarily to rods in both turtles and cats (Leeper, personal communication; Kolb, 1974). The axon terminals also respond consistently to any wavelength of light, and therefore have been classified as L-type horizontal structures (Saito et al, 1974; Nelson et al,

1974; Leeper, personal communication). In turtle, the axonless horizontal cells have been identified as the site of C-potentials by correlating Saito's data with Leeper's anatomical studies (personal communication). Using anatomical methods, Leeper found the C-type horizontal cells to be postynaptic to blue (450 nm) and green (520 nm) single cones, which is consistent with Yazulla's observation that blue and green cones mediate the chromaticity systems in turtles (Yazulla, 1976).

Data from studies of fish and turtle retinas, in which spectral sensitivity of photoreceptors can be determined from morphological characteristics, indicate that cone inputs to H1 and H2 cell homologues differ. Furthermore, anatomical evidence suggests that additional interconnections between horizontal cells exist in the outer plexiform layer. While the fine detail of pre- and postsynaptic connections to horizontal cells varies somewhat with species, the function and gross structure of these cells seem to be similar among the vertebrate classes studied to date. More recently evolved species (e.g. mammals) show more clearly defined cell bodies and more extensive dendritic and axonal ramifications, however.

Bipolar cells. Bipolar cells observed in the present study were classified on the basis of axonal termination pattern in the inner plexiform layer. Early authors

classified cells according to depth of dendrites within the outer plexiform layer, a variable which was thought to have functional significance. That is, bipolars with "deep" dendritic fields, extending sclerally into the outer rows of the receptor bases were thought by Cajal (1892) to be "rod" bipolars, while shallower bipolars were thought to be "cone" bipolars. Obviously, establishing a correspondence between the bipolars described here and those described by other authors is difficult for that reason.

As described above, many of the early classification schemes evolved at a time when the concept of the duplex retina was widely accepted. The speculations of Cajal (1892) and Polyak (1941) as to the synaptic inputs to bipolar cells was undoubtly influenced by their conviction that maximal utilization of the diverse information available from rods and cones would require separate retinal pathways. The techniques available to those authors did not permit the direct examination of synaptic relationships existing within the retinas of the species they studied.

As Gallego et al, (1975) have pointed out, the electron microscope is necessary tool for the reliable identification of photoreceptor types in Golgi impregnated retinas, and for the determination of the location of their synaptic bases within the outer plexiform layer. Although those authors did report that different receptors ended in

different strata for diurnal birds, complete segregation of rod and cone inputs was not observed, as double cones and rods were found to terminate in the most scleral rows. In nocturnal species, all photoreceptors terminated in a single layer. Other authors (e.g. Morris and Shorey, 1967) have found two layers of photoreceptor bases in diurnal birds, which differed from the three layers reported by Gallego et al (1975). The retinal locus from which samples were obtained could affect these observations since the peripheral retina is thought to have more rods than the central retina, however, that type of information has not been specified by most authors. Whether the layering patterns of receptor cell bases varies systematically as a function of retinal locus has not been determined.

Photoreceptor outer segments are rarely completely impregnated using Golgi procedures (Pedler, 1965). By dark-adapting subjects, some completely stained receptors were obtained in flatmount tissue in the present study. However, given the similarities in receptor base configuration found for rods, cones and double cones in this study, I was unable to establish a convincing dichotomy between possible "rod" and "cone" bases in transverse sections. Hence, while stratification of pedicles was observed, establishing which photoreceptors terminated in which layers was impossible. It therefore seemed inappropriate to attempt

to classify bipolars as "rod" or "cone" bipolars on the basis of small differences in depth of dendritic field.

The morphology of bipolar cells has not been as widely studied as has that of other retinal cells, perhaps because of the presumed dichotomy between rod and cone bipolars mentioned above. In recent schemes, the number of bipolar cell categories has proliferated as authors include level of termination, number of axonal terminations, depth of cell body and dendritic field and width of dendritic field as defining characteristics. Most of these distinctions seem to be somewhat arbitrary, since the dimensions involved define continua rather than discrete classes. The possible functional significance of these criteria has not been specified.

In the inner plexiform layer, avian bipolars were found to terminate in several discrete strata, as observed by Yazulla (1974). My observations, together with his, suggest that avian "bipolar axons" shown by Shen et al (1956) and Hazlett et al (1975) may be examples of incompletely impregnated cells, since cells showing no terminal arborization were found to terminate randomly within the inner plexiform layer. Extensive layering within the inner plexiform layer is characteristic not only of birds, but also of many other nonmammalian species (Cajal, 1892; Polyak, 1941, 1957; Boycott and Dowling, 1969; Dubin, 1970).

Electron microscope examinations of bipolar cells suggest that quantitative differences in cellular dimensions observed with the light microscope do not imply qualitatively different cells. An examination of Rhesus monkey retinas by Boycott and Dowling (1966) led those authors to conclude that all bipolar cells exhibit a distinctive ribbon within their synaptic terminals. In another study, Boycott and Kolb (1973) distinguished only three types of bipolars in cats on the basis of photoreceptor input. Flat and invaginating cone bipolars could not be reliably discriminated using a light microscope, as each class assumed a wide and overlapping range of forms. Stell has investigated bipolar connections in fish and finds that small bipolars receive input from cones, while larger "rod" bipolars receive both rod and cone inputs. Most horizontal cells are known to make synaptic contacts with a spectrally restricted set of photoreceptors (see page 111f.). Whether a similar situation obtains in terms of bipolar connections has yet to be determined using anatomical methods.

Intracellular recording from bipolars does indicate that some cells respond differentially to changes in wavelength. Early electrophysiological studies found bipolar receptive fields to be concentrically organized, with antagonistic centers and surrounds, which responded similarly to different wavelengths (Werblin and Dowling,

1969; Kaneko, 1970; Schwartz, 1974). Recently, authors have reported spectrally sensitive bipolar cells in fish (Kaneko, 1973), mudpuppy (Fain, 1975) and turtle (Yazulla, 1976). In this respect, the two known classes of bipolars resemble the luminosity and chromaticity horizontal cells, leading some authors to speculate that horizontal cells may mediate the surround characteristics of the bipolar cells receptive field (Fuortes et al, 1973; Fuortes and Simon, 1974; Sjostrand, 1976). Again, attempts to correlate electrophysiological response characteristics to gross morphological features have not been successful as yet, possibly due to the scarcity of data bearing upon bipolar cell structure and function.

Amacrine cells. Several varieties of monostratified amacrines were observed in pigeons and blue jays, as were multistratified and diffuse cells. The multistratified and diffuse cells were relatively rare in both species, being all but absent from the foveal area, where displaced amacrine cells were more common. My observations confirm the suggestions of Binggeli and Paule (1969) that displaced amacrine cells and glial cells may comprise a significant proportion of the cell bodies found in the ganglion cell layer. In his study of avian amacrines, Cajal (1892) further divided cells according to their level of termination within the inner plexiform layer, as did Yazulla (1974). My observations

also indicate that monostratified amacrines may show a specified layer pattern, but dendritic depth is difficult to evaluate in flatmounted tissue, and precise estimates of dimensions cannot be obtained from transverse sections.

The amacrine cells presented the greatest variety of morphologically distinct subcategories, and are among the most difficult retinal cells to classify. Monostratified and diffuse varieties have been observed in all vertebrates studied, but the distinctive A1 configuration and multistratified cells have not been found in mammalian species (Cajal, 1892; Polyak, 1941, 1957; Boycott and Dowling, 1969). Amacrine cells are among the largest cells found in the avian retina, sometimes having diameters of up to 1.5 mm. (The retina of these species is approximately 23-25 mm in length.) These cells exhibit numerous varicosities along their processes, which some authors feel may be sites for synaptic interaction (e.g. Stell and Lightfoot, 1975).

Dowling and his colleagues have emphasized the importance of amacrine cells in determining ganglion cell receptive field characteristics in vertebrates (Dowling, 1968, 1970; Dubin, 1970). Dowling and Boycott (1966) found amacrine cells in primates to be presynaptic in what they termed "conventional" synapses (see Kidd, 1962). In this respect, amacrine cells differed from bipolar cells, which

exhibited ribbon synapses within the inner plexiform layer.

Amacrine cells have only rarely been the target of intracellular recordings. In amphibians, amacrine cells were found to respond best to transient stimuli, although in fish, responses to both sustained and transient stimuli were observed (Werblin and Dowling, 1969; Kaneko, 1970). The amacrine response takes the form of a low amplitude, long duration spike, making the amacrine the most distal retinal cell to exhibit spiking activity. As would be predicted from their large size, amacrine cells have been found to have large receptive fields (Kaneko, 1970). Efforts to determine the precise effect of amacrine cells on ganglion and bipolar cells has been hindered by the difficulty in isolating their inputs from those of other retinal cells.

In extra-cellular recordings, Burkhardt (1970) identified amacrine cells as the site of the proximal negative response (PNR, a component of the electroretinogram) in frogs, but Holden, was unable to unequivocally confirm that finding in pigeon (1972). Holden found the receptive fields for the PNR to be approximately 3-4° in diameter, which is comparable to the size of some of the larger mono-stratified amacrine cells. However, the observation of large field displaced ganglion cells within the inner nuclear layer makes precise identification of the source of the PNR even more difficult, since its origin is

determined primarily by the depth of penetration of the recording electrode.

Ganglion cells. The ganglion cells observed in these avian species comprised three groups, deep (G1), stratified (G2) and displaced ganglion cells. Cajal (1892) found monostratified and multistratified cells in the avian retinas he investigated, as well as displaced ganglion cells. Cajal did not describe diffuse ganglion cells, however, although diffuse ganglions were found in all other vertebrate classes by him, and in primates by Polyak (1941) and Boycott and Dowling (1969). The G1 cell could be a diffuse ganglion cell, although its processes are usually fewer in number than those of the diffuse ganglion cells in other species. As noted above, the cell's structure suggests that it may instead be a partially impregnated mono- or multi-stratified cell. Both stratified and displaced ganglion cells have been found in all vertebrate classes (e.g. Cajal, 1892; Polyak, 1941, 1957; West and Dowling, 1972; Stell and Witkovsky, 1973; Boycott and Wassle, 1974; Bunt, 1976).

Ganglion cell receptive fields differ in size as a function of retinal locus, and in complexity as a function of both locus and species. Naturally, many authors have speculated that this variability in response characteristics may correspond to differences in cellular morphology. Shkolnic-Yarros (1971) suggested that ganglion cell

asymmetry might determine directional selectivity, for example. More ambitious efforts have attempted to establish a precise correlation between morphologically and electrophysiologically distinct cell classes (e.g. Lettvin et al, 1961; Boycott and Wassle, 1974; Kalinina, 1976). However, none of these analyses is without problems, since they require assumptions concerning both staining procedures and the general relationship between dendritic and receptive field size. Usually, it is assumed that cells are stained randomly and that the smallest receptive fields should be associated with those cells which have the smallest dendritic spreads. (Brown and Major, 1966; Kalinina, 1976). Thus, Kalinina (1976), who studied frog ganglion cells, argued that the smallest cells were probably convex edge detectors, which respond to small moving objects, since those cells have very small receptive fields (Lettvin et al, 1959; Maturana et al, 1960).

In cats, Boycott and Wassle (1974) suggested that their α, β, and γ cells corresponded to Y, X and W units, respectively. Both X and Y units have concentrically organized receptive fields, but X cells are insensitive and Y cells are sensitive to changes in lunimance pattern. W units have more complex receptive field characteristics and slower conduction times (Enroth-Cugell, and Robson, 1966; Stone and Hoffman, 1972). Later, however, Cleland and

Levick (1974) described a new dimension for cat ganglion cells (brisk vs sluggish responses) and argued, on the basis of conduction velocity, receptive field size and variance with retinal eccentricity, that β cells might be their "brisk-sustained" cells, while α cells were the "brisk-transient" units. Presumably the more variable γ cells corresponded to the "sluggish" cells. Thus, two alternative schemes have emerged. Interestingly, Boycott and Wassle found three morphological types of cat ganglion cells at a time when many authors believed that three major classes of ganglion cell receptive fields were present in cats. With the addition of the "brisk/sluggish" dimension to the "sustained/transient" and "on-center/off-center" dichotomies, at least eight categories of ganglion cell receptive fields can now be distinguished in the cat.

Attempts to correlate anatomical with electrophysiological features serve to underscore the limitations inherent in each methodology. As discussed above (see: "Limitations of Golgi Techniques") currently available anatomical methods may yield partially impregnated cells, and cannot provide information as to the distribution of various cell types. Further, classification of cells is an incredibly difficult and subjective task, for which there seem to be no "right" answers. Nor are electrophysiological procedures without potential sources of bias.

Various laboratories use different procedures for determining receptive field sizes and characteristics (see, for example, Rodieck, 1973, for a discussion of this point). In many cases, cells can be "held" for only a short period of time, so the number of characteristics which can be evaluated is limited. Also, larger cells are more likely to be sampled than small cells.

These problems have led many authors to conclude that anatomical features which determine intracellular response characteristics exist at the synaptic level. Certainly, in a functional analysis, synaptic similarities or differences are more important than gross morphological features. However, some anatomical features observed with the light microscope may suggest synaptic inputs. For example, cells with more processes or larger fields might be expected to contact a larger number of cells, covering a greater expanse of retinal area. Again, our ability to establish correlations between synaptic inputs and receptive field characteristics is limited by a relatively rudimentary understanding of synaptic structure.

West and Dowling (1972) investigated the synaptic input to nine of fifteen morphologically distinct varieties of ganglion cell which they identified in the retina of the ground squirrel. Grouping on the basis of synaptic relations reduced the number of classes from nine to two. One class of cells was postsynaptic to amacrine cells, almost

exclusively; while the other class had nearly equal bipolar and amacrine input, as determined by the proportion of ribbon and conventional synapses (West and Dowling, 1972). With presently available techniques it has not been possible to determine which of several bipolar and amacrine cell types account for the connections to individual cells. Possibly ganglion cells with qualitatively different receptive fields will be found to receive input from different types of bipolar and amacrine cells. Whether the criteria used by West and Dowling (1972) to determine cell classes do in fact produce qualitatively different groups is open to question, however. Dimensions such as dendritic depth, level of inner plexiform layer termination, dendritic diameter and texture, and branching pattern define quantitative continua, and cannot, in my opinion, be expected to generate qualitatively discrete classes.

A survey of several papers which describe receptive field characteristics of ganglion cells in pigeons (Maturana, 1962; Maturana and Frenk, 1963; Holden, 1969; Pearlman and Hughes, 1976) suggests that attempts to systematically correlate anatomical features with the fragmentary electrophysiological data would be premature at this time. (Nonetheless, I expect to do exactly that in the section on the midget system!) Most receptive fields are believed to be relatively complex in character,

although some concentrically organized fields have been observed (Pearlman and Hughes, 1976). Receptive fields ranging from a few minutes to seventeen degrees of visual angle have been reported (Maturana, 1962; Holden, 1969). The largest ganglion cells observed here had maximum field diameters of 750 μ, or about 5.5 visual degrees. Cleland and Levick (1974) and Boycott and Dowling (1969) reported a similar relationship between ganglion cell dendritic spread and receptive field sizes in cat and monkey. That is, receptive fields are often larger than would be predicted from the diameter of ganglion cell dendritic fields. The increase in receptive field area is attributed to lateral influences mediated by amacrine or horizontal cells. Abundant possibilities for such interactions are present in the bird retinas studied, since both horizontal and amacrine cells are numerous.

Retinal circuitry

The most consistently observed differences between vertebrate visual systems relates to the complexity of ganglion cell receptive field characteristics. Species vary widely with respect to the relative proportions of complex (edge detectors, directionally selective units, etc.) and simple (concentric, center/surround organization) ganglion cells found in their retinas. While it is possible that this difference is an artifict of sampling procedures

or of recording techniques, it seems more likely that there are distinct species differences in this respect. Most ganglion cells in frogs and pigeons exhibit responses to complex stimuli, while most cat and monkey ganglion cells appear to respond to simpler stimuli. "Intermediate" retinas, which have many cells of each type, are found in ground squirrel, mudpuppy and rabbit. (See also p. 16).

Naturally, comparative physiologists have been concerned with elaborating the structural basis for this difference. At present, the most widely accepted hypothesis ascribes the primary role of mediating ganglion cell receptive field complexity to the circuitry of the inner plexiform layer. Dowling (1968) noted that the thickness of the inner plexiform layer, as well as its stratification, varied across species. More specifically, receptive field complexity is believed by Dowling and his colleagues to relate to the contribution of amacrine cells to processing in the inner plexiform layer (Dowling, 1970; Dubin, 1970).

Kidd (1962) found several different presynaptic configurations in the inner plexiform layer. Dowling and Boycott (1966) reported that "ribbon" synapses were associated with bipolar cells, and that "conventional" synapses belonged to amacrine cells in Rhesus monkeys. Dubin (1970) confirmed the postulated correspondence of conventional synapses to amacrine cell processes and

ribbon synapses to bipolar cell processes in several additional species. As a result, the paired terms have been treated as synonymous by subsequent authors (e.g. Werblin, 1972; West and Dowling, 1972; Yazulla, 1974). Dubin's paper also provided the most convincing evidence in support of Dowling's (1968) hypothesis that those species with predominantly simple receptive fields would have lower amacrine to bipolar ratios than those with a majority of complex receptive fields. As predicted, species termed intermediate had ratios between those of the two extreme groups.

Whether the amacrine cells which terminate in the inner plexiform layer are, in fact, the primary determinant of ganglion cell receptive fields cannot be demonstrated by correlational evidence alone, however. As yet, electrophysiological techniques have not been able to provide a more direct evaluation of this hypothesis. In addition, evidence has begun to accumulate which suggests that the amacrine-conventional and bipolar-ribbon identities represent an oversimplification. Allen (1969) reported that some human bipolar cells made conventional contacts in the inner plexiform layer; and Wong-Riley (1973) found that up to 30% of the bipolar synapses in salamander were of the conventional type. Since Wong-Riley based this claim on serial reconstructions of complete synaptic terminals, it seems unlikely

that synaptic ribbons could have been overlooked. Finally, Dowling and Cowan (1966) found that centrifugal fibers formed conventional synapses in the inner plexiform layer of pigeons.

While the observation that cells other than amacrine cells make conventional contacts in the inner plexiform layer does not alter the correlation between the conventional-to-ribbon ratio and ganglion cell receptive field characteristics, it does raise the possibility that cells other than amacrines could account for the increased ratios, and possibly for the change in receptive fields, as well. Of particular importance are the observations of alternative sources of conventional contacts in amphibian and avian species, since those classes were found to have the highest proportion of conventional to ribbon synapses. A careful reexamination of the synaptic structures of amacrine and bipolar cells in the inner plexiform layer is clearly warranted, in order to substantiate the observations of Dowling and his colleagues, who based their conclusions on circumstantial evidence, rather than on serial reconstructions of a number of cells (Dowling and Boycott, 1966; Dowling, 1968; Dubin, 1970).

Reevaluation of Dowling's (1970) formulation is further necessitated by the development of alternative theories as to the origin of ganglion cell receptive field

characteristics. Sjöstrand (1976) has suggested that outer plexiform connections may be more critical in that process than heretofore thought. Following a serial reconstruction of the outer plexiform layer of the rabbit, Sjostrand concluded that circuitry there was capable of mediating edge detection and directional selectivity, complex responses usually thought to be processed through the inner plexiform layer.

Sjöstrand's (1976) logical arguments regarding the importance of the outer plexiform layer are also powerful. He points out that the synaptic terminals in the outer plexiform layer are substantially smaller than those in the inner plexiform layer. If outer plexiform terminals were comparable in size to those of the inner plexiform layer, the thickness of the outer plexiform layer would be increased by a factor of ten, making it thicker than the inner plexiform layer. In fact, Sjöstrand found the compact circuitry of the outer plexiform later to be more complex than inner plexiform layer circuitry. Finally, Sjöstrand notes that processing complex information in the outer plexiform layer would allow the system to utilize maximal resolution available there, while assigning such processing to the inner plexiform layer requires that layer to reestablish resolution lost between receptor and bipolar cells in addition to coding complex stimulus attributes.

At present, the Sjöstrand analysis is simply a reasonable hypothesis. The serial reconstructions necessary to evaluate circuitry within the outer and inner plexiform layers of other species are tedious and have yet to be accomplished. Furthermore, the extreme difficulty of recording from bipolar cells limits the information available from that technique. Clearly, Sjostrand's hypothesis requires that bipolar cells exhibit more complex receptive fields than have been demonstrated, particularly in species with complex retinas.

One of the more provocative aspects of Sjöstrand's (1976) model concerns the advantages obtained by assigning significant information processing to the outer plexiform layer. His suggestion that such processing could be used to maintain fine spatial resolution which is available at the level of the receptor mosaic has direct implications as to the role of the non-mammalian fovea, and could possibly account for the absence of an extensive midget system in nonprimates. This point will be elaborated as part of the discussion of the avian "midget system," which follows.

The midget system

Evidence described earlier (pp. 20-22) indicated that the primate fovea is simultaneously the area of highest visual acuity and the region where receptors are most densely packed. Clearly, the density of the receptor mosaic

is one potentially important factor in determining maximal acuity. It remained for Polyak (1941) to demonstrate a mechanism by which the fine grain obtained at the level of the receptors could be maintained into the central nervous system. The nearly one-to-one ratio between receptors and ganglion cells in the foveal region first suggested that a one-to-one structural relationship might exist. In 1941, Polyak reported his observations of "midget bipolar cells" and "midget ganglion cells" which together formed a "pure" or "private" cone system in the primate fovea. The midget bipolar was thought to be synaptically related to only a single foveal cone, and the midget ganglion cell to only a single midget bipolar.

The midget system notion advanced by Polyak (1941; 1957) has most frequently been criticized on the grounds that electron microscopic analyses demonstrate that an individual foveal cone contacts two or more midget bipolar cells (Pedler, 1965a; 1965b; Kolb, 1970; Missotten, 1974). However, the one-to-one-to-one relationship of interest to Polyak was not that between receptor, bipolar and ganglion cells, but rather that between ganglion, bipolar and receptor cells. Ultimately, the concern was that information from an individual receptor be transmitted relatively intact to the central nervous system. While a single ganglion cell must receive input from an individual receptor

to accomplish this, the receptor in question may also provide information to other cells.

It is with regard to the inner plexiform layer connections of the midget system that Polyak is most often misunderstood and misrepresented. For example, some authors have demanded that potential "midget ganglion cells" make contact only with one midget bipolar (Bunt, 1976). However, Polyak wrote:

> The individual relationship of the midget bipolar cell and the midget ganglion cell, . . . although it appears to be most important and an indispensible prerequisite for the transmission of individual mono-neuronal impulses is, however, not the only relation of the neurons in question . . . (1941, p. 284, emphasis added).

Later in the same volume, he concluded:

> In the primate retina there is a system of neurons, the "pure, or private, cone system," which in a paradigmatic way exhibits an individual relationship on not one but two synaptic levels; although the actual relationships, as discussed, are much more complex than here-to-for thought, since, besides the "one-to-one synapse," the same neurons possess other spatially less restricted or "diffuse" relationships. (1941, p. 390, emphasis added).

Polyak's belief that midget bipolars were synaptically related to amacrine cells and to diffuse ganglion cells, and that midget ganglion cells received input from diffuse bipolars and amacrine cells, as well as from midget bipolars has been confirmed by Boycott and Dowling (1969) in the primate and West and Dowling, (1972) in ground squirrel.

Some birds exhibit static acuity which equals or surpasses that of humans and Rhesus monkeys (Fite, personal communication; Fox et al, 1976). This finding has led authors to speculate that the foveal connections of avian species may be similar to those of primates, including high receptor cell density and a midget system. Fite and Rosenfield-Wessels (1975) reported that receptor densities in various hawks were two or three times that observed in the Rhesus monkey; however, the values they obtained for Rhesus monkey were more than twice as high as those reported by Rolls and Cowey (1970) and Adams et al (1974) for the same species. Using Osterberg's data, Adams et al (1974) estimated human cone densities in the foveal area to be approximately 12,500 cones per square degree. Fite and Rosenfield-Wessels (1975) reported values of 13,700 receptors per square degree and 18,500 receptors per square degree for Goshawk and Red-tailed hawk, respectively. Although Cajal (1892) reported small field (possibly "midget") bipolars in the sparrow fovea, no "midget" ganglion cells were observed by that author. The possibility that a foveal "midget system" might exist in birds which is structurally and functionally comparable to that of primates has not been directly evaluated by previous authors.

The light microscope analysis presented here

suggests that the two avian species studied may possess foveal "midget systems" which are in some ways comparable to that observed in primate foveal areas. One type of small field bipolars was similar in dendritic appearance and size to the invaginating midget bipolar of primates. Although the dimensions of these small field cells (hereafter, midget cells) were comparable to those of nearby foveal receptors, the cells exhibited a lateral displacement of the axonal terminal in excess of 300 μ. Primate midget bipolars from the foveal region show almost no lateral displacement (Polyak, 1941; 1957).

Avian small field ganglion cells differed from primate midget varieties in a number of dimensions which have been used by other authors as defining characteristics for potential midget ganglion cells (e.g. West and Dowling, 1972; Bunt, 1976). Small field ganglion cells impregnated in the bird foveas studied exhibited multiple dendrites, as well as relatively large cell soma and dendritic fields. A statistical analysis indicated that synaptic contact with more than one midget bipolar would be possible for those cells, also. As noted above, however, even primate midget ganglion cells are not connected to one and only one midget bipolar cell. Primate and ground squirrel midget ganglion cells may receive inputs from both diffuse bipolars and amacrine cells (Boycott-Dowling, 1969; West and Dowling,

1972). Since the synaptic relationships of a given cell are clearly more important in establishing a correspondence between analogous cells types than are structural characteristics, it would therefore appear that some of the small ganglion cells of the blue jay and pigeon foveas could function as midget ganglion cells. Ganglion cell dendritic field size, though larger than that of presumed midget bipolar axonal expansions could permit synaptic contacts with a single midget bipolar and additional diffuse bipolars or amacrine cells, rather than the multiple midget bipolars. It is important to note that such small field cells are relatively rare in the avian fovea, while midget ganglion cells comprise the majority of impregnated cells in the primate fovea.

Although the data presented here indicated that small bipolar cells and small ganglion cells could make synaptic contacts similar to those made by the midget cells of primates, a light microscope study cannot confirm that fact unequivocally. Dubin (1970) has noted that pigeons exhibit numerous amacrine synapses interposed between bipolar and ganglion cells on the basis of his electron microscopic analysis of the pigeon retina. Such interference between direct midget bipolar and midget ganglion cells connections would, of course, be inconsistent with Polyak's conception of the midget system. Yazulla (1974), who

determined the number of amacrine and bipolar synapses in the inner plexiform layer of pigeons at various retinal locations found that the ratio of amacrine (conventional) to bipolar (ribbon) synapses was relatively low in the foveal region. However, a comparison of the ratios obtained for pigeon fovea and parafovea (Yazulla, 1974) with those reported for Rhesus monkey fovea and parafovea (Dubin, 1970) indicates that the ratio is nearly twice as high in the former species. Those data suggest that the probability of direct midget bipolar to midget ganglion cell connection may be somewhat reduced in the pigeon fovea, and possibly in the foveas of other birds as well, unless bipolar cells make conventional contacts with ganglion cells there (Wong-Riley, 1973).

On the basis of the quantitative morphology described here, it appeared that a "midget system" might also be present in the red field of the pigeon retina. In fact, the data indicated that the "midget system" of the red field might be more highly developed than that of the pigeon fovea. This observation is particularly intriguing in light of Nye's (1968) and P. Blough's (1971) studies which suggest that the red field may mediate near-field acuity for the binocular frontal field of the pigeon. Interestingly, Yazulla (1974) found the central red field to have the highest ratio of conventional to

ribbon synapses of any retinal area of the pigeon. Thus, although both "midget" bipolars and "midget" ganglion cells may be present in the fovea and red field of the pigeon, there is reason to suspect that their relationships in the inner plexiform layer may differ.

The problems concerning synaptic relationships within the "midget system" of the two species studied are directly amenable to solution using electron microscopy in conjunction with the Golgi method. Analysis of bipolar and amacrine-synaptic contacts could be determined for Golgi-impregnated midget ganglion cells, if, indeed, bipolar and amacrine cells differ with regard to presynaptic terminal specializations (Dowling and Boycott, 1966; Dubin, 1970). A more difficult question involves the discrimination of whether direct bipolar inputs to midget ganglion cells (if such connections exist) are derived from midget, as opposed to diffuse, bipolar cells. Even in primates, direct midget bipolar to midget ganglion cells contacts have not been demonstrated, but are assumed to exist on the basis of light microscopic observations. Ultimate confirmation would undoubtedly require serial reconstruction of bipolars related to Golgi-impregnated midget ganglion cells, a particularly arduous task in birds, where midget bipolars may exceed 500 μ in length.

In summary, anatomical evidence suggests that the

two birds studied may possess foveal "midget" cells which are in some ways morphologically similar to those of primates. The proportion of "midget" to diffuse ganglion cells in the foveal area is considerably lower in birds, if the incidence of those cells in Golgi-impregnated tissue actually reflects their presence in the cell population. A similar situation may exist in the central portion of the pigeon's red field, as well.

Ultimately, of course, the primary concern is with the functional significance of the proposed avian "midget systems." The most parsimonious view would suggest that primate and avian "midget systems" subserve the same function; both mediating high spatial resolution. However, structural similarity between primate and avian "midget system" at the level of the light, or even the electron, microscope does not establish a corresponding functional identity. As noted earlier, Pumphrey (1948, 1961) suggested that deep avian foveas may mediate a form of dynamic acuity, acting as a mechanism aiding visual tracking. It may, therefore, be relevant to ask whether the foveal "midget systems" found in birds could be concerned with detecting movement, rather than with resolving static spatial detail.

Electrophysiological data as to the receptive field characteristics of "midget" cells are extremely provocative, yet inconclusive. Interestingly, Polyak's

(1941) early conception of midget ganglion cell inputs is more nearly consistent with currently available electrophysiological data from primate ganglions than is the strict one-to-one-to-one organization often attributed to him. Ganglion cell receptive field organization in primates typically involves a center/surround organization. In the foveal area, receptive field centers were found to be very small, often too small to measure. In fact, Hubel and Weisel (1966) noted that the receptive field centers approached the size of a single cone. Surround size was found to vary less as a function of retinal locus than did center size.

Gouras and his colleagues have suggested that the common type of small field color-opponent cell found in the Rhesus monkey fovea may represent output from midget ganglion cells (Gouras, 1968; de Monasterio and Gouras, 1975a; 1975b). These cells are believed to have one cone mechanism mediating the center and other cone mechanisms mediating the surround portions of the receptive field. This postulated input pattern would be consistent with Polyak's conception of midget system organization. Thus, it appears likely that midget ganglion cells in the primate may exhibit color-opponent responses over their small receptive fields.

Studies involving electrophysiological recording from avian ganglion cells are not as numerous as those in

primate. For the most part, ganglion cell characteristics have been found to be relatively complex, with individual units responding to movement, directionality or stimulus orientation. (in pigeon: Maturana, 1963; Maturana and Frenk, 1963; Holden, 1969; Pearlman and Hughes, 1976; in chicken, Miles, 1972), although recent studies have also found simple (concentrically organized) receptive fields (Miles, 1972; Pearlman and Hughes, 1976).

Donner (1953) described avian ganglion cell groups with limited spectral sensitivity when he recorded multiunit activity, yet only Maturana (1962) and Pearlman and Hughes (1976) have successfully recorded from individual color units. The latter authors reported that approximately 3% (10-11 cells) of their sample responded differentially to wavelength. Those authors described the cells as opponent-color cells, although they do not mention spontaneous activity or concentric center/surround field organization. Unfortunately, neither Maturana (1962) nor Pearlman and Hughes (1976) presented data as to the receptive field sizes of the color units they observed. However, Pearlman and Hughes (1976) did attribute the paucity of opponent-color cells in their sample to the small size of the cells in question, which is consistent with the hypothesis that these cells could be the "midget ganglion cells" of the pigeon.

Receptive field dimensions have been reported for other types of pigeon and chick retinal ganglion cells (Maturana, 1962; Maturana and Frenk, 1963; Holden, 1969; Miles, 1972). Fields greater than 1/2 degree diameter were found for all cell types except the convex edge detectors, Maturana's (1962) class 5 ganglion cells. Convex edge detectors, which responded strongly to small moving convex edges, but weakly to stationary spots, have "small receptive fields, only a few minutes in diameter." (Maturana, 1962, p. 175) Given the small field size of these cells (probably on the order of 10 μ on the retina), these ganglion cells could also correspond to the "midget ganglion cells" found in the pigeon retina.

Kalinina (1974, 1976) suggested that his class 1 (smallest) ganglion cells might correspond to the convex edge detectors found in frogs, and noted that those cells increased in frequency in the central areas. Although Kalinina did not use the Golgi procedure for impregnating his tissue, his class 1 and 2 cells closely resemble the small G1 cells found in the foveas of the two birds studied here. Both cells have small fields and a few diffuse dendrites extending into the inner plexiform layer.

Thus, on the basis of electrophysiological data, there appear to be two possible candidates for "midget-ganglion-cell" receptive fields, the opponent color cells

of Pearlman and Hughes (1976), and the convex edge detectors of Maturana (1962). Determining whether either or both of these cell varieties corresponds to the midget ganglion cells observed in birds would be of particular interest in light of the conflict between Pumphrey's (1948, 1961) hypothesis that the bird fovea (where many of the small ganglion cells are found) acts as a visual tracking device, and the more traditional view that it functions primarily to mediate spatial acuity, as does the primate fovea (e.g. Walls, 1942).

Equally interesting in this context is Sjöstrand's (1976) recent analysis of synaptic relations in the outer plexiform layer of the rabbit. The rabbit has many ganglion cells with complex receptive fields, as does the pigeon. Sjostrand's serial reconstruction of the outer plexiform layer delineated a complex circuitry which could provide the basis for edge detecting and directional selectivity. According to Sjöstrand, consigning visual processing to the outer plexiform layer "would secure that the resolution of visual information that is processed will be as high as possible." (Sjöstrand, 1976; p. 11). Note that this is precisely the function ascribed to the primate midget system. In primate species, most visual processing is believed to occur in cortical and subcortical areas of the central nervous system. In birds, however, substan-

tial processing is known to occur within the retina. To the extent that details of interest (whether static or dynamic in nature) are extracted at the level of the outer plexiform layer, the necessity for a "private" or midget system is mitigated. Thus, Sjöstrand's hypothesis could potentially account for the absence of true "midget" ganglion cells in nonmammalian retinas. Obviously, even in primate species the quality of the interreceptor mosaic cannot be maintained indefinitely within the central nervous system if complex patterns are to be coded.

Such an analysis is also consistent with Walls (1942) speculations as to the evolution of the mammalian visual systems. Walls (1942) suggested that early placental mammals were nocturnal, and as a result, photopic components of their visual systems degenerated, while scotopic functions were enhanced. The intraretinal summation required for scotopic vision greatly reduced the amount of pattern information that could be processed simultaneously. Carrying Wall's scenario a step further, as some species (primates) continued to evolve and began to fill diurnal niches, the necessity for devoting so much retinal processing to the coding of luminosity lessened, and more visual space could be devoted to processing more complex information. Rather than rebuild the complex outer plexiform layer circuitry, which had degenerated, this new processing was accomplished

within the rapidly expanding cortical centers. In order to retain maximal resolution into these centers, a retinal "midget system" for small bipolars and small ganglion cells developed, since fewer ganglion cells are needed to convey information about general luminance. Such an evolutionary analysis is of course highly speculative; however, it does tie together Sjostrand's hypothesis and Wall's account of mammalian evolution, while accounting for differences in gross anatomy observed between bird and primate foveas.

The gaps indicated by this analysis of the possible structural and functional significance of the "midget system" in birds are tremendous. The obvious need for an electron microscopic study of outer plexiform and inner plexiform layer connections has been discussed above. Also, there has been no electrophysiological recording from ganglion cells in the blue jay (or any other species with a deep fovea), and that recording which exists for pigeon is incomplete in many details. Data as to the location and receptive field size of opponent-color units is critical to evaluations of similarities between primate and avian "midget systems," as is further information bearing upon the characteristics of small field convex edge detectors.

Comparison of two avian retinas

Blue jays, which exhibited a deep, central fovea, were found to have a more highly differentiated retina than the pigeon. That is, foveal cells of all varieties had process-field dimensions only a fraction of the size found peripherally. Furthermore, the finding that cells of the dorso-temporal retina, in an area intermediate between the fovea and periphery, were intermediate in size suggested that a gradual and systematic increase in size occurred from the central to the peripheral retina in that quadrant. This increase in size may not be symmetric across all retinal areas, however, since, for example, horizontal cells of the inferior nasal quadrant were larger than those of the superior (dorso-) temporal quadrant. Additional confirmation of these observations would require more exact information as to retinal locus for each cell, as well as information regarding dimensions of cells located in other quadrants, of course.

The retinal elements of pigeons exhibited considerably less variability with respect to process field dimensions than did those of blue jays, indicating a more homogeneous (or less differentiated) retinal structure in the former species. In general, pigeon foveal cells were larger than their blue jay counterparts, while pigeon peripheral cells were smaller than blue jay peripheral cells. Such differences in field sizes might be related to species differences in

information processing or summation at the retinal level, in habitat, or in receptor distribution. Whether the differences in field size relate systematically to variation in receptor distribution, for example, would require more detailed information as to receptor density in various retinal areas. Direct counts of receptors might be obtained by viewing flatmounted tissue from dark-adapted retinas through a phase contrast microscope, since receptor nuclei and bases do not correspond to specific outer segment configurations.

The observations reported regarding foveal morphology in these birds provide information as to the functional significance of the shape of the fovea. For the most part, differences between blue jay (deep fovea) and pigeon (shallow fovea) foveal elements were quantitative rather than qualitative in nature. Evidence suggesting a possible "midget system" was present in both species, yet blue jay foveal cells were consistently smaller than their pigeon counterparts. Centrifugal displacement of receptor output from the foveal area was mediated by the lateral displacement of bipolar axons from their dendrites in both birds, rather than via oblique receptor descendant processes of receptors, as found in primates (Polyak, 1941; Boycott and Dowling, 1969). See Figure 7.

The primary qualitative difference between the

foveal areas was the apparent absence of H1 axon terminals from the blue jay foveas. This difference could relate to a difference in the distribution of photoreceptors, since the axon terminals are found to receive substantial input from rods in both turtles and cats (Leeper, personal communication; Kolb, 1974). I observed rods closer to the center of the pigeon fovea (200 μ) than to the center of the blue jay fovea (800 μ), but did not attempt a systematic study of receptor distribution since outer segments were so rarely stained. Alternately, it is possible that H1 terminals which exist in the blue jay fovea were not impregnated by the methods used here.

Overall, the shallow foveal region of the pigeon is more similar with respect to cellular anatomy to that of the deep-foveated blue jay than to the concaviclivate fovea of the primate. Both avian species show: (1) lateral processes emanating from receptor bases, even in the center of the fovea; (2) two types of horizontal cells; (3) substantial lateral displacement of both midget and diffuse bipolar cells; (4) multi-leveled terminations for bipolar cells; (5) numerous amacrine cells, including displaced varieties; and (6) multi-dendritic, small field (possibly midget) ganglion cells, with many process vericosities.

Perhaps the similarity between pigeons and blue jays is not surprising, despite differences in the depth of

the foveal clivus, since they are more closely related to each other than to primates. Furthermore, the absence of foveas from all other mammalian classes (Walls, 1924; Duke-Elder, 1958) suggests that the primate fovea may be a relatively recent adaptation, representing an instance of structural convergence, rather than being a homologous structure retained from a distant common ancester. Given the vast differences in the ecological habitat of primates and birds, it is unreasonable to expect that the shape or depth of the foveal clivus would override ancestral and ecological factors in determining foveal anatomy and function.

In addition to the fovea, a second area of high ganglion cell and receptor density has been described in the pigeon near the center of the red field (Galifret, 1968; Binggeli and Paule, 1969). Cellular dimensions for the two areas were found in this study to be remarkably similar. Interestingly, the major exceptions to this rule were found to be the amacrine and bipolar cell types. In the red field, amacrine cells were larger than those of the fovea, and two types of bipolar cells showed larger terminals in the red field. The increase in terminal size was larger for amacrine than for bipolar cells. The larger increase in the size of amacrine and bipolar cell fields may account for the increased ratio of conventional to ribbon synapses found in the red field by Yazulla (1974). As noted above, the red field

also resembled the fovea in exhibiting a possible "midget system."

The structural similarities of the red field and fovea, particularly at the level of the outer plexiform layer are especailly striking, yet the red field is usually considered to be involved in near-field acuity for the frontal field, while the central fovea serves a lateral field of view and mediates distance vision. Should the fovea and red field be found to have similar synaptic relations in the outer plexiform layer, the current status of the pigeon as an important model would be significantly enhanced, since its shallow fovea does not appear to be different morphologically from the deep fovea of the blue jay. Within a single species (pigeon), then, there appear to be two highly similar retinal areas which differ primarily with respect to synpatic relationships within the inner plexiform layer. Not only are most cells structurally similar, but cell counts indicate that receptors and ganglion cells may be equally numerous in the two areas (Galifret, 1968; Binggeli and Paule, 1969).

The potential correlation of behavioral investigations which tap the visual capabilities of each area, and intracellular recordings which describe ganglion cell receptive fields in the fovea and dorso-temporal retina with the few structural differences found may be of theoretical importance. Insights as to the role of amacrine

cells may be forthcoming. Also, investigation within a single species might permit the evaluation of Dowling's and Sjostrand's hypotheses concerning the primary source of receptive field complexity observed in pigeon ganglion cells. Finally, the role of the avian fovea could be further elucidated by studying a single species, the pigeon, since anatomical data indicate that the pigeon fovea does not differ qualitatively from deeper fovea of the blue jay.

Figure 1. This diagram shows the approximate relationship of the red and yellow fields in the Pigeon retina. Areas of increased cell density occur at the "area dorsalis" in the red field and at the fovea and surrounding area centralis in the yellow field. Exact size and location of the red field may vary somewhat from subject to subject, but the region is clearly discriminable as a result of its red hue. The left eye is shown here. (Adapted from Galifret, 1968; and Yazulla, 1974)

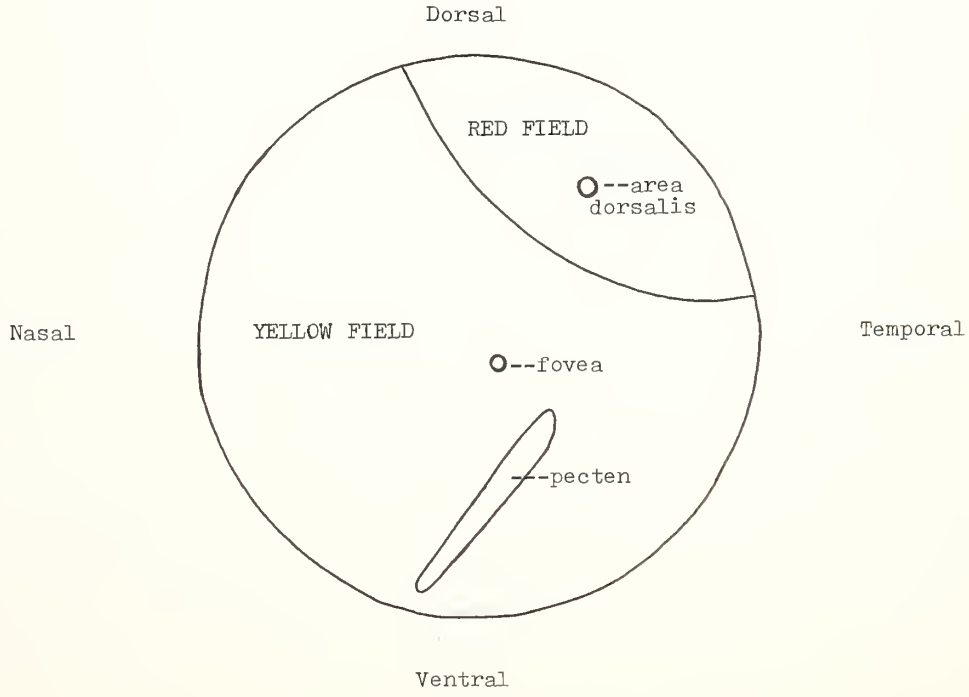

Dorsal
RED FIELD
--area dorsalis
Nasal
YELLOW FIELD
Temporal
--fovea
--pecten
Ventral

Figure 2. In order to assure random sampling of each cell type, a horizontal scanning pattern was adopted, as illustrated here. All cells which fell along horizontal scan lines and which met isolation criteria were evaluated. Scanning lines were separated by 2 mm. In addition, the foveal area was scanned horizontally and vertically, with scan separation of 0.3 mm.

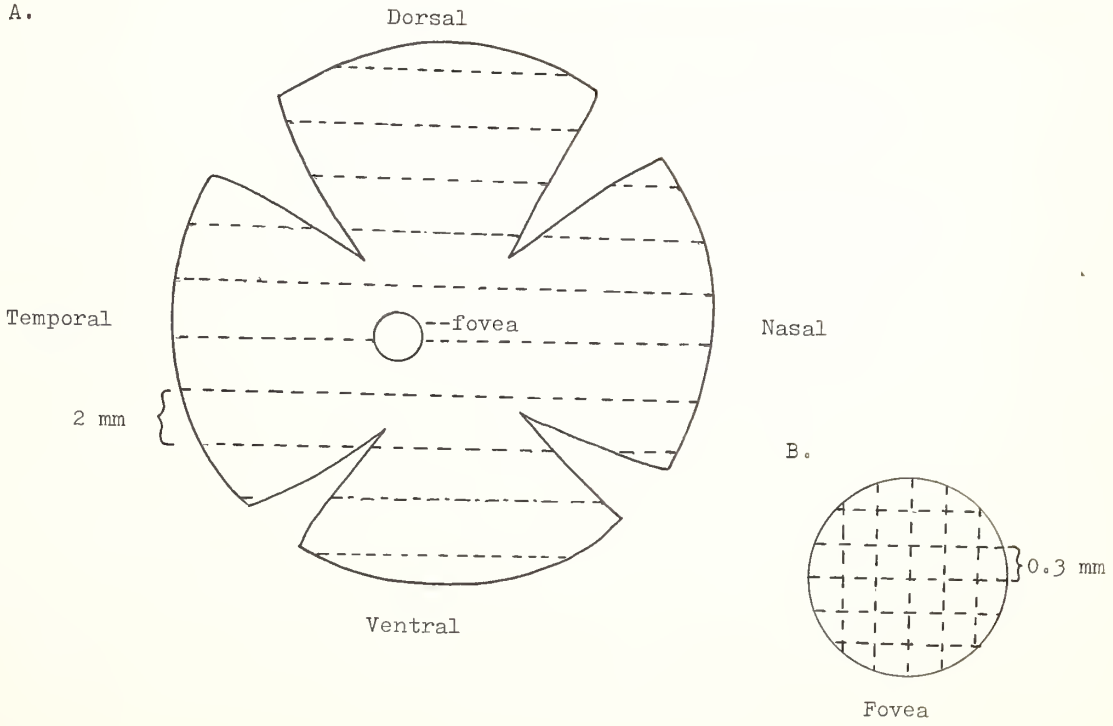
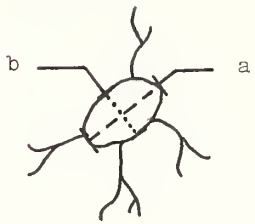
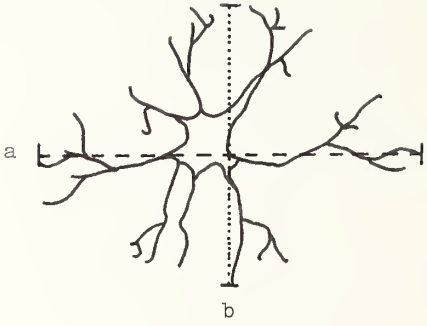

A.
Dorsal
Temporal
fovea
Nasal
2 mm
Ventral
B.
0.3 mm
Fovea

Figure 3. Procedures used for measuring cellular dimensions are illustrated. The longest diameter (a) is measured for a cell body (A) or dendritic field (B), then an additional diameter (b) is measured which is perpendicular to a and passes through the center of a. Similar procedures determine the size of receptor bases. C and D show procedures for measuring axonal length (c) in structures which possess and do not show clearly defined cell bodies, respectively.

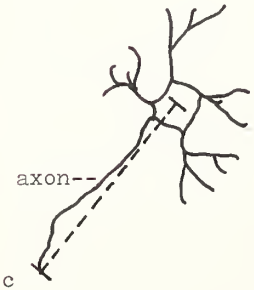
A.



B.



C.



D.

Figure 4. This figure summarizes measurements made of cells which were investigated in transverse sections. Depth of cell body or process field is measured perpendicular to the outer limiting membrane, while width is measured parallel to that structure. Displacement, as illustrated, is the horizontal distance between the center of a bipolar dendritic tree and the point of entry of its axon into the inner plexiform layer.

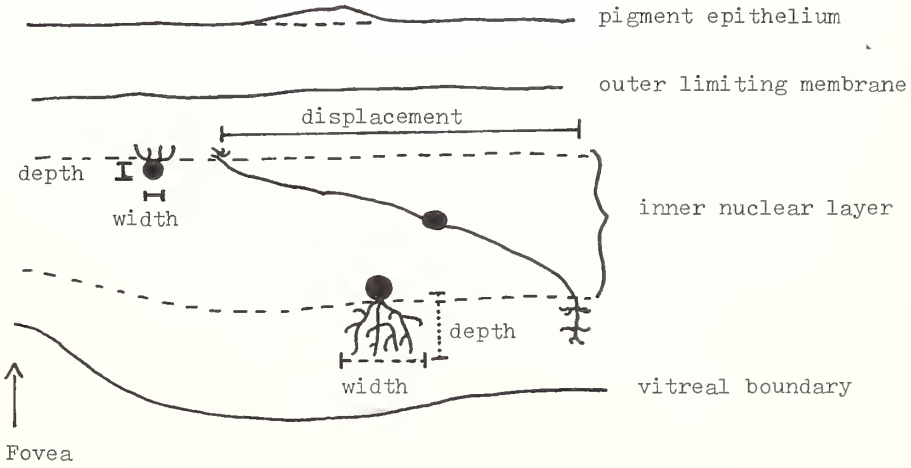
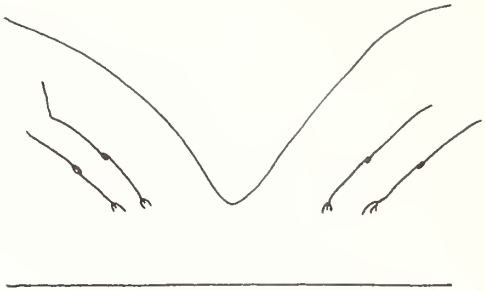

pigment epithelium
outer limiting membrane
displacement
depth
width
inner nuclear layer
depth
width
vitreal boundary
Fovea

Figure 5. Drawing of a retinal structure made with the microscope drawing attachment. A photograph of the same structure is shown in Figure 19.

Figure 6. Transverse sections through blue jay (A) and pigeon (B) foveas.

Figure 7. Lateral displacement of bipolar cells in the foveal region. A is a schematic diagram illustrating the phenomenon, while B shows foveal bipolar cells in the Golgi-impregnated retina of the blue jay. B is an enlargement of the bipolar group visible to the left of the fovea in Figure 6A.



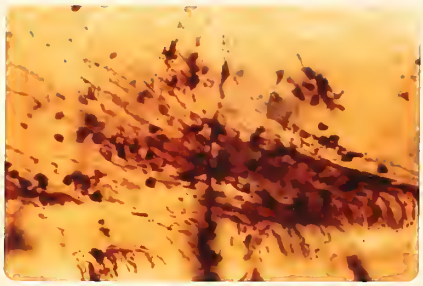
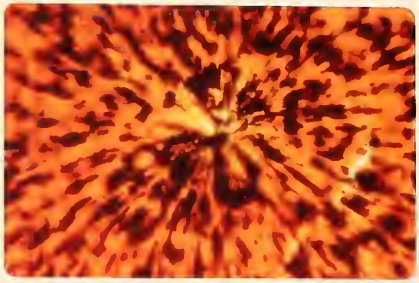


Figure 8. Views of blue jay (A) and pigeon (B) foveas in Golgi-impregnated, flatmounted tissue.



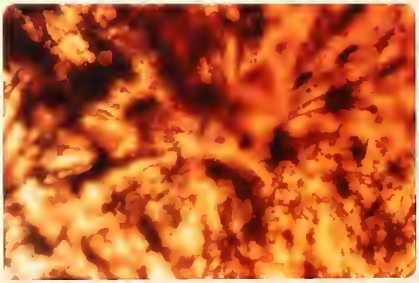


Figure 9. Photoreceptor base configurations. Tracings are of Golgi-impregnated cells of the blue jay dorso-temporal retina. (Drawn at X1000 magnification.)

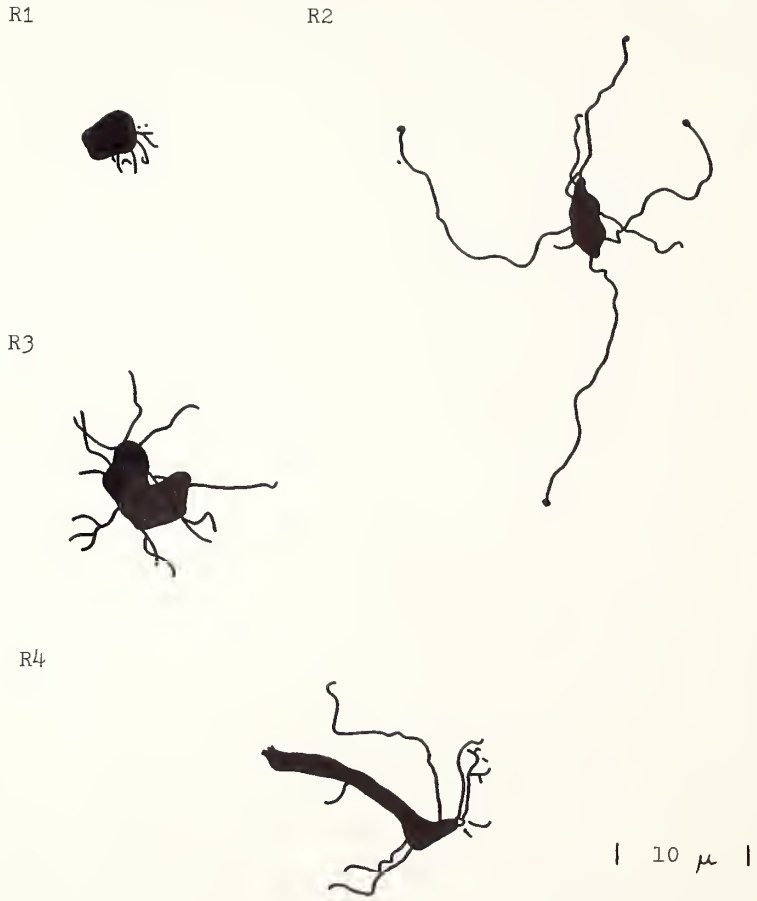

R1
R2
R3
R4
10 μ

Figure 10. Unstained photoreceptor outer segment from blue jay retinas. A is a rod outer segment from the peripheral retina; B is a cone outer segment from the same area.

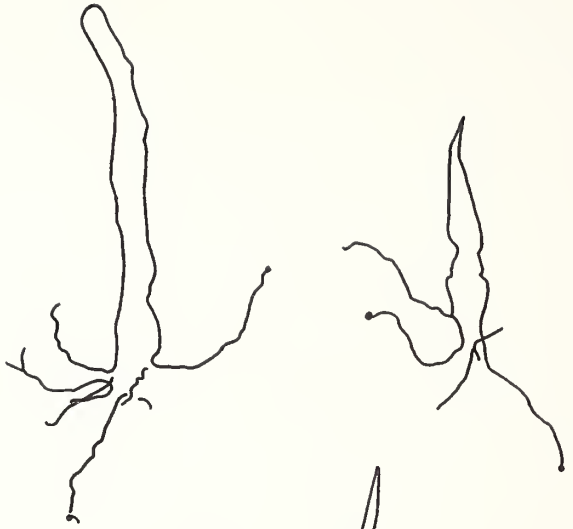
A.

B.

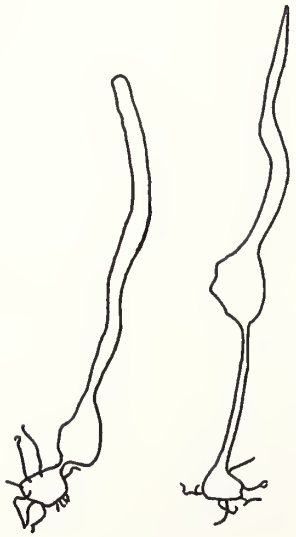
| 10 μ |

Figure 11. Drawings of completely impregnated transversely oriented receptor cells from blue jay retina.
A: rod and cone from the peripheral retina
B: rod and cone from the central retina
Note that all cells have R2 base configurations.

A.

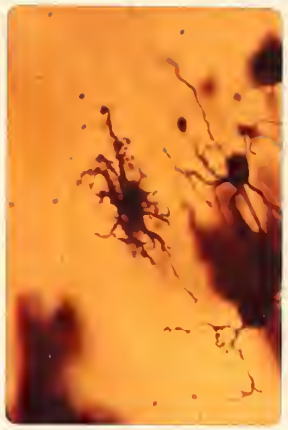


B.

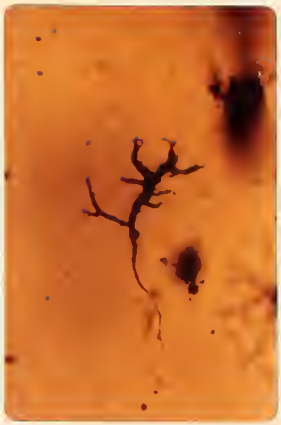


110 μl

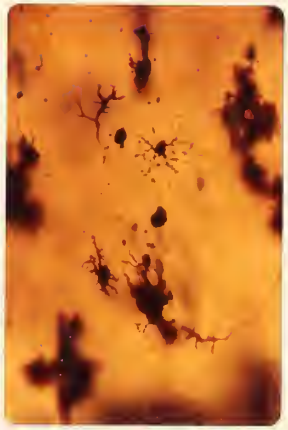
Figure 12. Horizontal cells.
A: A field of horizontal cells in the dorso-temporal retina of the pigeon (X400).
B, D: H1 cell and axon terminals.
C: H2 cell.
B, C, D are magnified X1000.



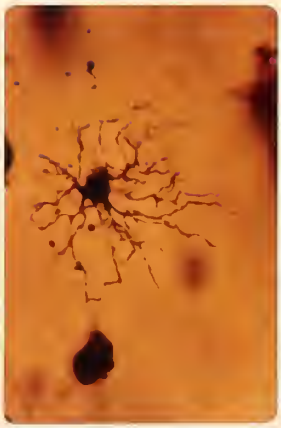
B



D



A



C

Figure 13. The axonal connection between the H1 cell and its terminal is clearly visible for this cell found in the blue jay peripheral retina.

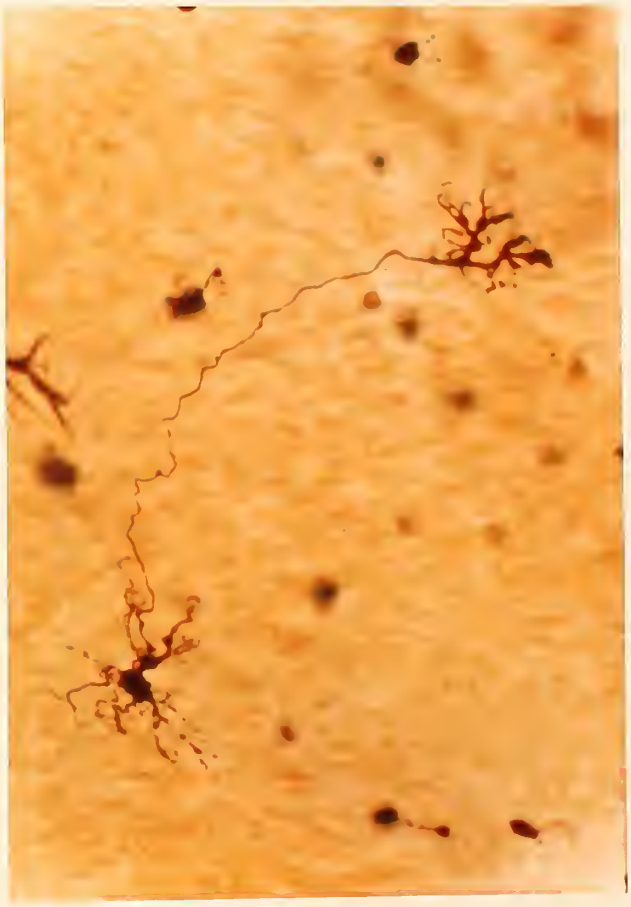


Figure 14. Examples of B1 and B2 cells in transverse (A) and flatmounted (B) views. In the flatmounted view of a B1 cell, the processes with varicosities are the axonal termination of the cell. In the flatmounted view of the B2 cell, the axonal terminations are shown below the cell body.

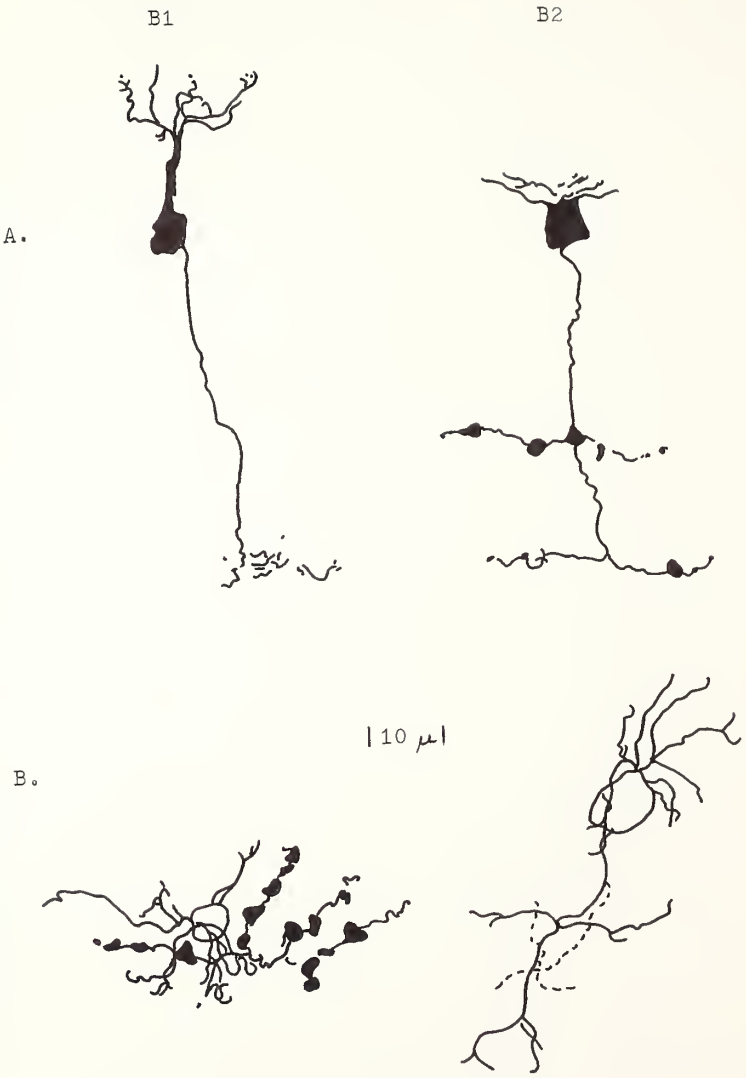

B1
B2
A.
B.
10 µl

Figure 15. Terminations of foveal bipolar cells in the inner plexiform layer. Note the distinct layering pattern exhibited by the processes.

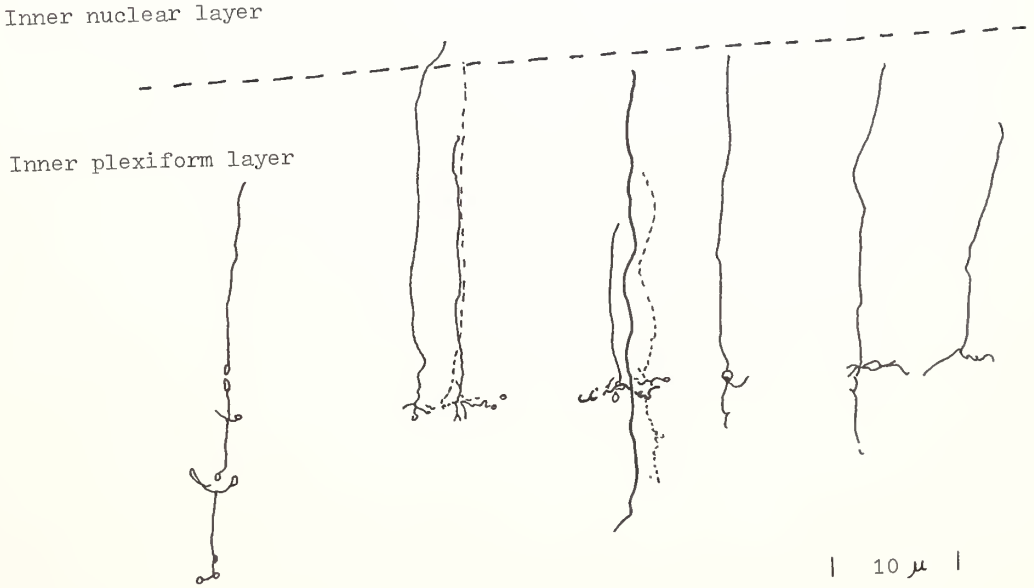
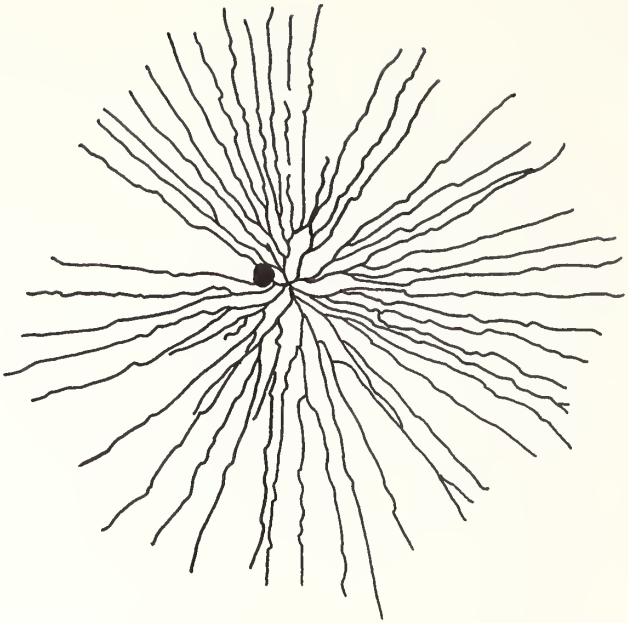

Inner nuclear layer
Inner plexiform layer
10 μ

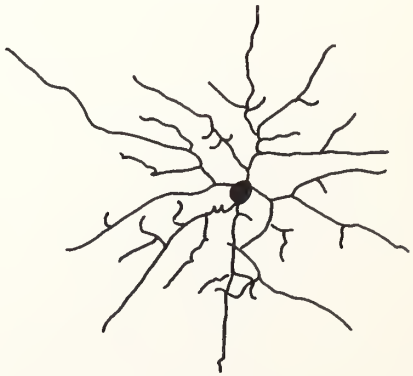
Figure 16. Monostratified amacrine cells. Drawn at magnification of X400.

A1



A2

A3



| 50 μ |

Figure 17. Multistratified (A,B) and diffuse (C) amacrine cells, drawn at X400 magnification.

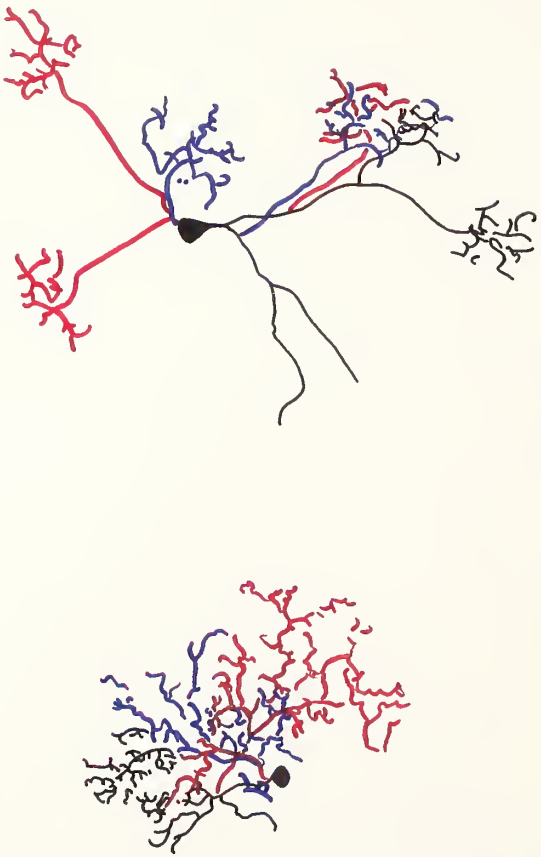


Figure 18. Ganglion cells, drawn at magnification of X400.

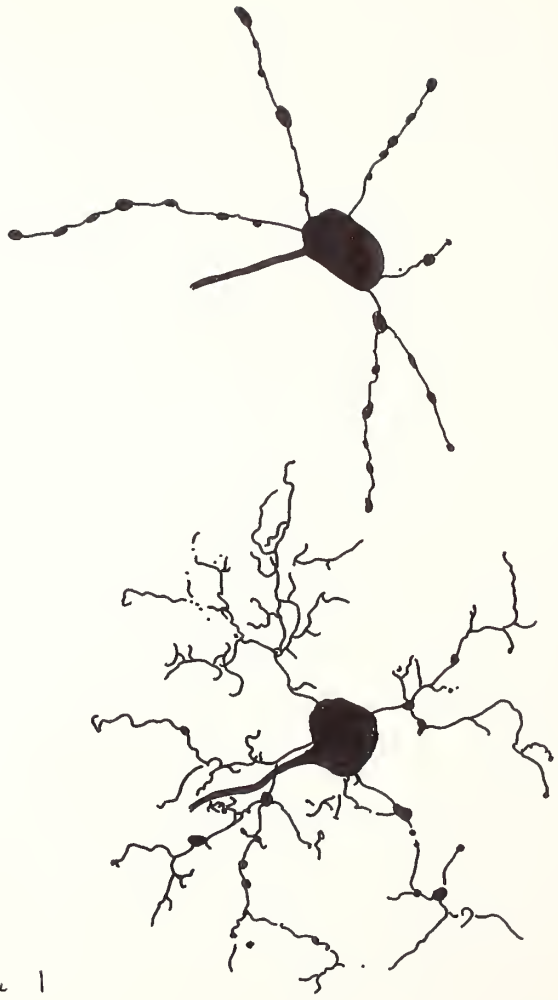

G1
G2
50 μ

Figure 19. Interspecies comparison of horizontal cells. H1 cell axon terminals are shown for pigeon (A) and blue jay (B). Both structures are from the peripheral retina. Other horizontal cells show comparable differences; that is, pigeon cells are thicker, showing fewer fine ramifications.

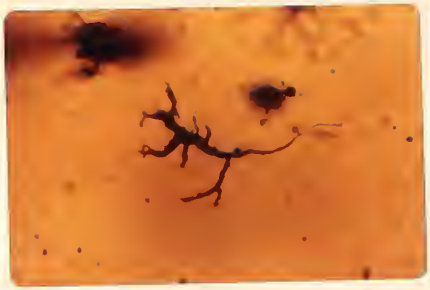
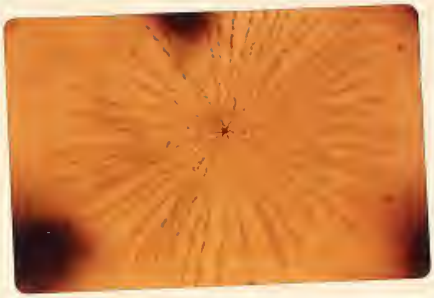
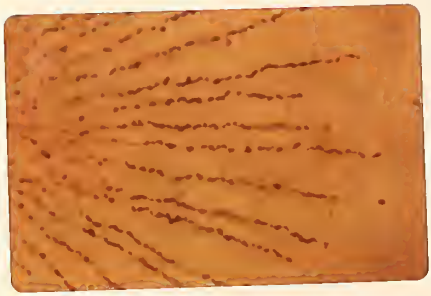


Figure 20. Photographs of A1 cells from pigeon (A) and blue jay (B) retinas. Note the greater density of varicosities on the pigeon amacrine cells.

A.



A'

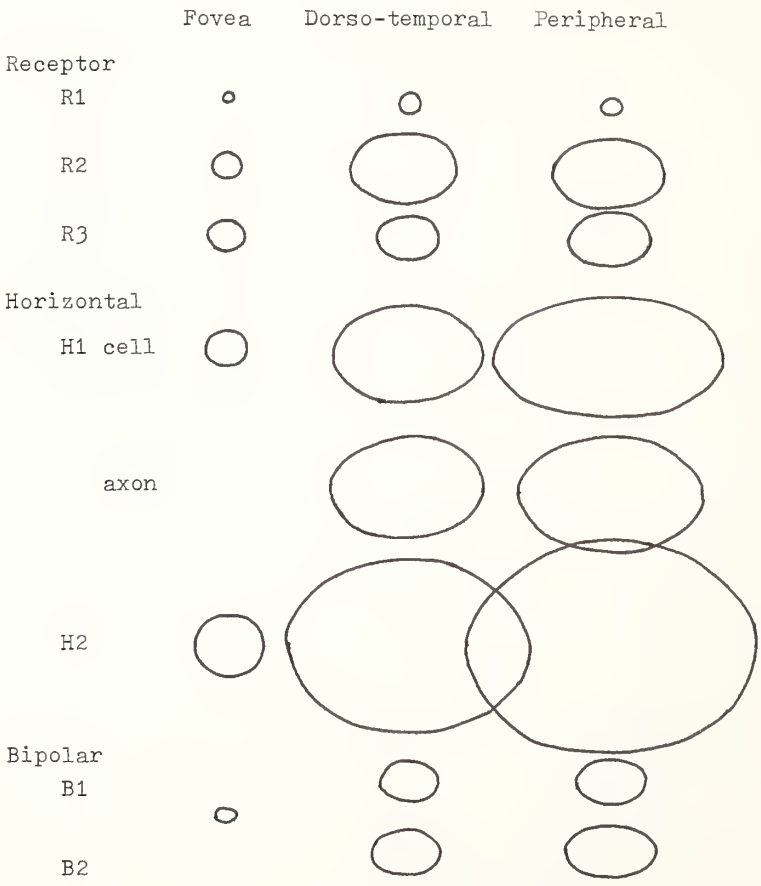


B.

Figure 21. Scale drawings illustrate the relative sizes of blue jay retinal cells. A shows dimensions of cells which terminate in the outer plexiform layer, while B shows dimensions of cells terminating in the inner plexiform layer. Process-field dimensions are illustrated for each cell type.

A. OUTER PLEXIFORM LAYER

Scale: 10 μ = ⊢



B. INNER PLEXIFORM LAYER

Scale: 50 μ = ⟼

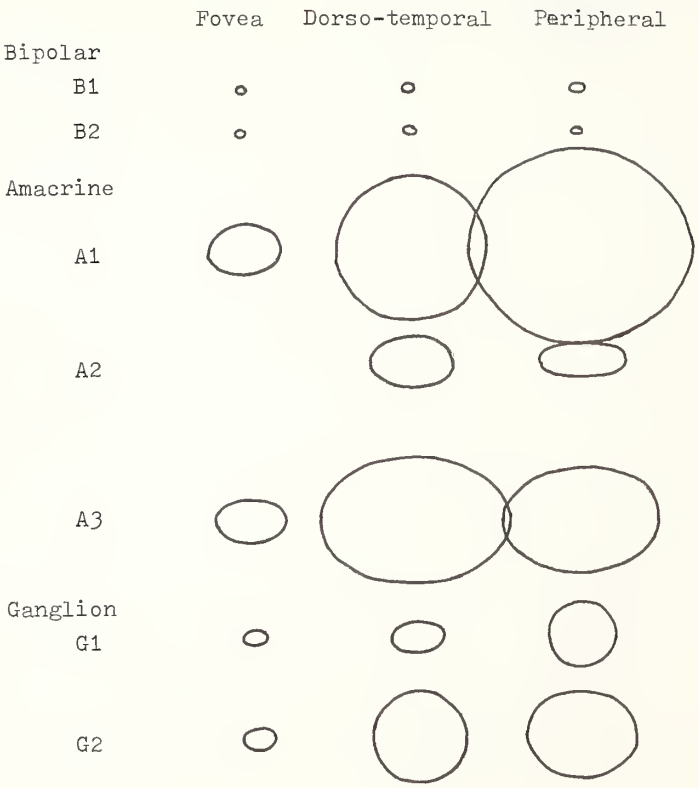
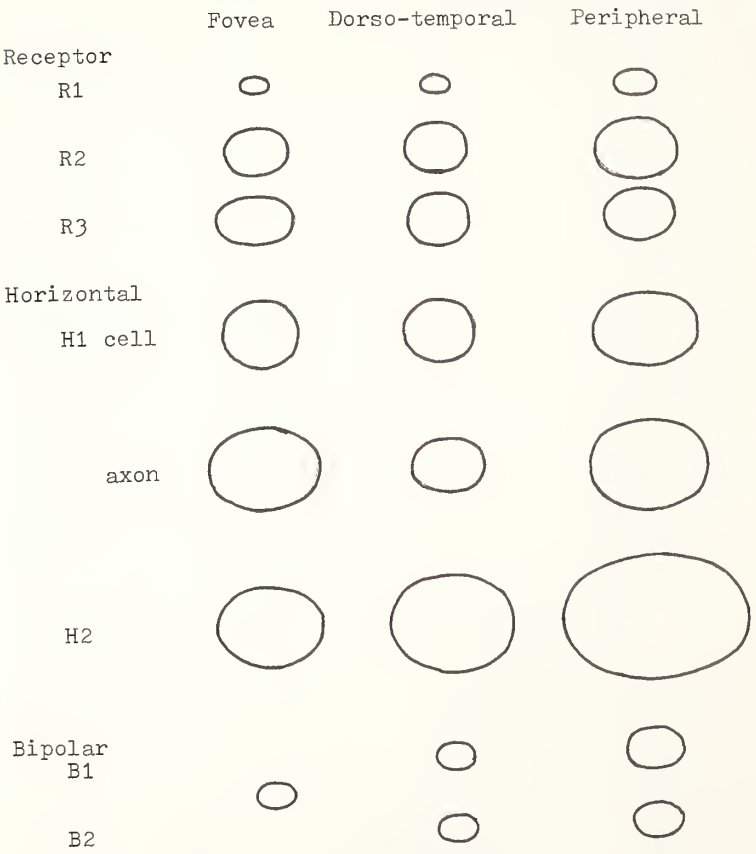


Figure 22. The relative sizes of retinal cells in the pigeon are illustrated with scale drawings. A shows process-field dimensions for cells which terminate in the outer plexiform layer, while B illustrates process-field dimensions for cells which terminate in the inner plexiform layer.

A. OUTER PLEXIFORM LAYER

Scale: 10 μ = ⟝



B. INNER PLEXIFORM LAYER

Scale: 50 μ = ⊢⊣

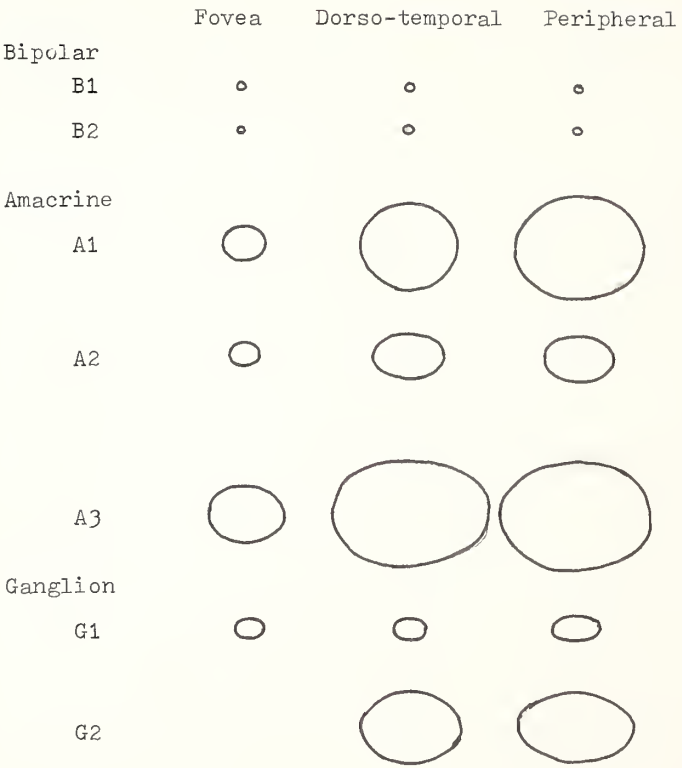
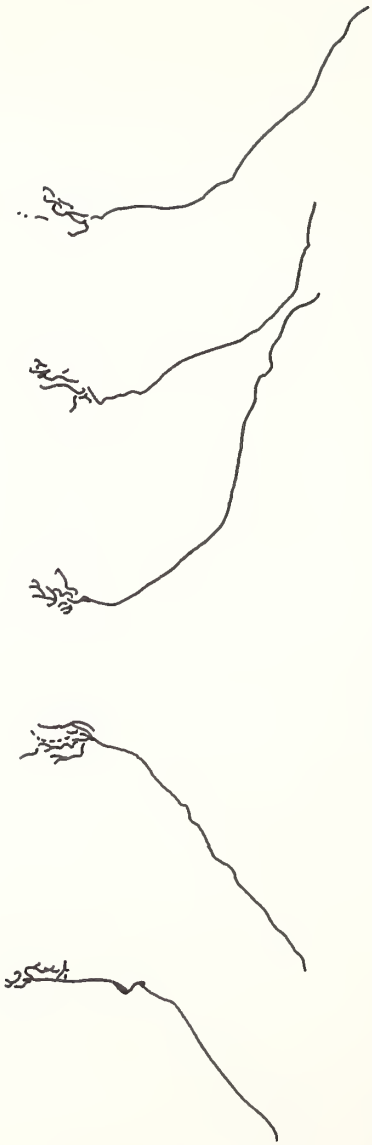


Figure 23. Distal (dendritic) expansions of small field foveal bipolar cells. Drawn at X1000.



| سر 10 |

Figure 24. Primate and avian small field foveal ganglion cells. A shows midget ganglion cells from the primate fovea and parafovea, and is redrawn from Polyak, 1941. B shows the two smallest ganglion cells observed in avian foveas. The scale is approximately the same for the two drawings.

A.

B.

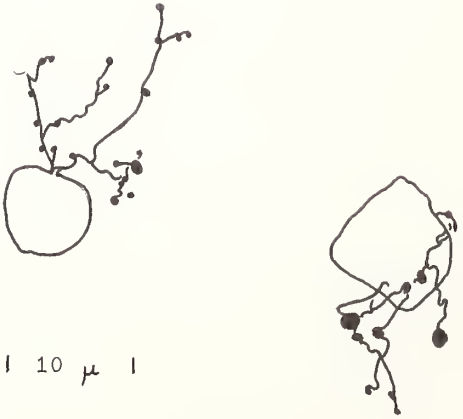
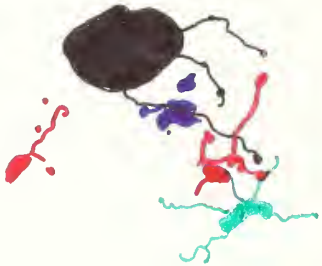


Figure 25. Small field ganglion cells from the foveal area and nearby bipolar terminal processes. Depth at which processes occurred in the inner plexiform layer is indicated by the color of the cells. The large, black central cells are ganglion cells. Using the vitreal border of the inner plexiform layer as a baseline, the depths of the processes are as follows:

For A,	ganglion dendrites	(Black)	= 16
	bipolar axons	(Blue)	= 24
		(Red)	= 31
		(Green)	= 41
For B,	ganglion dendrites	(Black)	= 22
	bipolar axons	(Blue)	= 18
		(Red)	= 35

A.



B.

10 µ

Figure 26. Distribution of foveal bipolar dendritic field sizes for the blue jay. The area of bipolar fields was determined and rounded to the nearest micron. Brackets in the upper left corner indicate range and mean sizes of receptor cell synaptic bases. The arrow at the lower baseline indicates the mean size of primate midget bipolar dendritic fields, corrected for eye size and visual field dimensions (derived from Boycott and Dowling, 1969 and Dowling, 1965).

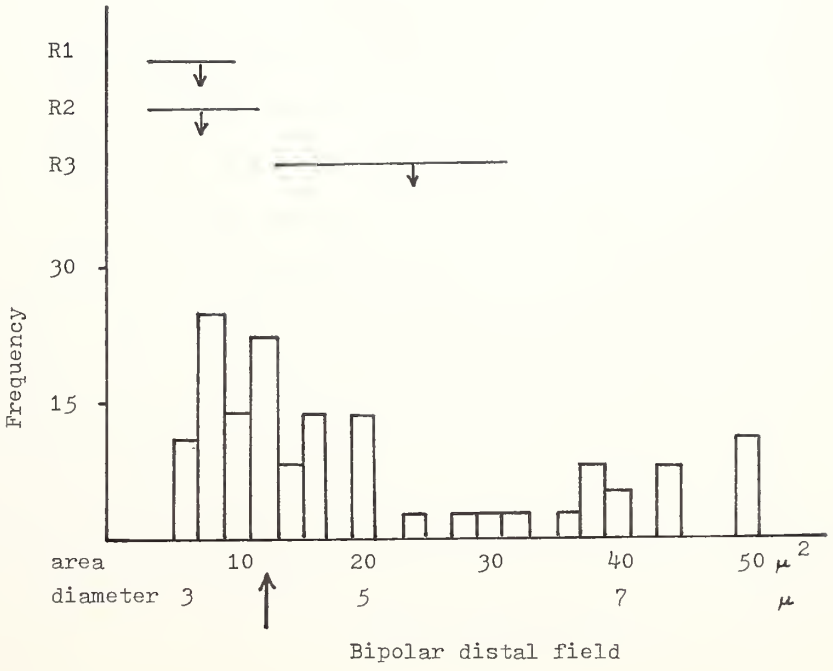

R1
R2
R3
30
15
Frequency
area
10
20
30
40
50 μ 2
diameter 3
5
7
μ
Bipolar distal field

Figure 27. Distribution of foveal bipolar dendritic field sizes for the pigeon. See caption for Figure 26.

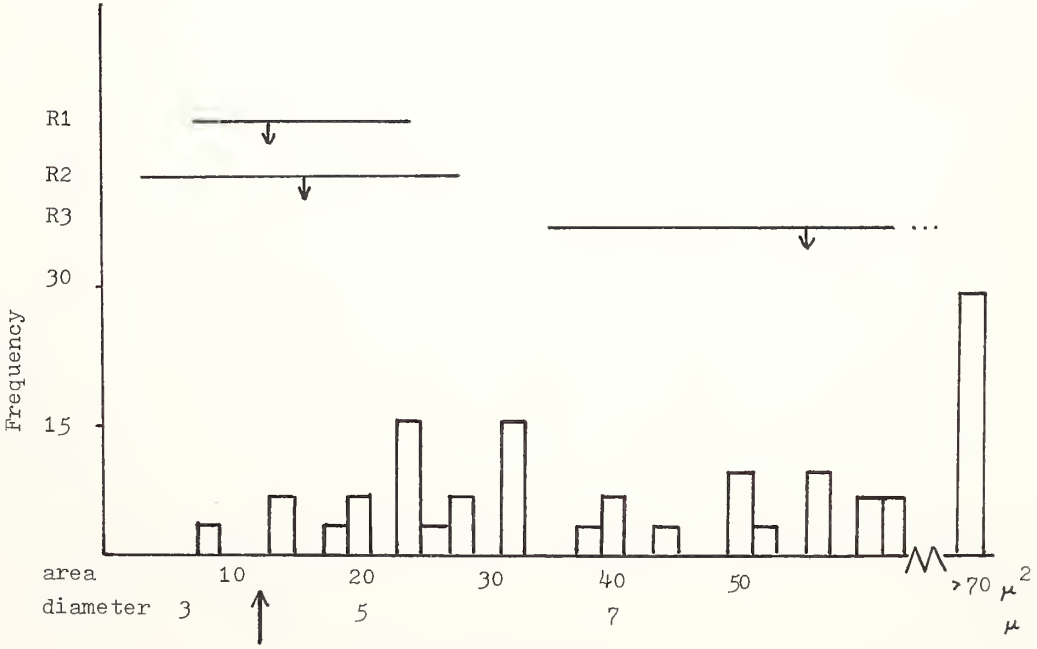

R1
R2
R3
30
15
Frequency
area
diameter
10
20
30
40
50
>70 μ²
3
5
7
μ
Bipolar distal field

Figure 28. Distribution of ganglion-cell field sizes in the blue jay fovea. Areas of G1 cell dendritic fields were determined, since they are smaller than G2 fields. The range of bipolar axonal areas for the foveal region is shown in the upper left corner of the graph. The arrow indicates the mean value for each cell type. Both B2 field sizes were averaged to yield a single value. The arrow at the baseline indicates the maximum areal extent for primate midget ganglion cell dendritic fields, as reported by Boycott and Dowling, 1969. The primate value has been corrected for differences in eye size and field of vision.

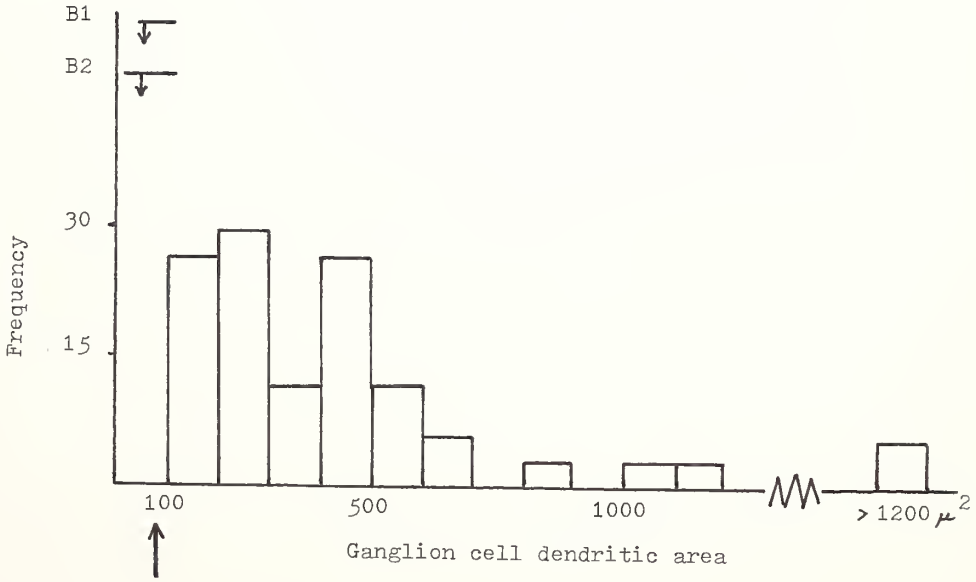

B1
B2
30
15
Frequency
100
500
1000
> 1200 μ2
Ganglion cell dendritic area

Figure 29. Distribution of ganglion-cell dendritic field areas in the pigeon fovea. See caption for Figure 28.

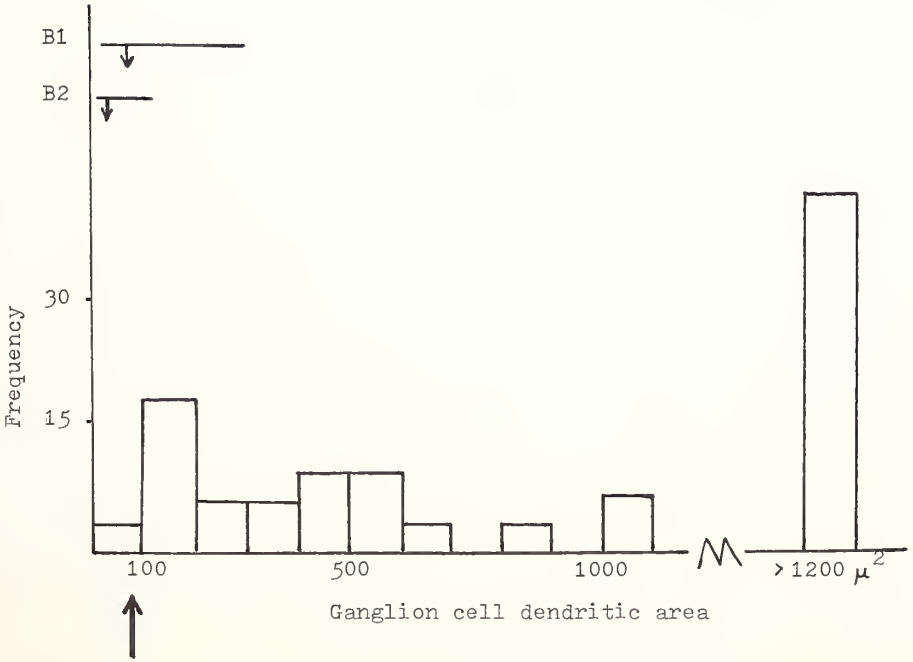

B1
B2
30
15
Frequency
100
500
1000
> 1200 μ²
Ganglion cell dendritic area

TABLE 1: Retinal Dimensions in Pigeon and Blue Jay

Species	Retinal Length (mm)	Visual Field (one eye, °)	Mean Microns Per Visual Degree	Corrected For 20% Shrinkage
Pigeon	23.3	166	140	175 μ/°
Blue Jay	22.8	168	136	170 μ/°

TABLE 2: Numbers of Cells Measured for Quantitative Comparisons

OUTER PLEXIFORM LAYER

CELL TYPE:		R1	R2	R3	H1 cell	H1 axon	H2	B1	B2
Pigeon	Foveal	63	71	34	126	88	46	- 138 -	
	Dorso-temporal	29	137	36	108	85	42	99	94
	Peripheral	32	181	75	103	63	61	104	102
Blue Jay	Foveal	45	107	32	48	--	37	- 89 -	
	Dorso-temporal	35	116	43	103	105	39	85	152
	Peripheral	31	146	37	100	47	28	156	91

INNER PLEXIFORM LAYER

CELL TYPE:		B1	B2	A1	A2	A3	multi A	G1	G2
Pigeon	Foveal	91	26	29	26	49	--	97	--
	Dorso-temporal	38	56	44	30	77	62	151	28
	Peripheral	79	61	28	46	108	75	125	30
Blue Jay	Foveal	61	45	42	--	120	--	135	28
	Dorso-temporal	63	128	67	62	77	47	78	24
	Peripheral	56	110	32	63	87	27	93	42

TABLE 3: Process-field Diameter of Photoreceptor Cells, in microns.

Species	Cell Type		Location: Foveal	Dorso-temporal	Peripheral
Pigeon	R1	mean	4X9	5X8	6X13
		range	3X3 - 10X12	3X5 - 5X13	3X5 - 7X22
	R2	mean	13X19	13X18	17X24
		range	8X8 - 22X25	7X11 - 18X27	7X11 - 28X32
	R3	mean	14X23	15X19	14X21
		range	12X15 - 16X44	10X16 - 20X22	10X12 - 22X27
Blue Jay	R1	mean	2.5X3	5X7	5X7
		range	2X2 - 3X4	3X4 - 8X10	3X4 - 10X10
	R2	mean	7X8	19X31	20X32
		range	5X5 - 10X10	12X12 - 30X58	6X13 - 37X75
	R3	mean	8X10	12X17	16X23
		range	5X8 - 10X14	10X12 - 15X22	12X18 - 20X35

TABLE 4: Diameter of Photoreceptor Synaptic Bases, in microns.

Species	Cell Type		Location: Foveal	Dorso-temporal	Peripheral
Pigeon	R1	mean	4X4	4X4	5X5
		range	2X2 - 5X6	3X3 - 6X6	4X4 - 8X8
	R2	mean	4X5	5X5	4X5
		range	2X2 - 6X6	3X4 - 5X7	3X3 - 5X7
	R3	mean	7X10	6X7	7X9
		range	6X8 - 8X15	5X6 - 6X9	5X7 - 7X10
Blue Jay	R1	mean	3X3	5X6	5X6
		range	2X2 - 3X4	4X4 - 7X8	2X4 - 7X8
	R2	mean	3X3	4X6	5X6
		range	2X2 - 3X5	4X4 - 7X8	4X4 - 10X12
	R3	mean	5X6	6X9	8X11
		range	4X4 - 7X7	5X7 - 6X12	7X9 - 8X14

TABLE 5: Number of Basal Processes for Photoreceptor Cells

Species	Cell Type		Location: Foveal	Dorso-temporal	Peripheral
Pigeon	R2	mean	13	11	11
		range	6-17	5-20	5-20
	R3	mean	11	13	13
		range	8-20	9-15	8-19
Blue Jay	R2	mean		8	8
		range		4-20	5-21
	R3	mean		10	12
		range		10-16	8-15

TABLE 6: Process-field Diameters for Horizontal Cells, in microns

Species	Cell Type		Location: Foveal	Dorso-temporal	Peripheral
Pigeon	H1 Cell	mean	19X23	17X21	21X32
		range	12X14 - 30X30	10X13 - 19X36	17X19 - 27X53
	Terminal				
		mean	24X31	14X20	25X34
		range	23X25 - 32X37	10X13 - 22X35	18X20 - 38X44
	H2 Cell	mean	22X32	27X36	34X55
		range	12X15 - 38X60	15X17 - 55X65	15X17 - 45X70
Blue Jay	H1 Cell	mean	10X12	27X43	33X67
		range	9X10 - 20X24	20X20 - 45X78	20X27 - 45X75
	Terminal				
		mean	--	28X44	32X53
		range		22X25 - 38X78	30X45 - 38X78
	H2 Cell	mean	17X19	56X70	59X85
		range	11X14 - 20X26	20X31 - 125X140	25X40 - 110X150

TABLE 7: Length of Horizontal Cell "Axons", in microns

Species	Cell Type	Location		
		Foveal	Dorso-temporal	Peripheral
Pigeon	H1 Cell mean	26	26	34
	range	12 - 50	14 - 52	17 - 150
	H1 Terminal			
	mean	44	20	32
	range	10 - 115	10 - 63	12 - 63
Blue Jay	H1 Cell mean	9	85	95
	range	8 - 10	20 - 160	20 - 200
	H1 Terminal			
	mean	--	86	123
	range		10 - 230	50 - 240

TABLE 8: Cell Body Diameters for Horizontal Cells, in microns

		Location		
Species	Cell Type	Foveal	Dorso-temporal	Peripheral
Pigeon	H1 mean	6X6	5X6	6X7
	range	4X5 - 8X8	4X5 - 6X8	4X5 - 7X10
	H2 mean	6X6	5X7	7X9
		5X5 - 6X10	5X5 - 5X10	5X5 - 10X20
Blue Jay	H1 mean	5X5	8X9	8X10
	range	4X4 - 6X8	6X6 - 10X12	7X7 - 10X12
	H2 mean	6X6	7X8	8X9
		5X5 - 8X8	5X5 - 10X10	7X7 - 9X10

TABLE 9: Field Diameters of Distal Processes of Bipolar Cells, in microns

Species	Cell Type	Location		
		Foveal	Dorso-temporal	Peripheral
Pigeon	B1 mean		8X11	12X17
	range	7X10	4X6 - 14X20	5X5 - 23X25
	B2 mean	3X3 - 13X18	8X12	10X14
	range		6X6 - 12X24	6X6 - 12X24
Blue Jay	B1 mean		12X17	12X21
	range	4X6	3X5 - 31X28	3X10 - 28X31
	B2 mean	3X3 - 13X15	13X20	14X27
	range		4X6 - 32X42	6X12 - 32X42

TABLE 10: Diameters of Bipolar Cell Bodies, in microns

Species	Cell Type	Location		
		Foveal	Dorso-temporal	Peripheral
Pigeon	B1 mean		5X6	6X6
	range	6X7	5X5 - 8X8	5X5 - 7X8
	B2 mean	5X5 - 8X8	6X7	6X7
	range		5X5 - 7X8	5X5 - 7X8
Blue Jay	B1 mean		6X7	7X7
	range	6X8	5X6 - 8X9	5X5 - 8X10
	B2 mean	4X6 - 7X9	6X7	6X7
	range		5X5 - 8X10	4X5 - 8X10

TABLE 11: Field Diameters of Proximal Processes of Bipolar Cells, in microns

Species	Cell Type	Location: Foveal	Dorso-temporal	Peripheral
Pigeon	B1 mean	7X11	10X15	9X14
	range	5X6 - 15X25	4X7 - 18X42	3X5 - 42X18
	B2 -Outer			
	mean	7X9	11X15	11X15
	range	3X3 - 10X12	3X6 - 24X36	4X6 - 24X36
	-Inner			
	mean	5X8	6X8	6X14
	range	3X3 - 5X12	3X4 - 7X30	3X4 - 12X18
Blue Jay	B1 mean	6X10	12X17	10X18
	range	6X7 - 12X13	6X6 - 22X45	3X7 - 23X45
	B2 -Outer			
	mean	6X11	10X20	11X21
	range	4X5 - 7X20	2X7 - 24X26	2X7 - 23X35
	-Inner			
	mean	5X10	10X17	12X22
	range	3X4 - 7X20	2X5 - 19X36	2X7 - 20X45

TABLE 12: Diameters of Amacrine Cell Process Fields, in microns

Species	Cell Type	Location		
		Foveal	Dorso-temporal	Peripheral
Pigeon	A1 median	48X60	125X138	150X190
	range	20X25 - 160X325	25X50 - 225X320	75X140 - 240X260
	A2 median	33X45	58X105	60X98
	range	20X30 - 100X125	50X65 - 135X160	30X40 - 100X150
	A3 median	78X113	150X225	150X218
	range	50X70 - 450X650	50X55 - 225X500	60X70 - 600X1000
	multi median	---	43X75	50X75
	range		15X35 - 100X200	15X35 - 100X170
Blue Jay	A1 median	70X103	200X220	280X325
	range	30X60 - 200X200	40X75 - 1200X1500	70X75 - 800X1000
	A2 median	---	75X125	85X125
	range		50X50 - 200X225	25X60 - 100X200
	A3 median	58X100	175X275	150X230
	range	25X35 - 140X220	20X25 - 400X800	60X90 - 650X1200
	multi median	---	50X65	50X100
	range		30X35 - 160X250	25X50 - 125X150

TABLE 13: Diameter of Amacrine Cell Bodies, in microns

Species	Cell Type	Location: Foveal	Location: Dorso-temporal	Location: Peripheral
Pigeon	A1 mean	--	9X10	10X12
	A2 mean	6X7	9X10	8X9
	A3 mean	10X11	10X11	10X11
	multi mean	--	9X9	9X9
Blue Jay	A1 mean	8X9	9X10	10X10
	A2 mean	--	7X8	9X10
	A3 mean	7X8	9X10	11X12
	multi mean	--	8X8	9X9

TABLE 14: Process-field Diameters of Ganglion Cells, in microns

Species	Cell Type		Location: Foveal	Dorso-temporal	Peripheral
Pigeon	G1	median	25X42	30X45	35X70
		range	10X10 - 300X335	5X7 - 125X600	10X15 - 375X750
	G2	median		100X152	100X172
		range		50X75 - 175X325	25X50 - 240X275
Blue Jay	G1	median	16X35	45X75	90X100
		range	10X15 - 80X90	12X24 - 250X340	16X25 - 250X340
	G2	median	27X45	130X135	127X165
		range	12X23 - 60X90	60X60 - 175X200	70X100 - 150X240

TABLE 15: Diameters of Ganglion Cell Bodies, in microns.

Species	Cell Type	Location		
		Foveal	Dorso-temporal	Peripheral
Pigeon	G1 median	10X12	9X13	11X14
	range	8X8 - 20X22	8X8 - 20X30	5X5 - 25X25
	G2 median	--	12X14	12X17
	range		8X8 - 25X25	6X15 - 20X23
Blue Jay	G1 median	9X11	12X15	16X19
	range	7X7 - 12X16	6X7 - 25X25	8X8 - 25X25
	G2 median	9X11	15X19	20X25
	range	4X10 - 10X12	6X6 - 20X25	15X20 - 25X27

TABLE 16: Mean Length of Ganglion Cell Axons and Proportions of Cells with Axon.

Species	Cell Type	Location		
		Foveal	Dorso-temporal	Peripheral
Pigeon	G1 length ($\bar{X}$)	29 μ	48 μ	56 μ
	percent	46	57	68
	G2 length ($\bar{X}$)	--	53 μ	45 μ
	percent		75	50
Blue Jay	G1 length ($\bar{X}$)	21 μ	34 μ	43 μ
	percent	36	46	48
	G2 length ($\bar{X}$)	19 μ	45 μ	31 μ
	percent	38	71	66

TABLE 17: Dimensions of "Midget" Bipolar Cells in the Pigeon Red Field

Cell Type	Proportion in Red Field	Mean Distal Field Area	Mean Proximal Field Area
"Midget" B1	0.21	24 μ^2	42 μ
"Midget" B2	0.19	28 μ^2	vitreal: 19 μ scleral: 110 μ

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