CHAPTER

1

Sensory Physiology: Vision

ONUR GÜNTÜRKÜN

AE Biopsychologie
Fakultät für Psychologie
Ruhr-Universität Bochum
44780 Bochum
Germany

I. INTRODUCTION

Birds are the most visually dependent class of vertebrates and the phrase of Rochon-Duvigneaud (1943) that a pigeon is nothing else but two eyes with wings is probably valid for most avian species. Man, a highly visual primate, sees the world with the information transmitted by about one million fibers within each of his optic nerves. This is only 40% of the number of retinal axons counted in a single optic nerve of pigeons and chicks (Binggeli and Paule, 1969; Rager and Rager, 1978). The acuity of many birds of prey surpasses that of other living beings (Fox *et al.,* 1976) and even the unspecialized pigeon excels relative to humans in its ability to discriminate luminances (Hodos *et al.,* 1985) and discern subtle color differences (Emmerton and Delius, 1980). Food-storing birds like Clark's nutcracker store 33,000 seeds in about 6,600 caches to survive in winter (Vander Wall and Balda, 1977). Pigeons acquire visual concepts of, for example, "animals" (Roberts and Mazmanian, 1988), "same versus different" (Wright *et al.,* 1988), and even cartoon figures such as "Charlie Brown" (Cerella, 1980). They communicate using visual symbols (Lubinski and MacCorquodale, 1984) and are able to rank optic patterns by using transitive inference logic (von Fersen *et al.,* 1992). If we, on the basis of countless evidence, assume that the visual system of amniotes has evolved only once (Shimizu and Karten, 1993), the avian visual system is a remarkable model to explore its morphology, its modes of operations, and the unanticipated complexity of its function.

II. STRUCTURE AND FUNCTIONS OF THE EYE

Avian eyes take up a considerable volume of the bird's head and are very large in relation to brain size (Figure 1). In general terms, the structure of their eyes is not much different from that of other vertebrates. Incoming light has to pass through four media: the cornea, the anterior chamber, the lens, and the vitrous body, before reaching the retina, where photoreceptors convert light energy into electric impulses by bleaching of visual pigments. All four optic media are remarkably transparent, transmitting wavelengths down to at least 310 nm in the near-ultraviolet range (Emmerton *et al.,* 1980).

The avian retina is completely avascularized to prevent shadows and light scattering. This arrangement is associated with the presence of an unusual nutritional device specific for birds—the pecten. This black pig-

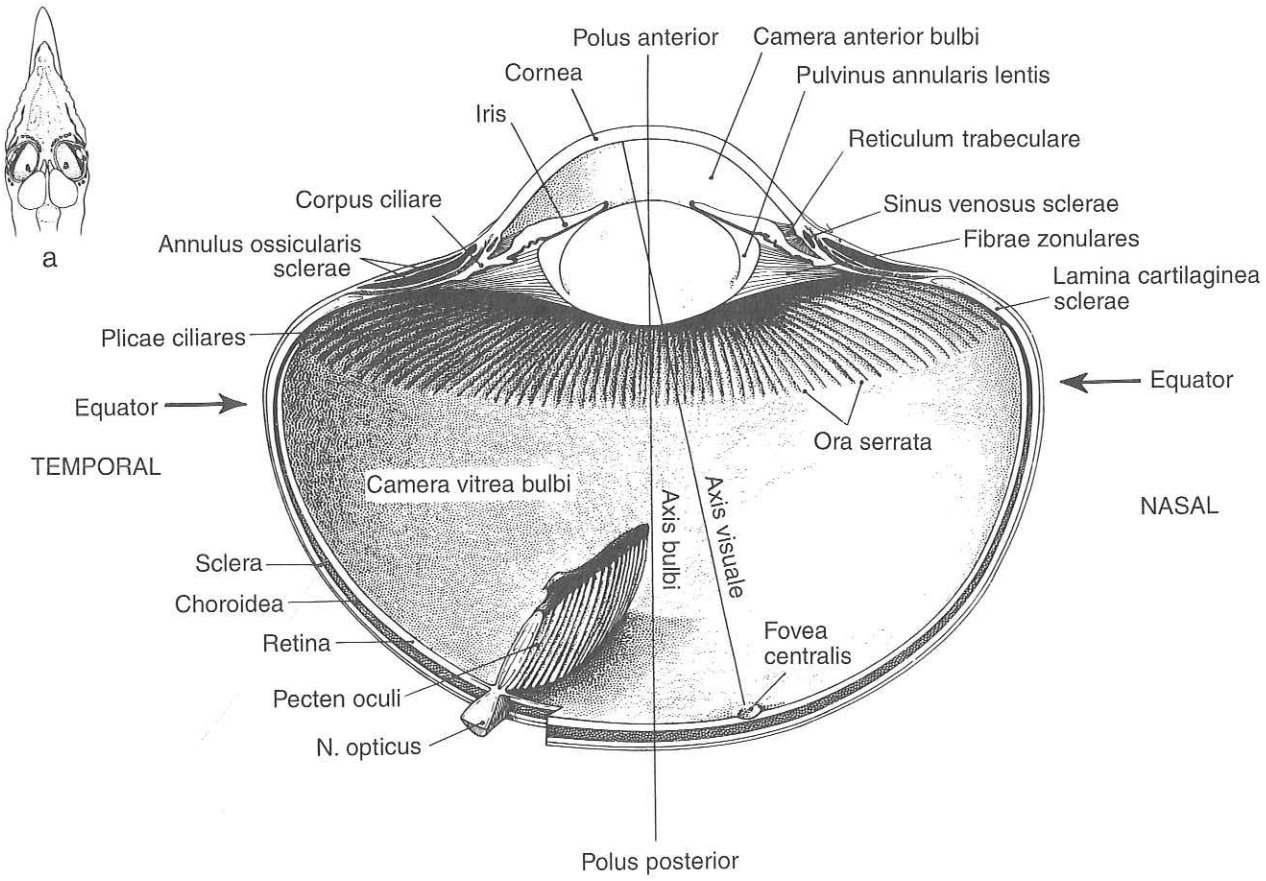

FIGURE 1 Drawing of a horizontal section of the chicken eye showing the position of the eyes within the head. (From H. Evans, 1996.)

mented and manifoldly pleated structure projects from the ventral retina above the exit of the optic nerve toward the lens and is completely made up of blood vessels and extravascular pigmented stromal cells. There is evidence that it also has a nutritive function. This is shown by the presence of an oxygen gradient from the pecten to the retina, the passing of nutrients from the pecten into the vitreous, and the observation that fluorescent markers pass from the pecten into the vitreous (Bellhorn and Bellhorn, 1975). Also, Pettigrew *et al.* (1990) posit that the inertia of the pecten during saccadic eye movements could be used like a shaker to propel oxygen and nutrients within the eye.

A. Eye Shape, Stereopsis, and Acuity

The eyeshapes of birds are a result of ecological requirements (Figure 2). Generally, acuity can be maximized by increasing the anterior focal length of an eye; the optic image is then spread over a larger retinal surface and thus over a larger number of photoreceptors (Martin, 1993). Increasing the number of photorecep-

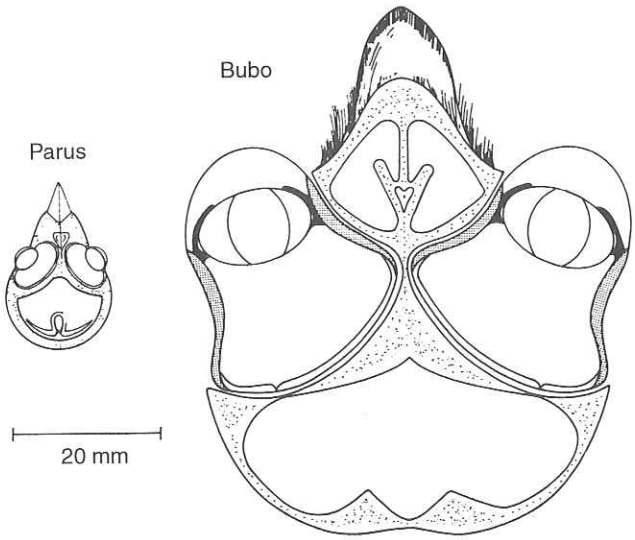

FIGURE 2 Horizontal section through the head of the black-capped chickedee (*Parus atricapillus*) and the great owl (*Bubo virginianus*). (From *Perception and Motor Control in Birds,* Form and function in the optical structure of bird eyes, G. R. Martin, pp. 5–34, Fig. 1.2, 1994, © Springer-Verlag.)

tors also makes it possible to connect several receptors to single bipolar cells and thus to maximize visual detection even under low light conditions. Since an increase in eye size is advantageous, birds, which rely heavily on vision, generally have the largest absolute and relative eyes within the animal kingdom. The eye of the ostrich, for example, has an axial length of 50 mm, the largest of any land vertebrate and twice that of the human eye (Walls, 1942). The tube-shaped eyecups of birds of prey, which create an extremely large image on the retina, represent another extreme version of biological optimization to achieve high acuity. These eyes generally also have a low retinal convergence ratio (receptors per ganglion cell) so that the receptor inputs are not pooled to increase visual resolution (Snyder *et al.,* 1977). However, these optimizations are limited by trade-offs for brightness sensitivity. Retinae in which receptors are not pooled function only optimally at high light intensities and, indeed, resolution of birds of prey deteriorates at dusk (Reymond, 1985).

Visual acuity measurements in pigeons (*Columba livia*) have shown that the acuity in the frontal field depends on stimulus time (Bloch and Martinoya, 1982), wavelength of light (Hodos and Leibowitz, 1977), luminance (Hodos *et al.,* 1976; Hodos and Leibowitz, 1977), and age of the pigeon (Hodos *et al.,* 1991a). Under favorable conditions 1-year-old pigeons reach a frontal acuity of 12.7 c/deg, increase this value to 16–18 c/deg at 2 years, and decline to 3 c/deg at 17 years (Hodos *et al.,* 1985, 1991b). The frontal binocular visual field of pigeons is represented in the superiotemporal area dorsalis, while the lateral monocular visual field is observed via the area centralis (both lack a true foveal depression). These two retinal regions seem to subserve different visual functions with differing capacities for optic resolutions. Behavioral studies show that many avian species, including pigeons, fixate distant objects preferentially with their lateral and monocular field (pigeon: Blough, 1971; dove: Friedman, 1975; kestrel: Fox *et al.,* 1976; eagle: Reymond, 1985; passerine birds: Bischof, 1988; Kirmse, 1990). This behavior is often pronounced; birds orient themselves sideways in order to achieve a lateral orientation to the inspected object. This behavior, together with the fact that retinal ganglion cell densities reach peak values in the central fovea, suggest that resolution is maximal in the lateral visual field. However, the acuity of young pigeons is 12.6 c/deg in their lateral visual field and thus identical with the values obtained for frontal vision in same aged subjects (Hahmann and Güntürkün, 1993). However, lateral acuity measurements are naturally obtained under monocular conditions, while frontal acuity is generally tested binocularly. In humans, binocular sensitivity can almost double that of one-eyed viewing (Pirenne, 1943). This same effect is known in pigeons and possibly depends on probability summation of the input of both eyes (DiStefano *et al.,* 1987; Kusmic *et al.,* 1991). The power of this mechanism is visible when pigeons are frontally tested under monocular conditions. Their acuity then drops to a mean of 6.5 c/deg and thus to less than half the value obtained under binocular conditions (Güntürkün and Hahmann, 1994). If only monocular data are used to compare frontal and lateral acuity, resolution in the lateral field (12.6 c/deg) is considerably higher than in the frontal field (6.5 c/deg). These psychophysical data are in perfect accord with the observations that many bird species prefer to use their lateral visual field for a detailed inspection of distant objects.

These acuity data are easily surpassed by some birds of prey. The wedge-tailed eagle *Aquila audax* reaches a maximum acuity of 143 c/deg, more than two times higher than the human optic resolution measured under identical conditions (Reymond, 1985). These values are even surpassed by the American kestrel *Falco sparverius.* The acuity threshold of this falcon was measured to be 160 c/deg, which would enable this animal to discriminate 2-mm insects from 18-m-high treetops (Fox *et al.,* 1976). In both studies, these birds of prey were reported to be considerably luminance dependent with acuity dropping to 58 c/deg at 2 cd/m^2 in the wedge-tailed eagle (Reymond, 1985). Thus, while visual adaptations allow for high acuity they necessitate a loss of optical sensitivity. Not all birds of prey, however, reach high acuity values. The nocturnal barn owl *Tyto alba,* which heavily relies on auditory cues to detect prey, reaches an acuity of only 8.4 c/deg as predicted from its retinal ganglion cell density (Wathey and Pettigrew, 1989).

The ability to focus the eye to see objects at various distances sharply is called accomodation; it is achieved by alterations in corneal curvature and by lens deformation and constitutes one of the most important mechanisms of achieving high visual resolution. In addition to these dynamic accommodation mechanisms, some birds possess static mechanisms which keep objects along the ground in focus, irrespective of their distance. This is achieved by asymmetries of the eye such that it is emmetropic in its superior parts but increasingly myopic with decreasing elevation (Fitzke *et al.,* 1985). As a result, objects along the horizon or in the upper visual field are in focus together with objects at various distances on the ground. The degree of this lower-field myopia seems to adjust to the height of the head of the animal so that cranes can also benefit from its effect (Hodos and Erichsen, 1990). The presence of a lower field myopia would not be advantageous for raptors which pursue and capture their mobile prey, the prey often being seen with their lower field of view. Conse-

quently, Murphy *et al.* (1995) demonstrated that raptors lack lower-field myopia.

B. Retina

1. Oil Droplets, Photoreceptors, and Color Vision

Differing from those of placentalia, avian eyes are characterized by the presence of oil droplets within the distal end of the inner segment of their cones. Microspectrophotometric studies show that oil droplets act as cut-off filters and absorb light below their characteristic wavelength of transmission (Emmerton, 1983b). Colored oil droplets thus provide a protective shield against UV light, similar to the yellowish lenses of mammals. Additionally they probably act as lenses which focus light onto the photoreceptor, thus increasing the quantum reception of visual pigments (Young and Martin, 1984). A detailed inspection shows at least five different-colored types of oil droplets depending on the presence, mixture, and concentration of different carotenoids: red, orange, greenish-yellow, pale, and transparent (Varela *et al.,* 1993).

The spectral sensitivity of an avian cone is the result of the relation between the spectral transmittance of the oil droplets and the spectral absorptance of the visual pigments. This condition creates the possibility that birds can increase the number of their chromatic channels by varying the combinations of oil droplets and cone pigments. Indeed, there is evidence that at least some bird species have two absorption maxima operating with one visual pigment which is associated with two different oil droplets (Jane and Bowmaker, 1988). Birds studied up to now have at least three to four cone pigments which, together with their associated oil droplets, create spectral sensitivity maxima reaching from 370 to 580 nm (Chen and Goldsmith, 1986).

Another feature that increases the complexity of color perception in birds is the differential distribution of oil droplets across the retina. This hererogeneous distribution reaches an extreme in pigeons where the dorsotemporal "red field," with large numbers of red and orange droplets, is clearly separated from the remaining "yellow field," which is characterized by a high density of greenish-yellow droplets (Galifret, 1968). Bowmaker (1977) showed that the transmission curves of oil droplets in the red field are shifted 10 nm toward longer wavelengths. These data may indicate differences in color perception between different retinal areas in pigeons and, indeed, behavioral experiments demonstrate that colors backprojected onto two pecking keys are treated differently by pigeons when both are seen with the red field or when one is viewed with the red and the other with the yellow field (Delius *et al.,* 1981). The authors suggest that their results are due to a subjective discrepancy, as the birds perceived the two keys illuminated with light of identical spectral composition as being of different color when one was seen with the yellow and the other with the red field. However, probably the most important differentiation of color perception between retinal areas is related to UV sensitivity. Remy and Emmerton (1989) showed in a behavioral study with head-fixed pigeons that UV sensitivity is high in the yellow and low in the red field. Emmerton (1983a) additionally demonstrated that pigeons perform excellent pattern discrimination in UV. Thus, pigeons and several other avian species may use their UV sensitivity to view objects such as plumage or fruits reflecting UV light (Burkhardt, 1989).

2. Neuronal Wiring

The basic design of all vertebrate retinae is essentially the same and those of birds are no exception. Light passes through the neural retina and is transduced in the outer segments of photoreceptors to electrical signals which are relayed via bipolar cells to the ganglion cells and thus to the brain. Horizontal intraretinal interactions are provided by horizontal and amacrine cells which in birds are also partly responsible for long intraretinal projections. But imposed on this basic uniformity, there is wide variation in details (Thompson, 1991) (Figure 3).

In the diurnal pigeon, rods and principal members of the double cones terminate in the outer sublayer of the outer plexiform layer (OPL), the straight single cones in the middle sublayer, and the oblique single cones terminate exclusively in the inner sublayer of the OPL (Mariani and Leure-du Pree, 1978; Mariani, 1987; Nalbach *et al.,* 1993). According to morphological criteria, Mariani (1987) distinguished four types of horizontal and eight types of bipolar cells with each bipolar cell showing a distinct type of termination within the five sublayers of the inner plexiform layer (IPL). The diversity of amacrine cells described by Golgi techniques in the early 1980s (Mariani, 1983) turned out to be an extreme oversimplification as shown by immunocytochemical studies within the past decade. These experiments revealed amacrine cells specific for substance P (Ehrlich *et al.,* 1987), tyrosine hydroxylase (Keyser *et al.,* 1990), enkephalin (Britto and Hamassaki-Britto, 1992), glucagon (Keyser *et al.,* 1988), somatostatin Morgan *et al.,* 1983), 5-hydroxytryptamine (Kiyama *et al.,* 1985), avian pancreatic polypeptide (Katayama *et al.,* 1984), choline acetyltransferase (Millar *et al.,* 1987), neuropeptide Y (Verstappen *et al.,* 1986), neurotensin-related hexapeptide LANT-6 (Reiner, 1992), and GABA (Hamassaki-Britto *et al.,* 1991). Some of the substance

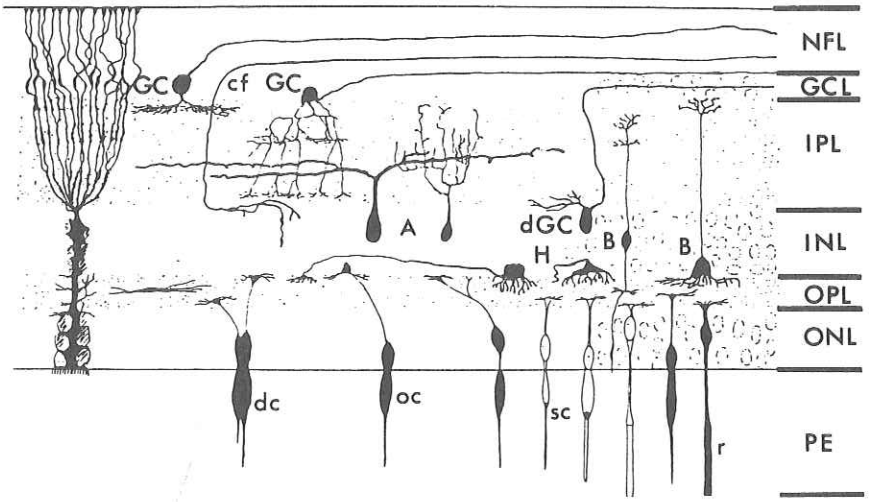

FIGURE 3 Schematic drawing of the avian retina. A, amacrine cell; B, bipolar cell; cf, centrifugal fiber; dc, double cone; dGC, displaced ganglion cell; GC, ganglion cell; GCL, ganglion cell layer; H, horizontal cell; INL, inner nuclear layer; IPL, inner plexiform layer; oc, oblique cone; ONL, outer nuclear layer; OPL, outer plexiform layer; PE, pigment epithelium containing the outer parts of the photoreceptors; r, rod; and sc, single straight cone. (From Nalbach *et al.,* 1993, *Vision, Brain and Behavior,* The MIT Press. © 1993 The MIT Press.)

P and/or glucagon-positive amacrine cells are the "bullwhip" neurons with long thin processes directed toward the posterodorsal pole of the retina (Ehrlich *et al.,* 1987; Keyser *et al.,* 1988). Catsicas *et al.* (1987a) could show that some amacrine cells, of which the bullwhip neurons probably represent a subclass, are localized within the central and ventral retina and project toward the superiodorsal retina. They suggested that the intraretinal connections may be involved in a system for switching attention between the upper and lower halves of the visual field, which could be modulated by centrifugal axons entering the retina from the contralateral tegmentum (Fritzsch *et al.,* 1990). It is interesting to note that these experiments demonstrate a one-way route from central and ventral retinal areas to the red field, but not vice versa. Mallin and Delius (1983) showed that pigeons can transfer information about discriminatory cues from the central retina to the red field, but not from the red field to the area centralis. Behaviorally, this asymmetry makes sense since pigeons spot seeds from a distance (central retina) and approach to peck them after making a final inspection in the binocular field (superiodorsal red field). The reverse behavioral pattern never occurs. There may be a neural basis for this behavioral constraint.

A subpopulation of ganglion cells is located within the inner nuclear layer (INL) and they are thus called "displaced ganglion cells" (DGCs) (Brecha and Karten, 1981). Medium-sized and large DGCs have dendrites which arborize for considerable distances in the outermost lamina of the IPL (Britto *et al.,* 1988), are predominantly distributed in the peripheral retina (Prada *et al.,* 1989; Prada *et al.,* 1992), and project to the avian accessory optic nucleus (Fite *et al.,* 1981; Yang *et al.,* 1989). A part of the DGCs are substance P positive (Britto and Hamassaki-Britto, 1991), while others are cholinergic (Britto *et al.,* 1988). Further aspects of the accessory optic system will be discussed in Chapter 4. Additionally, a population of DGCs appears to exist in the avian retina, which exhibit smaller soma sizes, are located centrally in the retina, and whose central connections are uncertain (Hayes and Holden, 1983).

Cajal (1892) described two main types of ganglion cells in the chicken retina: mono- and polystratified neurons. More modern attempts to classify avian retina ganglion cells into categories similar to that developed by Boycott and Wässle (1974) and Fukuda and Stone (1974) in cats did not lead to unequivocal results (Ikushima *et al.,* 1986). Hayes and Holden (1980) suggested, on the basis of perikaryal morphology and electrophysiological properties (Holden, 1978), that retinal ganglion cells projecting to the optic tectum would be comparable to W-cells. Studies in owls (Bravo and Pettigrew, 1981) and pigeons (Remy and Güntürkün, 1991) demonstrated that indeed the tectum receives its input from a large number of very small and a few very large ganglion cells while the GLd is characterized by its afferents from medium-sized and very large retinal neurons. These conditions suggest similarities to the differential sizes and central projections of cat alpha, beta, and gamma cells (Illing and Wässle, 1981). It should, however, be remarked that these assumptions rest on observations of soma diameters and projections and do not include any

data on dendritic morphology and axonal diameters. Additionally, electrophysiological studies demonstrated various ganglion cell properties in avian retinae with important deviations from the usual schema known from mammals (Maturana and Frenk, 1963, Miles, 1972a).

As outlined for amacrine cells, immunocytochemical analyses have demonstrated a very large number of diverse ganglion cells specific for certain transmitters or neuromodulators. Among them are neurons positive for cholecystokinin (Britto and Hamassaki-Britto, 1991), tyrosine hydroxylase (Keyser *et al.,* 1990), substance P (Britto and Hamassaki-Britto, 1991), dopamine (Karten *et al.,* 1990), GABA (Hamassaki-Britto *et al.,* 1991), LANT6 (Reiner, 1992), enkephalin (Britto and Hamassaki-Britto, 1992), and glutamate (Morino *et al.,* 1991). Such diversity in ganglion cell transmitters/modulators implies a far more heterogeneous influence of retinal axons on central targets than previously imagined and may require revision of the broadly held concept that ganglion cell classifications based on frequency coding and dendritic morphology provide sufficient information on the type of central effects of retinal inputs.

The retinae of birds are characterized by a large variation of different regional specializations (Figure 4). In pigeons the density of cells in the outer nuclear layer (ONL) and the inner nuclear layer (INL) as well as the ganglion cell layer (GCL) increase in the area centralis and the dorsotemporal red field, while a streak of slightly increased ganglion cell densities connects these two areas of enhanced vision (Galifret, 1968). This arrangement is typical for granivorous birds (pigeons: Binggeli and Paule, 1969; quail: Budnik *et al.,* 1984; but see chicks: Ehrlich, 1981) which probably have to switch

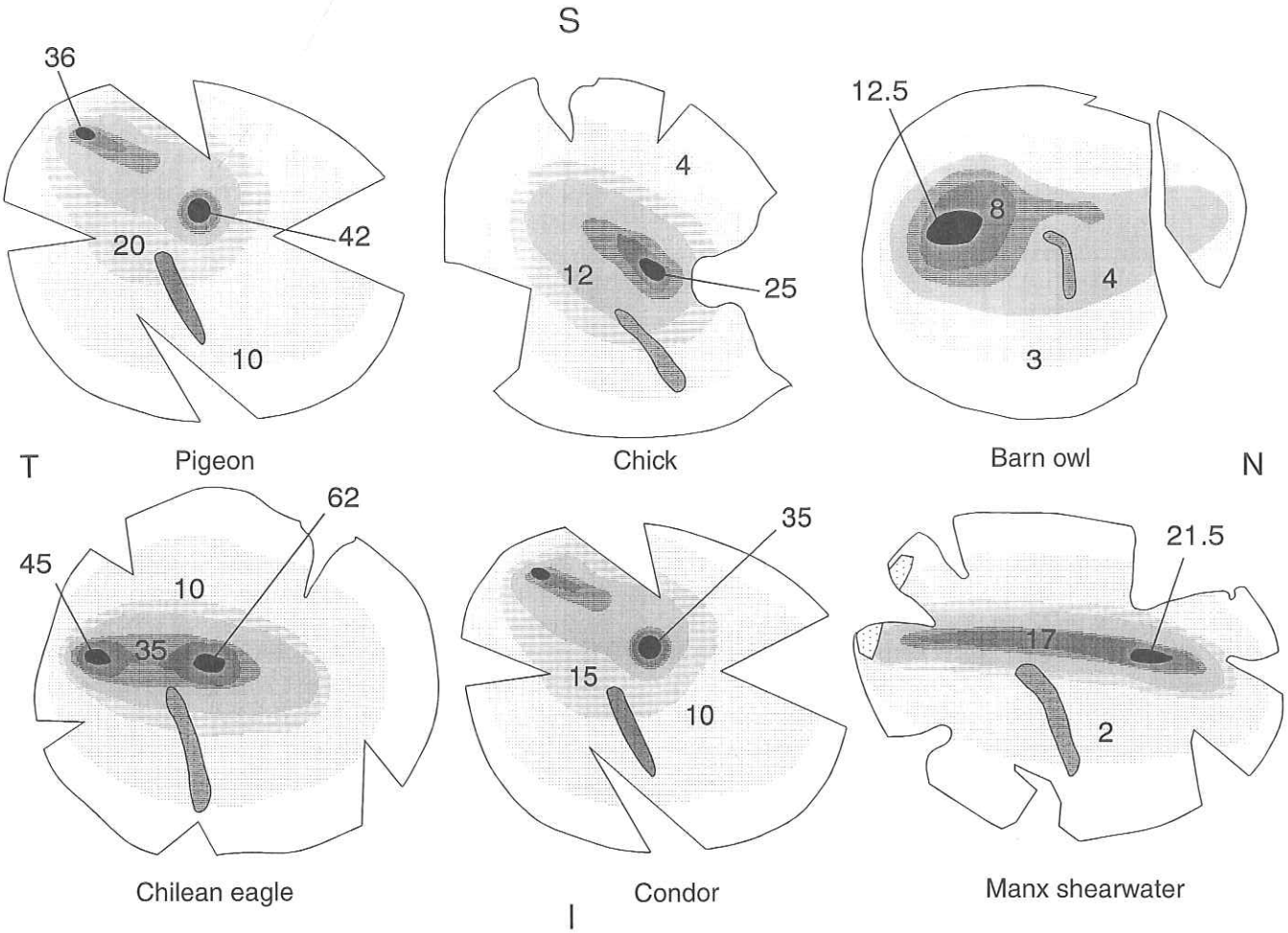

FIGURE 4 Distribution of ganglion cell densities in the retinae of six different bird species. All retinae are drawn to the same size and gray shadings indicate neuronal densities. Drawings according to Binggeli and Paule (1969; pigeon), Ehrlich (1981; chick), Wathey and Pettigrew, 1989; barn owl), Inzunza *et al.* (1991; chilean eagle and condor), and Hayes et al. (1991; Manx shearwater). The dark gray stippled structure is the pecten. The dotted region in the most superiotemporal retina of Manx shearwater is the area giganto cellularis. Numbers indicate 1.000/mm^2. Abbreviations: I, inferior; N, nasal; S, superior; and T, temporal.

between monocular lateral and binocular frontal vision. With regard to synaptic interactions, the dorsotemporal red field seems to be the most complex one, while the area centralis displays a very low synaptic complexity (Yazulla, 1974). Golgi studies make it likely that this is probably due to the area centralis being specialized for precise point-to-point interactions by a midget-like system that does not require extensive horizontal processing by amacrine cells (Lockhart, 1979, Quesada *et al.,* 1988).

A streak with two real foveae can be found in birds of prey like the American kestrel or the Chilean eagle *Buteo fuscenses,* which attack birds or rodents directly from flight and have to combine panoramic sight with excellent stereoscopic vision (Inzunza *et al.,* 1991). The density of ganglion cells reaches up to 65,000 mm^2 in the central fovea of these animals, which surpasses foval values from mammals with high acuity (human: 38,000 mm^2, Curcio and Allen, 1990; macaque: 33,000 mm^2, Perry and Cowey, 1985). Carrion-eating birds like the condor *Vultur gryphus* or the black vulture *Coragyps atratus* pursue their prey from the ground and are not in need of high stereoscopic vision. Consequently they not only have reduced ganglion cell densities within their visual streak but they also have lost their temporal fovea (Inzunza *et al.,* 1991). A single temporal fovea characterizes nocturnal predators like owls (Oehme, 1961, Wathey and Pettigrew, 1989), which have to summate light from both eyes under dim conditions. Diurnal birds living in open country generally have a pronounced streak aligned with the horizon (Duijm, 1985, Kirmse, 1990). According to phylogenetic conditions (Nalbach *et al.,* 1993) or the ecological habitat, specializations within this streak can be found. A prominent example is the area giganto cellularis along the ora serrata of the dorsotemporal retina in procellariiform seabirds (Hayes *et al.,* 1991). These are pelagic seabirds which come ashore only to breed and spend most of their life wandering close to the surface of the oceans, often within the troughs of the waves. According to Hayes *et al.* (1991), the location of this specialized retinal area and the morphology of its cells suggest a function in the detection of prey due to relative movements within a small binocular field projecting below and around the bill tip (Martin, 1993).

III. CENTRAL PROCESSING—ANATOMY AND FUNCTION

A. Centrifugal Pathway

The centrifugal visual system of birds originates in two different mesencephalic cell groups: the isthmo-optic nucleus (ION), a folded bilaminate structure in the dorsolateral midbrain tegmentum, and the nucleus of the ectopic isthmo-optic neurons (EION), a loosely scattered array of cells with reticular appearance surrounding the ION (Hayes and Webster, 1981, Wolf-Oberhollenzer, 1987). Both structures are part of a closed loop consisting of a projection from the retinal ganglion cells to the contralateral tectum, the efferents of which in turn project both to the ipsilateral ION and EION, whence back-projections lead to the contralateral retina (Clarke, 1992) (Figure 5). All projections within this system seem to be topographically organized (McGill *et al.,* 1966a,b; Catsicas *et al.,* 1987b). Weidner *et al.* (1987) showed in a comparative study in different bird species important differences between raptors and ground-feeding birds. In seed- or fruit-eating birds, the ION was always large, well differentiated, and laminated. In raptors, the ION was small, poorly differentiated, and reticular in appearance. The authors suggested from their observations that the centrifugal system is probably involved in pecking and visual food selection among static stimuli at a short viewing distance.

The cell bodies of quail tecto-ION neurons are located in layer 9 of the tectum and with their dendrites branching outside the retinorecipient superficial layers (Uchijama and Watanabe, 1985). Thus, tecto-ION neurons have to receive their retinal input via intratectal mechanisms. Uchijama et al. (1987) could demonstrate that electrical stimulations of the Wulst elicited ION neurons, indicating a forebrain influence on activity patterns within this structure. The situation seems to be slightly different in pigeons and chicks, where tecto-ION neurons reach up to layer 2 with their dendrites and could thus pick up direct retinal input (Woodson *et al.,* 1991).

The ION consists of a highly convoluted lamina in which two perikaryal layers are separated by a neuropil in which the dendrites from opposing layers branch toward the middle of the two layers (Güntürkün, 1987) (Figure 6). Afferent axons of presumably tectal origin pass through this dendritic field and synapse topographically on small dendritic appendages and spines providing virtually all excitatory synapses in the ION (Cowan, 1970; Angaut and Repérant, 1978). Additionally, large numbers of inhibitory synapses on ION dendrites are found, which partly originate from a small number of GABAergic neurons within the ION (Miceli *et al.,* 1995). Axons from ION cells emerge at opposing ends of the two laminae and proceed, together with those from the EION, to the contralateral retina. The number of efferent axons within the optic nerve is supposed to be about 12,000 in the pigeon, of which the ION contributes about 10,000 (Cowan, 1970; Weidner *et al.,* 1987; Wolf-Oberhollenzer, 1987). Since the tecto-ION and the tecto-EION pathways also consist of about 12,000 neurons, a 1:1 ratio of tectal and centrifugal

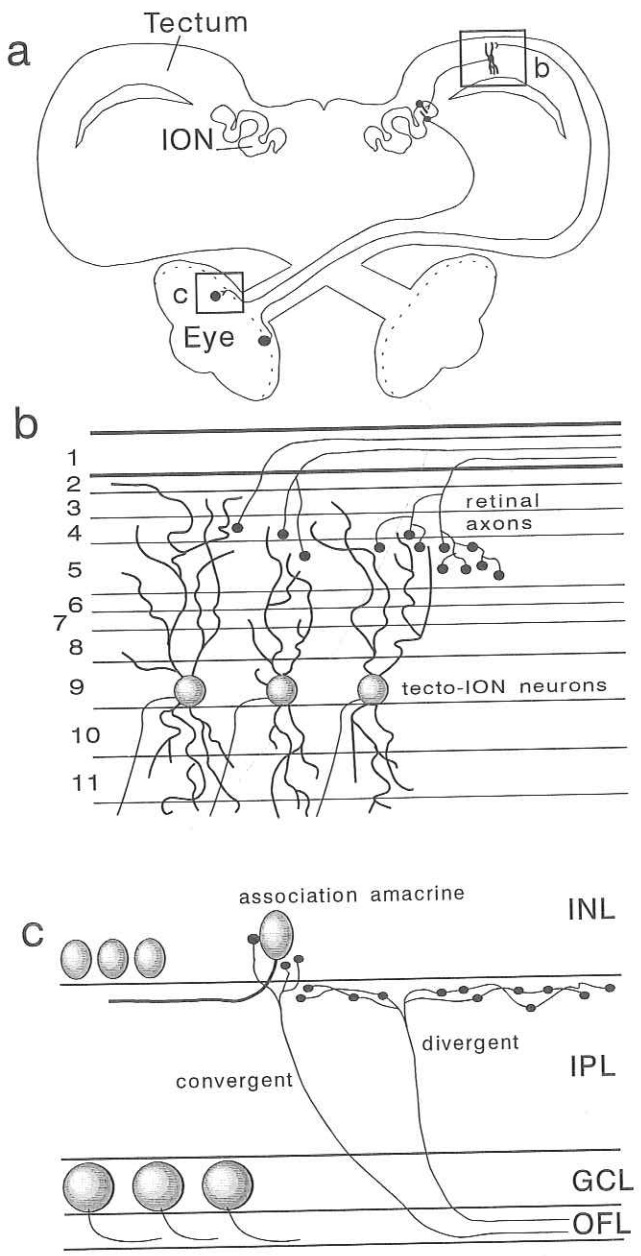

FIGURE 5 Schematic view of different aspects of the avian centrifugal system. (a) Overview of the centrifugal system with retinal ganglion cells projecting to the contralateral tectum, the tectal cells constituting the tecto-ION projection, and the ION neurons, which project back to the contralateral tectum. Components of the schema are not drawn to scale. The EION, which would take a position surrounding the ION, is not depicted. b and c give the position of the drawings with the same letters. (b) Schematic view of the tectum with layers 1 to 11 showing some retinal axons and the position of tecto-ION neurons as described by Woodson *et al.* (1991); (c) schematic view of the retina showing the two types of centrifugal axons. Abbreviations: ION, n. isthmo-opticus; and OFL, optic fiber layer or as in the legend to Figure 3.

neurons is likely (Woodson *et al.*, 1991). The centrifugal axons terminate near the IPL/INL border in the horizontal and ventral retina, barely penetrating the red field (Hayes and Holden, 1983; Catsicas *et al.*, 1987b; Fritzsch *et al.*, 1990). They are composed of two distinct types, with very different degrees of topographic localization. The "convergent" type of axon probably stems from the ION and generally gives rise to a single restricted type of terminal fiber, which forms a dense pericellular nest covering the perikaryon of a single association amacrine cell (Maturana and Frenk, 1965; Dowling and Cowan, 1966; Fritzsch *et al.*, 1990; Uchijama and Ito, 1993; Uchiyama *et al.*, 1995). Association amacrines have long intraretinal axons, are mainly located in the horizontal plus ventral retina, and project dorsally (Catsicas *et al.*, 1987a). In pigeons their projections are directed toward the red field (Ehrlich *et al.*, 1987). The fibers from the ION could thus be involved in a mechanism for switching attention between the upper and the lower field of view (Catsicas *et al.*, 1987a). In contrast, the "divergent" centrifugal axons from the EION give rise to several terminal branches, each constituting an extensive and highly branched arbor of up to 1 mm^2 in the IPL, such that the total termination field of these axons must be several square millimeters (Chmielewski *et al.*, 1990; Fritzsch *et al.*, 1990).

Electrophysiological data are only available for the ION. Miles (1972b) and Holden and Powell (1972) demonstrated that a large number of ION units show a preference for target movements in the anterior visual field and accomodate rapidly to repetitive stimulations, indicating a role in the analysis of transient and dynamic features of the visual environment. Miles (1972c) additionally demonstrated an effect of ION stimulation on the disinhibition of retinal ganglion cell surrounds and activation of ganglion cell centers. This would indicate a role in the modulation of local contrast and luminance sensitivities. Most ION cells have their receptive fields in the inferior anterior visual field and are thus related to the upper posterior parts of the retina, where paradoxically, ION terminals are virtually absent (Hayes and Holden, 1983; Catsicas *et al.*, 1987a).

Several authors tried to establish the functional importance of the ION and EION in behavioral studies. Hodos and Karten (1974), Jarvis (1974), Shortess and Klose (1977), and Knipling (1978) observed only mild or no deficits in visual intensity and pattern discrimination experiments after bilateral centrifugal lesions. However, using a different approach Rogers and Miles (1972) demonstrated profound deficits in the detection of suddenly occuring moving stimuli and the perception of grain on the black squares of a checkerboard. These authors suggested that the centrifugal system may play a role in detecting moving objects and in enhancing contrast under dim light conditions through a mechanism of dynamic adaption at the retinal level. A study of Hahmann and Güntürkün (1992) could not confirm

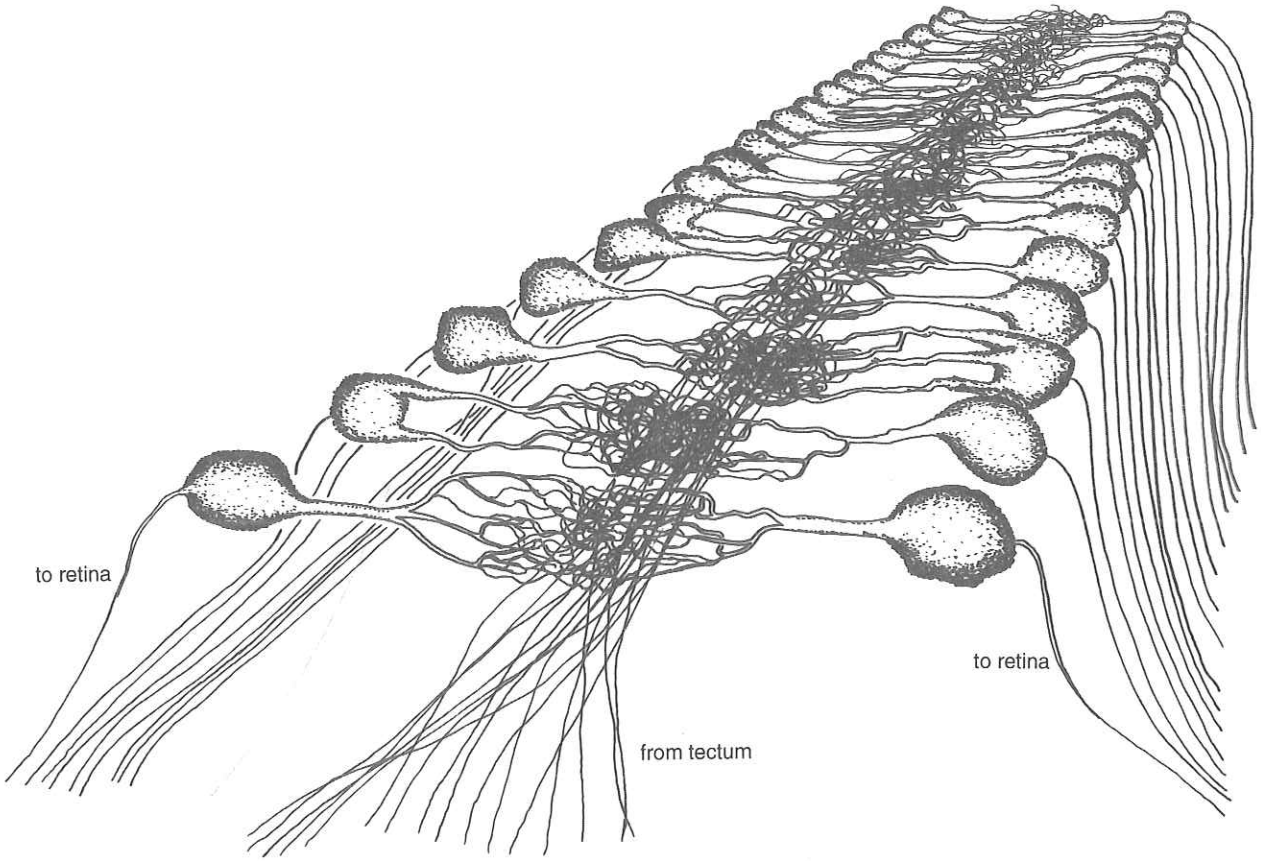

FIGURE 6 Simplified model of the cellular organization of the ION. Only two opposing cell rows separated by dendritic arborizations are shown. Axons entering the system are of presumably tectal origin. (From *Cell Tissue Res.,* A Golgi study of the isthmic nuclei in the pigeon (*Columba livia*), O. Güntürkün, **248,** 439–448, Fig. 5, 1987, © Springer-Verlag.)

the first result but provided additional evidence for the second. Three different behavioral experiments, each testing different aspects of visual analysis, were performed in this study. In the first two experiments, a grain–grit discrimination task and a visual acuity determination, stimuli were presented in the frontal binocular visual field. A third experiment investigated the early detection of moving objects, introduced into the monocular lateral visual field. After bilateral ION and EION lesions a multiple linear regression analysis was employed to correlate the postoperative performance in all three tasks with the amount of structure loss within ION and EION. Deficits in the grain–grit discrimination procedure were a function of the ION lesion extent and did not depend on EION damage. Thus, these two structures could be functionally differentiated. However, neither the ION nor the EION seemd to be involved in visual acuity performance or the early detection of large shadows moving through the visual field. These data support the hypothesis that at least the ION in pigeons is involved through its projections onto the association amacrines in pecking and food selection among static stimuli in the inferior frontal visual field (superiotemporal retina). The electrophysiological study of Miles (1972c) demonstrated an effect of ION stimulation on the disinhibition of retinal ganglion cell receptive field surrounds and the facilitation of the exciatory field centers. The first mechanism would sacrifice contrast sensitivity for responsiveness to a wide range of target forms and would thus confer improved detectability. The second mechanism, on the other hand, would increase sensitivity to small objects without loosing constraints on shape and size, thus facilitating the discriminative capacity of the visual system. Both mechanisms would enable birds to adapt to local optic background variations within the context of feeding or to "highlight" the object of choice as supposed by Uchiyama (1989).

B. Tectofugal Pathway

The tectofugal pathway is composed of optic nerve axons which decussate virtually completely in the chiasma opticum and end in the optic tectum (TO). The

tectum projects bilaterally to the thalamic nucleus rotundus (Rt), which itself sends efferent fibers to the ipsilateral ectostriatum (E). Ectostriatal cells project to a surrounding shelf area, the ectostriatal belt (Eb), from where intratelencephalic projections lead to different forebrain structures (Figure 7).

In probably most avian species the majority of retinal ganglion cells project to the optic tectum. The exact proportion is difficult to estimate but according to the data of Bravo and Pettigrew (1981) in the barn owl *Tyto alba* and Remy and Güntürkün (1991) in pigeons, 75–95% of ganglion cells have axons leading to the tectum. With regard to these numbers, the burrowing owl *Speotyto cunicularia* is an exception. This bird is supposed to rely heavily on its thalamofugal pathway and consequently seems to have less than 50% tectally projecting ganglion cells (Bravo and Pettigrew, 1981).

Retinal axons, which constitute the first of the 15 tectal laminae, innervate only superficial layers 2–7 and reach their highest synaptic density in layer 5 (Hayes and Webster, 1985). The retinal projection onto the tectum is strictly topographical in all species studied with the inferior retina projecting to the dorsal tectum while the posterior tectum is reached by the nasal retina (Clarke and Whitteridge, 1976; Frost *et al.,* 1990a; Remy and Güntürkün, 1991). The tectal representation of the foveae or the areas of enhanced vision are considerably expanded (Clarke and Whitteridge, 1976; Frost *et al.,* 1990a). Single-unit recordings in the optic tectum demonstrate that the visual receptive fields of neurons in the superficial layers are small (0.5–4°) but increase to up to 150° in deeper laminae (Jassik-Gerschenfeld *et al.,* 1975; Frost *et al.,* 1981). Despite this modulation in the z-axis, changes in the x- and y-axes also occur: Frost *et al.* (1990a) could demonstrate that receptive field sizes increase from foveal to peripheral representations in the tectum of the American kestrel. Most responses to stationary targets have typical on–off characteristics, and in a large number of cells the activating area is surrounded by an inhibitory region (Hughes and Pearlman, 1974). Using moving bars of monochromatic light, Letelier (1983) could show that 30% of the recorded tectal units had specific wavelength preferences, mostly for short wavelengths. The majority of cells (70%) are movement sensitive with about 30% of them having directional preferences (Jassik-Gerschenfeld and Guichard, 1972). Directionally responsive units are either narrowly tuned or, more commonly, they respond to a wide range of directions, with the majority being inhibited by backward movement (Frost and DiFranco,

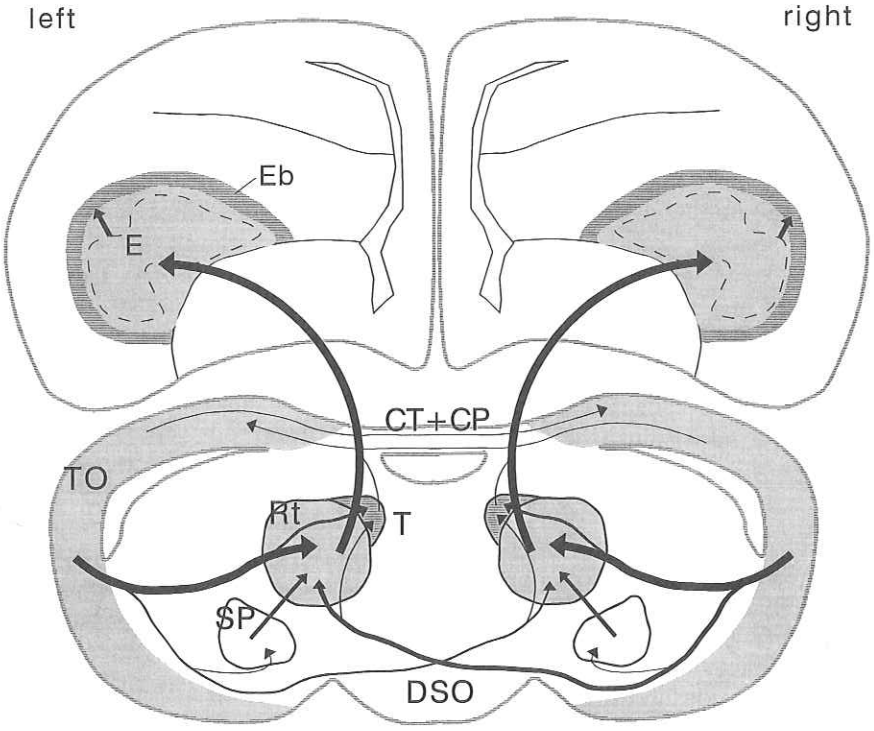

FIGURE 7 Schematic view of the avian tectofugal system. The broken lines within E gives the borderline between the subcomponents as described by Hellmann *et al.* (1995). Abbreviations: CP, commissura posterior; CT, commissura tectalis; DSO, dorsal supraoptic decussation; E, ectostriatum; Eb, ectostriatal belt; Rt, n. rotundus; SP, n. subpretectalis; T, n. triangularis; and TO, tectum opticum.

1976). If the stimulus is positioned on a random-dot background, tectal cells are activated when the background is moved out of phase to the stimulus, while a profound inhibition is produced by an in-phase motion of background and stimulus (Frost and Nakayama, 1983). These data strongly suggest that tectal cells play an important function in figure–ground segregation through discontinuities in velocity (Frost *et al.,* 1990b). If kinematograms (motion equivalents of random dot stereograms) are presented, tectal cells in deep laminae respond only to virtual "objects" shearing above the surface of the background and not to virtual "holes" in the background through which a further texture is visible (Frost *et al.,* 1988). Thus, deep tectal units seem to prefer moving objects rather than movement per se.

Tectal cells also respond selectively to the spatial frequency of drifting sine wave gratings, with most neurons having their optima between 0.45 and 0.6 c/deg (Jassik-Gerschenfeld and Hardy, 1979). Most of these cells are more selective to spatial frequencies than they are to single bar stimuli (Jassik-Gerschenfeld and Hardy, 1980). Birds therefore appear to be able to perform Fourier analysis of patterns in visual space. Recently, Neuenschwander and Varela (1994) could additionally prove the presence of visually triggered gamma oscillations in the pigeon's tectum. This oscillatory activity had characteristics similar to those reported in the mammalian neocortex in the context of synchronization of unit responses as a putative physiological basis of perceptual binding (Singer, 1993).

In pigeons, up to layer 12, most, if not all, cells are purely visually driven, while deeper neurons are often bi- or multimodal, integrating visual, auditory, and somatosensory afferents (Cotter, 1976). This seems to be different in the barn owl, in which the majority of superficial and deep tectal units are bimodal and have their auditory and visual receptive fields in the same space coordinates (Knudsen, 1982).

Visual information is transmitted either directly by axodendritic contacts or with interneurons to the cells of layer 13, which project to the Rt in the thalamus (Hardy *et al.,* 1985). Within Rt they end in synaptic glomerulilike structures constituted by the end-claws of several dendrites and bundles of tectal fibers (Thin *et al.,* 1992; Tömböl *et al.,* 1992). As demonstrated by Bischof and Niemann (1990) and Güntürkün *et al.* (1993a), the tectal projection is bilaterally organized with the efferents to the contralateral TO crossing through the dorsal supraoptic decussation. Accordingly, Engelage and Bischof (1988) could demonstrate the existence of ipsi- and contralaterally evoked potentials in the Rt of zebra finches. The Rt seems to consist of several distinct subfields as shown by histochemical (Martinez-de-la Torre *et al.,* 1990) and electrophysiological results (Revzin, 1979, Wang *et al.,* 1993). In anterior sections Rt units seem to be specialized successively from dorsal to ventral to color, luminance, and 2D motion, while in posterior sections looming cells can be found in the most dorsal portion of the Rt (Wang *et al.,* 1993). These looming cells seem to signal time to collision with an activity peak about 1 sec before virtual collision with the object (Wang and Frost, 1992).

Rt- and T-cells project ipsilaterally and in a topographic manner onto the ectostriatum (E) in the forebrain, from where projections lead to the surrounding ectostriatal belt (Eb) (Benowitz and Karten, 1976). Due to a Wulst projection onto Eb, this structure seems to be the first forebrain entity in which thalamo- and tectofugal systems interact (Ritchie, 1979). Kimberly *et al.* (1971) established that E-cells have properties similar to those of Rt, that is, most respond preferentially to moving stimuli with wide receptive fields. Engelage and Bischof (1988) revealed ipsi- and contralaterally evoked potentials in the E of zebra finches and even showed an intraectostriatal differentiation in the current source density profile of ipsi-, contra-, and binocularly evoked potentials (Engelage and Bischof, 1989). Hellmann *et al.* (1995) demonstrated that the E can be parceled according to the long-term activity pattern of its neurons into at least two components which might reflect ocular dominance areas within this structure.

Lesions of tectum or Rt cause pronounced deficits in pattern (TO: Jarvis, 1974; Hodos and Karten, 1974; Rt: Hodos and Karten, 1966; E: Hodos and Karten, 1970), intensity (TO: Hodos and Karten, 1974; Rt: Hodos and Karten, 1966; E: Hodos and Karten, 1970), or color discrimination (Rt: Hodos, 1969). Psychophysical techniques confirmed the drastic elevation of acuity or intensity thresholds after tectofugal lesions (Rt: Hodos and Bonbright, 1974; Macko and Hodos, 1984; E: Hodos *et al.,* 1984, 1988). The data of Güntürkün and Hahmann (1998) make it likely that the tectofugal system operates according to asymmetric principles. Their unilateral lesions of the Rt revealed that only structure loss within the left Rt correlates significantly with right- or left-sided acuity losses, while right-sided Rt lesions had no impact on monocular acuity. These behavioral data thus confirm the anatomical results of Güntürkün and Melsbach (1992), who demonstrated that left-sided Rt injection of retrograde tracers revealed a twice-as-numerous contingent of contralaterally projecting tectal neurons than after right-sided injections. Since each tectum represents the input from the contralateral eye, asymmetries in the contralateral tectal afferents could create asymmetries in the degree of the visual bilateral integration at the rotundal level. Despite these left–right asymmetries, behavioral studies additionally show a frontal–lateral difference within the tectofugal system.

According to Güntürkün and Hahmann (1998), Rt lesions interfere with acuity in the frontal but not in the lateral visual field. At the same time GLd lesions attenuate lateral but not frontal acuity. Thus, frontal and lateral visual acuity seem to depend on tecto- and thalamofugal mechanisms, respectively.

C. Thalamofugal Pathway

The thalamofugal pathway consists of the retinal projection onto the n. geniculatis lateralis pars dorsalis (GLd), a group of nuclei in the contralateral dorsal thalamus, and the bilateral projection of the GLd onto the Wulst ("bulge") in the anteriodorsal forebrain (Güntürkün *et al.,* 1993b). Most people agree that the avian thalamofugal pathway corresponds due to its anatomical, physiological, and functional properties to the mammalian geniculostriate system (Shimizu and Karten, 1993) (Figure 8).

While the tectofugal pathway receives afferents from the complete extent of the retina, the retinal location of ganglion cells projecting onto the GLd differs in various species. In birds of prey, ganglion cells in the temporal retina subserving frontal vision project primarily onto the GLd (Bravo and Pettigrew, 1981; Bravo and Inzunza, 1983). Consequently, many neurons in the visual Wulst of owls, kestrels, and vultures possess binocular visual fields and detect retinal disparity (Pettigrew, 1979; Porciatti *et al.,* 1990). In pigeons, however, mainly ganglion cells outside the "red field" of superiotemporal retina have efferents to the GLd (Remy and Güntürkün, 1991). The paucity of afferents from the red field should render the thalamofugal pathway of pigeons largely frontally blind, an assumption supported by electrophysiological results (Miceli *et al.,* 1979). Thus, while the GLd of several birds of prey seems to be specialized for the frontal binocular visual field, the GLd of pigeons mainly receives afferents from the lateral monocular field. This functionally important difference is not the result of the laterally placed eyes of pigeons, since the kestrel, a diurnal raptor that has lateral eyes, is also characterized by an overrepresentation of the frontal binocular visual field within its thalamofugal pathway (Pettigrew, 1978). The "frontal blindness" of the pigeon's thalamofugal system is very likely the reason for the virtual absence of behavioral deficits in a variety of discrimination tasks after GLd or Wulst lesions (Güntürkün, 1991). Generally in these experiments the pigeons were required to perform discriminative pecking responses to patterns presented upon response keys. Pigeons pecking a key fixate it with their red field (Goodale, 1983). Since the red field has only limited projections onto the GLd, thalamofugal lesions are likely to produce minimal deficits when tested with this procedure. When using discriminations of laterally presented stimuli, GLd lesions produce severe deficits (Güntürkün and Hahmann, 1998).

The differing ecological demands of seed-eating versus hunting birds are probably the reason for the different thalamofugal specialization to only one visual field. Pigeons and many other seed- or fruit-eating birds fixate novel or complex and distant stimuli laterally and only switch to frontal binocular vision to peck the scrutinized object (Bischof, 1988; Bloch *et al.,* 1988). Thus, in these species visual detection and analysis is mainly performed by those parts of the neural apparatus which represent the lateral visual field, while the frontal binocular area is only involved during the last visually guided sequences before and within pecking bouts. The lateral specialization of the thalamofugal pathway in pigeons could therefore be related to the fact that it is mainly the lateral visual field which requires fine analysis of the visual scenery. The frontal specialization of the thalamofugal system in birds of prey could be related to their more complex feeding habits which require them to specify the distance of objects with great precision through flow-field variables while moving with high speed (Davies and Green, 1990). Although eagles and falcons fixate distant objects mainly laterally (Reymond, 1985, 1987) they switch to frontal vision when approaching prey. The need for complex and fast visual information analysis of moving objects could explain the specialization of the thalamofugal pathway to the frontal visual field in birds of prey.

The GLd is composed of six components, of which only four constitute the core portion since they are retinorecipient and project onto the visual Wulst: n. dorsolateralis anterior thalami, pars lateralis (DLL), n. dorsolateralis anterior thalami, pars magnocellularis (DLAmc), n. lateralis dorsalis nuclei optici principalis thalami (LdOPT), and the n. suprarotundus (SpRt), with DLL and DLAmc being the two largest substructures (Güntürkün and Karten, 1991). Avian GLd neurons are also characterized by relatively small receptive fields (1° in owls, 2°–4° in pigeons, 3° in chicks), by center-surround organization and by a low adaptation to stimulus repetition (Pateromichelakis, 1981; Britten 1987). Aditionally, in pigeons and chicks many directionally selective cells with large receptive fields have been encountered (Wilson, 1980; Britten, 1987).

The GLd-Wulst projection is bilateral and topographically organized in all species studied, but the relative contribution of both sides probably depends on the orientation of this system to the frontal or the lateral field of view (Bagnoli *et al.,* 1990; Miceli *et al.,* 1990; Güntürkün *et al.,* 1993b). In owls with their essentially frontal eyes and the frontal thalamofugal orientation, the ipsi- and contralateral sides contribute an approximately equal number of fibers to the forebrain projec-

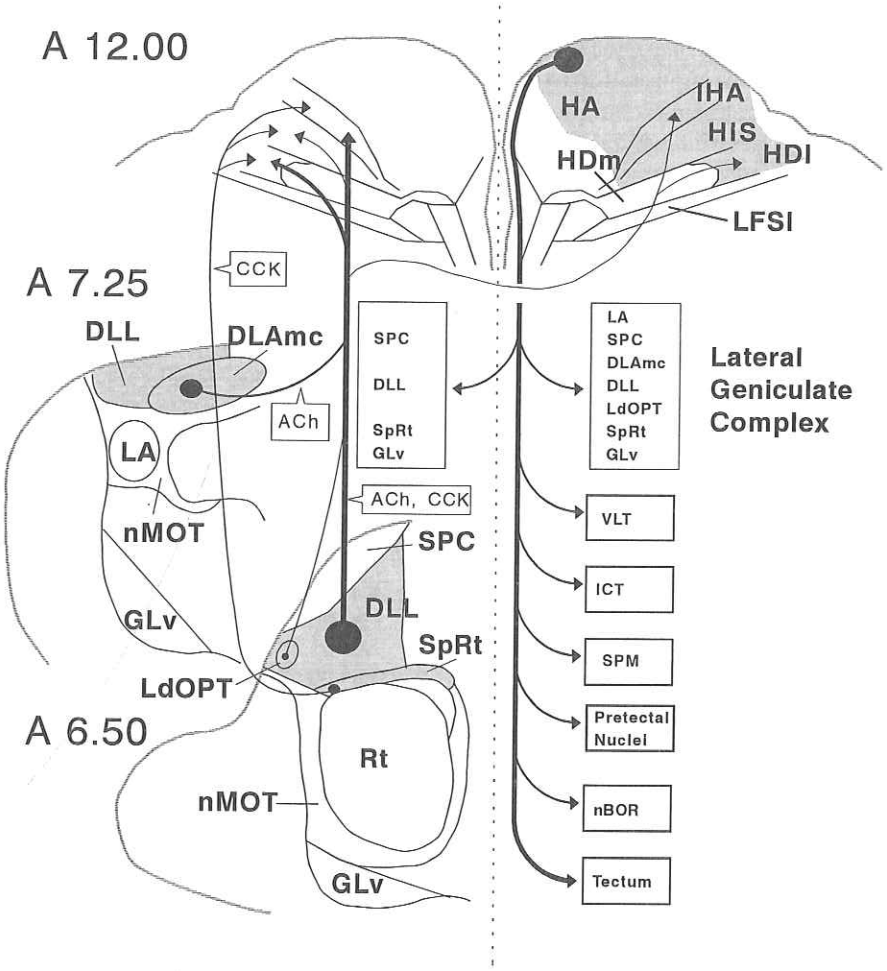

FIGURE 8 Schematic view of the avian thalamofugal pathway. The various core components of the dorsolateral geniculate complex (gray shading) are depicted to the left together with the ascending projections onto the ipsi- and contralateral Wulst and the neurotransmitters/modulators of the relay neurons. Note that the SpRt projects only ipsilaterally. The sizes of the black circles indicate the relative number of neurons contributing to the depicted projections. At the top the subdivisions of the Wulst are given with the nomenclature and the presumed extent of the visual components to the right (gray shading). To the right, the descending Wulst projections via the TSM are depicted. The broken line is the partition between the hemispheres. Each section represents a frontal plane of the atlas of Karten and Hodos (1967). Abbreviations: ACh, acetylcholine; CCK, cholecystokinin; DLAmc, n. dorsolateralis anterior thalami, pars magnocellularis; DLL, n. dorsolateralis anterior thalami, pars lateralis; GLv, n. geniculatus lateralis, pars ventralis; HA, hyperstriatum accessorium; HDl, lateral portion of the hyperstriatum dorsale; HDm, medial portion of the hyperstriatum dorsale; HIS, Hyperstriatum intercalatus superior; ICT, n. intercalatus thalami; IHA, n. intercalatus hyperstriati accessorii; LA, n. lateralis anterior; LdOPT, n. lateralis dorsalis nuclei optici principalis thalami; LFSl, lateral portion of the lamina frontalis superior; nBOR, n. of the basal optic root, pars dorsalis; nMOT, n. marginalis tractus optici; Rt, n. rotundus; SPC, n. superficialis parvocellularis; SPM, n. spiriformis medialis; SpRt, n. suprarotundus; and VLT, n. ventrolateralis thalami. (After Güntürkün *et al.,* 1993b, in *Vision, Brain and Behavior,* The MIT Press. © 1993 The MIT Press.)

tion (Bagnoli *et al.,* 1990). In lateral-eyed birds like pigeons, only a few contralateral projections can be found (Hahmann *et al.,* 1994).

The Wulst can be subdivided into a rostral somatosensory, a medial hippocampal, and a caudal visual division. The visual Wulst is organized from dorsal to ventral in four laminae: hyperstriatum accessorium (HA), intercalated nucleus of the hyperstriatum accessorium (IHA), hyperstriatum intercalatus superior (HIS), and hyperstriatum dorsale (HD). These subdivisions are

based on the cytoarchitectonics of the Wulst and do not reflect the full complexity of the structure, since Shimizu and Karten (1990) were able to distinguish at least eight subdivions using immunocytochemical techniques. The granular IHA and probably also lateral HD are the major recipients of the cholinergic and colecystokinergic GLd input (Watanabe *et al.,* 1983; Güntürkün and Karten, 1991). Electrophysiological studies demonstrate similarities between the visual Wulst of birds of prey and the striate cortex of mammals. In the visual Wulst of raptors most neurons are primarily concerned with binocular visual processing, are selectively tuned to stereoscopic depth cues, are sensitive to visual experience during the neonatal period, and have small receptive fields of about 1° (Pettigrew and Konishi, 1976a,b; Pettigrew, 1979). This is not the case for species like pigeons, chickens, and zebra finches in which binocular neurons are rare or in which ipsilaterally evoked visual responses are very weak and irregular (Bredenkötter and Bischof, 1990a,b). Additionally, the receptive fields encountered are considerably larger in nonraptors (pigeons: 2°, Revzin, 1969; chickens: 10°–20°, Wilson, 1980).

Raptors especially need stereoscopic depth cues. However, the distance of a visual target cannot be directly determined from its retinal location but has to be computed by comparing inputs from both eyes. The fundamental problem for a binocular system is to find the correct correspondence; that is, to identify the pair of image segments that belong to the same visual target (Pettigrew, 1993). With repeated stimuli like from a certain spatial frequency the phase ambiguity has thus to be resolved by the nervous system. Wagner and Frost (1993) proposed a solution to this problem by assuming that disparity sensitive neurons in the Wulst of barn owls might be tuned to a characteristic disparity. Indeed, they found that in many disparity-sensitive neurons the reaction peak to visual noise at a certain disparity did not change when using stimuli of different spatial frequencies (Wagner and Frost, 1994). Thus, disparity-sensitive cells in the barn owl's Wulst have a characteristic disparity which could be used to detect the depth plane of a stimulus which exhibits the appropriate combinations of spatial frequency and interocular phase.

The extratelencephalic Wulst efferents project primarily to the GLd, pretectal nuclei, the basal optic root nucleus, and the tectum opticum (Miceli *et al.,* 1987). Within GLd, the terminal fields partially overlap with those areas which both receive direct retinal input and project to the visual Wulst. The Wulst thus modulates its own GLd- input either by direct excitation of relay neurons or by inhibition of GABAergic interneurons (Watanabe, 1987). The Wulst projection onto the tectum is probably of great functional importance. Leresche *et al.* (1983) could demonstrate that many tectal cells depend for their receptive field properties upon input from an intact Wulst. Cryogenic block of the Wulst caused a reversible response depression of a majority of tectal cells and drastically diminished the directional tuning of half of the directionally selective neurons. Thus, the visual properties of tectal cells are not solely a reflection of the retinal afferents and the intratectal circuitry, but also depend on the thalamofugal input.

References

Angaut, P., and Repérant, J. (1978). A light and electron microscopic study of the nucleus isthmo-optic in the pigeon. *Arch. Anat. Mikr.* **67,** 63–78.

Bagnoli, P., Fontanesi, G., Casini, G., and Porciatti, V. (1990). Binocularity in the little owl, *Athene noctua.* I. Anatomical investigation of the thalamo-Wulst pathway. *Brain Behav. Evol.* **35,** 31–39.

Bellhorn, R. W., and Bellhorn, M. S. (1975). The avian pecten. *Ophtalmic Res.* **7,** 1–7.

Benowitz, L. I., and Karten, H. J. (1976). Organization of tectofugal visual pathway in pigeon: Retrograde transport study. *J. Comp. Neurol.* **167,** 503–520.

Binggeli, R. L., and Paule, W. J. (1969). The pigeon retina: Quantitative aspects of the optic nerve and ganglion cell layer. *J. Comp. Neurol.* **137,** 1-18.

Bischof, H. J. (1988). The visual field and visually guided behavior in the zebra finch (*Taeniopygia guttata*). *J. Comp. Physiol. A* **163,** 329–337.

Bischof H. J., and J. Niemann, (1990). Contralateral projection of the optic tectum in the zebra finch (*Taenopygia guttata castanotis*). *Cell Tissue Res.* **262,** 307–313.

Bloch, S., and Martinoya, C. (1982). Comparing frontal and lateral viewing in the pigeon. I. Tachistoscopic visual acuity as a function of distance. *Behav. Brain Res.* **5,** 231–244.

Bloch, S., Jäger, R., Lemeignant, M., and Martinoya, C. (1988). Correlations between ocular saccades and headmovements in walking pigeons, *J. Physiol.* (*London*) **406,** 173.

Blough, P. M. (1971). The visual acuity of the pigeon for distant targets. *J. Exp. Anal. Behav.* **15,** 57–67.

Bowmaker, J. K. (1977). The visual pigments of oil droplets and spectral sensitivity of the pigeon. *Vision Res.* **17,** 1129–1138.

Boycott, B. B., and Wässle, H. (1974). The morphological types of ganglion cells of the domestic cat's retina. *J. Physiol.* **240,** 397–419.

Bravo, H., and Inzunza, O. (1983). Estudio anatomico en las vias visuales parallelas en falconiformes. *Arch. Biol. Med. Exp.* **16,** 283–289.

Bravo, H., and Pettigrew, J. D. (1981). The distribution of neurons projecting from the retina and visual cortex to the thalamus and tectum opticum of the barn owl, *Tyto alba,* and the burrowing owl, *Speotyto cunicularia. J. Comp. Neurol.* **199,** 419–441.

Brecha, N. C., and Karten, H. J. (1981). Organization of avian accessory optic system. *Ann. N.Y. Acad. Sci.* **374,** 215–229.

Bredenkötter, M., and Bischof, H.-J. (1990a). Differences between ipsilaterally and contralaterally evoked potentials in the visual Wulst of the zebra finch. *Vis. Neurosci.* **5,** 155–163.

Bredenkötter, M., and Bischof, H.-J. (1990b). Ipsilaterally evoked responses of the zebra finch visual Wulst are reduced during ontogeny. *Brain Res.* **515,** 343–346.

Britten, K. H. (1987). Receptive fields of neurons of the principal optic nucleus of the pigeon (*Columba livia*). Ph.D. thesis, SUNY, Stony Brook.

Britto, L. R. G., and Hamassaki-Britto, D. E. (1991). A subpopulation of displaced ganglion cells of the pigeon retina exhibits substance P-like immunoreactivity. *Brain Res.* **546,** 61–68.

Britto, L. R. G., and Hamassaki-Britto, D. E. (1992). Enkephalin-immunoreactive ganglion cells in the pigeon retina. *Vis. Neurosci.* **9,** 389–398.

Britto, L., and Hammassaki, D. E. (1991). A subpopulation of displaced ganglion cells of the pigeon retina exhibits substance P-like immunoreactivity. *Brain Res.* **546,** 61–68.

Britto, L. R. G., Keyser, K. T., Hamassaki, D. E., and Karten, H. J. (1988). Catecholaminergic subpopulation of retinal displaced ganglion cells projects to the accessory optic nucleus in the pigeon (*Columba livia*). *J. Comp. Neurol.* **269,** 109–117.

Britto, L. R. G., Hamassaki, D. G., Keyser, K. T., and Karten, H. J. (1989). Neurotransmitters, receptors, and neuropeptides in the accessory optic system: An immunohistochemical survey in the pigeon (*Columba livia*). *Visual Neurosci.* **3,** 463–475.

Budnik, V., Mpodozis, J., Varela, F. J., and Maturana, H. R. (1984). Regional specialization of the quail retina: ganglion cell density and oil droplet distribution. *Neurosci. Lett.* **51,** 145–150.

Burkhardt, D. (1989). UV vision: A bird's eye view of feathers. *J. Comp. Physiol. A* **164,** 787–796.

Cajal, S. R. (1892). La rétine des vertébrés. *La Cellule* **9,** 119–257.

Catsicas, S., Catsicas, M., and Clarke, P. G. H. (1987a). Long-distance intraretinal connections in birds. *Nature* **326,** 186–187.

Catsicas, S., Thanos, S., and Clarke, P. G. H. (1987b) Major role for neuronal death during brain development: Refinement of topographical connections. *Proc. Natl. Acad. Sci. USA* **84,** 8165–8168.

Cerella, J. (1980). The Pigeon's analysis of pictures. *Pattern Recog.* **12,** 1–6.

Chen, D. M., and Goldsmith, T. H. (1986). Four spectral classes of cone in the retinas of birds. *J. Comp. Physiol. A* **159,** 473–479.

Chmielewski, C. E., Dorado, M. E., Quesada, A., Géniz-Galvéz, J.-M., and Prada, F. A. (1988). Centrifugal fibers in the chick retina. *Anat. Histol. Embryol.* **17,** 319–327.

Clarke, P. G. H. (1992). Neuron death in the developing avian isthmo-optic nucleus, and its relation to the establishment of functional circuitry. *J. Neurobiol.* **23,** 1140–1158.

Clarke, P. G. H., and Whitteridge D. (1976). Projection of retina, including Red Area onto optic tectum of pigeon. *Quart. J. Exp. Psychol.* **61,** 351–358.

Cotter, J. R. (1976). Visual and nonvisual units recorded from optic tectum of *Gallus domesticus. Brain Behav. Evol.* **13,** 1–21.

Cowan, W. M. (1970). Centrifugal fibres to avian retina. *Br. Med. Bull.* **26,** 112–119.

Curcio, C. A., and Allen, K. A. (1990). Topography of ganglion cells in human retina. *J. Comp. Neurol.* **300,** 5–25.

Davies, M. N. O., and Green, P. R. (1990). Optic flow-field variables trigger landing in hawk but not in pigeons. *Naturwissenschaften* **77,** 142–144.

Delius, J. D., Jahnke-Funk, E., and Hawker, A. (1981). Stimulus display geometry and colour discrimination learning by pigeons. *Curr. Psych. Res.* **1,** 203–214.

DiStefano, M., Kusmic, C., and Musumeci, D. (1987). Binocular interactions measured by choice reaction times in pigeons. *Behav. Brain Res.* **25,** 161–165.

Dowling, J. E., and Cowan, W. M. (1966). Electron microscope study of normal and degenerating centrifugal fibre terminals in pigeon retina. *Z. Zellforsch.* **71,** 14–28.

Duijm, M. (1958). On the position of a ribbon like central area in the eyes of some birds. *Arch. Neerl. Zool.* **13,** 128–145.

Ehrlich, D. (1981). Regional specialization of the chick retina as revealed by the size and density of neurons in the ganglion cell layer. *J. Comp. Neurol.* **195,** 643–657.

Ehrlich, D., Keyser, K. T., and Karten, H. J. (1987). Distribution of substance P-like immunoreactive retinal ganglion cells and their pattern of termination in opt tect of chick. *J. Comp. Neurol.* **266,** 220–233.

Emmerton, J. (1983a). Pattern discrimination in the near-ultraviolet by pigeons. *Percept. Psychophys.* **34,** 555–559.

Emmerton, J. (1983b). Vision. *In* "Physiology and Behaviour of the Pigeon" (M. Abs, ed.), pp. 245–266. Academic Press, London.

Emmerton, J., and Delius, J. D. (1980). Wavelength discrimination in the "visible" and ultraviolet spectrum by pigeons. *J. Comp. Physiol.* **141,** 47–52.

Emmerton, J., Schwemer, J., Muth, I., and Schlecht, P. (1980). Spectral transmission of the ocular media of the pigeon (*Columba livia*). *Invest. Ophtalmol. Visual Sci.* **19,** 1382–1387.

Engelage, J., and Bischof, H. J. (1988). Enucleation enhances ipsilateral flash evoked responses in ectostriatum of zebra fish. *Exp. Brain Res.* **70,** 79–89.

Engelage, J., and Bischof, H. J. (1989). Flash evoked potentials in ectostriatum of zebra finch: current source density analysis. *Exp. Br. Res.* **74,** 563–572.

Evans, H. E. (1996). Anatomy of the budgerigar and other birds. *In* "Diseases of Cage and Aviary Birds" (W. J. Rosskopf and R. W. Woerpel, eds.). Williams & Wilkins Co., Baltimore.

Fite, K. V., Brecha, N., Karten, H. J., and Hunt, S. P. (1981). Displaced ganglion cells and the accessory optic system of pigeon. *J. Comp. Neurol.* **195,** 279–288.

Fitzke, F. W., Hayes, B. P., Hodos, W., Holden, A. L., and Low, J. C. (1985). Refractive sectors in the visual field of the pigeon eye. *J. Physiol. (London)* **369,** 33–44.

Fox, R., Lehmkuhle, S. W., and Westendorf, D. H. (1976). Falcon visual acuity. *Science* **192,** 263–265.

Friedman, M. B. (1975). How birds use their eyes. *In* "Neural and Endocrine Aspects of Behaviour in Birds" (P. Wright, P. Cryl, and D. M. Volwes, eds.), pp. 182–204. Elsevier, Amsterdam.

Fritzsch, B., Crapon DeCaprona, M.-D., and Clarke, P. G. H. (1990). Development of two morphological types of retinopetal fibers in chick embryos, as shown by the diffusion along axons of a carbocyanine dye in the fixed retina. *J. Comp. Neurol.* **301,** 1-17.

Frost, B. J., and diFranco, D. E. (1976). Motion characteristics of single units in pigeon optic tectum. *Vision Res.* **16,** 1229–1234.

Frost, B. J., and Nakayama, K. (1983). Single visual neurons code opposing motion independent of direction. *Science* **220,** 744–745.

Frost, B. J., Cavanaugh, P., and Morgan, B. (1988). Deep tectal cells in pigeon respond to kinematograms. *J. Comp. Physiol. A* **162,** 639–647.

Frost, B. J, Scilley, P. L., and Wong, S. C. P. (1981). Moving Background patterns reveal double-opponency of directionally specific pegeon tectal neurons. *Exp. Brain Res.* **43,** 173–185.

Frost, B. J., Wise, L. Z., Morgan, B., and Bird, D. (1990a). Retinotopic representation of the bifoveate eye of the kestrel (*Falco sparverius*) on the optic tectum. *Vis. Neurosci.* **5,** 231–239.

Frost, B. J., Wylie, D. R., and Wang, Y.-C. (1990b). The processing of object and self-motion in the tectofugal and accessory optic pathways of birds. *Vision Res.* **30,** 1677–1688.

Fukuda, Y., Stone, J. (1974). Retinal distribution and central projections of Y-, X-, and W-cells of the cat's retina. *J. Neurophysiol.* **37,** 749–772.

Galifret, Y. (1968). Les diverses aires fonctionelles de la retine di pigeon. *Z. Zellforsch. Mikrosk. Anat.* **86,** 535–545.

Goodale, M. A. (1983).Visually guided pecking in the pigeon (*Columba livia*). *Brain Behav. Evol.* **22,** 22–41.

Güntürkün, O. (1987). A Golgi study of the isthmic nuclei in the pigeon (*Columba livia*). *Cell Tissue Res.* **248,** 439–448.

Güntürkün, O. (1991). The functional organization of the avian visual system. *In* "Neural and Behavioural Plasticity: The Use of the Domestic Chick as a Model" (R. J. Andrew, ed.), pp. 92–105. Oxford Univ. Press, Oxford.

Güntürkün, O., and Hahmann, U. (1994). Cerebral asymmetries and visual acuity in pigeons, *Behav. Brain Res.* **60,** 171–175.

Güntürkün, O., and Hahmann, U. (1998). Functional subdivisions of the ascending visual pathways in the pigeon. *Behav. Brain Res.,* in press.

Güntürkün, O., and Karten, H. J. (1991). An immunocytochemical analysis of the lateral geniculate complex in the pigeon (*Columba livia*). *J. Comp. Neurol.* **314,** 721–749.

Güntürkün, O., and Melsbach, G. (1992). Asymmetric tecto-rotundal projections in pigeons: Cues to the origin of lateralized binocular integration. *In* "Rhythmogenesis in Neurons and Networks" (N. Elsner and D. W. Richter, eds.), p. 364. Thieme, Stuttgart.

Güntürkün, O., Melsbach, G., Hörster, W., and Daniel S. (1993a). Different sets of afferents are demonstrated by the two fluorescent tracers Fast Blue and Rhodamine. *J. Neurosci. Meth.* **49,** 103–111.

Güntürkün, O., Miceli, D., and Watanabe, M. (1993b). Anatomy of the Avian Thalamofugal Pathway. *In* "Vision, Brain and Behavior in Birds" (H. P. Zeigler and H.-J. Bischof, eds.), p. 115–135. MIT Press, Cambridge.

Hahmann, U., and Güntürkün, O. (1992). Visual discrimination deficits after lesions of the centrifugal visual system in pigeons. *Visual Neurosci.* **9,** 225–234.

Hahmann, U., and Güntürkün, O. (1993). The visual acuity for the lateral visual field in the pigeon (*Columba livia*). *Vision Res.* **33,** 1659–1664.

Hahmann, U., Güntürkün, O., and Shimizu, T. (1994). Immunohistochemical analysis of the thalamofugal-Wulst projection of the pigeon (*Columba livia*). *In* "Göttingen Neurobiology Report" (N. Elsner and H. Breer, eds.), p. 488. Thieme, Stuttgart.

Hamassaki-Britto, D. E, Brzozowska-Prechtl, A., and Karten, H. J. (1991). GABA-like immunoreactive cells containing nicotinic acetylcholine receptors in the chick retina. *J. Comp. Neurol.* **313,** 394–408.

Hardy, O., Leresche, N., and Jassik-Gerschenfeld, D. (1985). Morphology and laminar distribution of electrophysiologically identified cells in the pigeon's optic tectum: An intracellular study. *J. Comp. Neurol.* **233,** 390–404.

Hayes, B., Martin, G. R., and Brooke, M. de L. (1991). Novel area serving binocular vision in the retinae of Procellariiform seabirds. *Brain. Behav. Evol.* **37,** 79–84.

Hayes, B. P., and Holden, A. L. (1980). Size classes of ganglion cells in the central yellow field of the pigeon retina. *Exp. Brain Res.* **39,** 269–275.

Hayes, B. P., and Holden, A. L. (1983). The distribution of displaced ganglion cells in the retina of the pigeon. *Exp. Brain Res.* **49,** 181–188.

Hayes, B. P., and Webster, K. E. (1981). Neurons situated outside the isthmo-optic nucleus and projecting to the eye in adult birds. *Neurosci. Lett.* **26,** 107–112.

Hayes, B. P., and Webster, K. E. (1985). Cytoarchitectural fields and retinal termination: an axonal transport study of laminar organization in the avian optic tectum. *Neuroscience* **16,** 641–657.

Hellmann, B., Waldmann, C., and Güntürkün, O. (1995). Cytochrome oxidase activity reveals parcellations of the pigeon's ectostriatum. *Neuroreport.* **6,** 881–885.

Hodos, W. (1969). Color discrimination deficits after lesions of the nucleus rotundus in pigeons. *Brain Behav. Evol.* **2,** 185–200.

Hodos, W., and Bonbright, J. L. (1974). Intensity difference thresholds in pigeons after lesions of the tectofugal and thalamofugal visual pathways. *J. Comp. Physiol. Psychol.* **87,** 1013–1031.

Hodos, W., and Erichsen, J. T. (1990). Lower field myopia in birds: An adaptation that keeps the ground in focus. *Vision Res.* **30,** 653–657.

Hodos, W., and Karten, H. J. (1966). Brightness and pattern discrimination deficits in the pigeon after lesions of nucleus rotundus. *Exp. Brain Res.* **2,** 151–167.

Hodos, W., and Karten, H. J. (1970). Visual intensity and pattern discrimination deficts after lesions of ectostriatum in pigeons. *J. Comp. Neurol.* **140,** 53–68.

Hodos, W., and Karten, H. J. (1974). Visual intensity and pattern discrimination deficits after lesions of the optic lobe in pigeons. *Brain. Behav. Evol.* **9,** 165–194.

Hodos, W., and Leibowitz, R. W. (1977). Near-field visual acuity of pigeons: Effects of scotopic adaption and wavelength. *Vision Res.* **17,** 463–467.

Hodos, W., Bessette, B. B., Macko, K. A., and Weiss, S. R. B. (1985). Normative data for pigeon vision. *Vision Res.* **25,** 1525–1527.

Hodos, W., Leibowitz, R. W., and Bonbright, J. C. Jr. (1976). Near-field visual acuity of pigeons: Effects of head location and stimulus luminance. *J. Exp. Anal. Behav.* **25,** 129–141.

Hodos, W., Macko, K. A., and Bessette, B. B. (1984). Near-field acuity changes after visual system lesions in pigeons. II. Telencephalon. *Behav. Brain Res.* **13,** 15–30.

Hodos, W., Miller, R. F., and Fite, K. V. (1991a). Age-dependent changes in visual acuity and retinal morphology in pigeons. *Vision Res.* **31,** 669–677.

Hodos, W., Miller, R. F., Fite, K. V., Porciatti, V., Holden, A. L., Lee, J.-Y., and Djamgoz, M. B. A. (1991b). Life-span changes in the visual acuity and retina in birds, *In* "The Changing Visual System" (P. Bagnoli and W. Hodos, eds.), pp. 137–148. Plenum, New York.

Hodos, W., Weiss, S. R. B., and Bessette, B. B. (1988). Intensity difference thresholds after lesions of ectostriatum in pigeons. *Behav. Brain Res.* **30,** 43–53.

Holden, A. L. (1978). Antidromic invasion of ganglion cells in the pigeon retina. *Vision Res.* **18,** 1357–1365.

Holden, A. L., and Powell, T. P. S. (1972). The functional organization of the isthmo-optic nucleus in the pigeon. *J. Physiol.* **233,** 419–447.

Hughes, C. P., and Pearlman, A. L. (1974). Single unit receptive fields and the cellular layers of the pigeon optic tectum. *Brain Res.* **80,** 365–377.

Ikushima, M., Watanabe, M., and Ito, H. (1986). Distribution and morphology of retinal ganglion cells in the Japanese quail. *Brain Res.* **376,** 320–334.

Illing, R. B., and Wässle, H. (1981). The retinal projection to the thalamus in the cat: A quantitative investigation and a comparison with the retinotectal pathway. *J. Comp. Neurol.* **202,** 265–285.

Inzunza, O., Bravo, H., Smith, R. L., and Angel, M. (1991). Topography and morphology of retinal ganglion cells in Falconiforms: A study on predatory and carrion-eating birds. *Anat. Rec.* **229,** 271–277.

Jane, S. D., and Bowmaker, J. K. (1988). Tetrachromic colour vision in the duck (*Anas platyrhynchos L.*): Microspectrophotometry of visual pigments and oil droplets. *J. Comp. Physiol. A* **62,** 225–235.

Jarvis, C. D. (1974). Visual discrimination and spatial localization deficits after lesions of the tectufugal pathway in pigeons. *Brain Behav. Evol.* **9,** 195–228.

Jassik-Gerschenfeld, D., and Guichard, J. (1972). Visual receptive fields of single cells in the pigeon's optic tectum. *Brain Res.* **40,** 303–317.

Jassik-Gerschenfeld, D., and Hardy, O. (1979). Single neuron responses to moving sine-wave gratings in the pigeon optic tectum. *Vision Res.* **19,** 993–999.

Jassik-Gerschenfeld, D., and Hardy, O. (1980). Single-cell responses to bar width and to sine-wave grating frequency in the pigeon. *Vision Res.* **21,** 745–747.

Jassik-Gerschenfeld, D., Guichard, J., and Tessier, Y. (1975). Localization of directionally selective and movement sensitive cells in the optic tectum of the pigeon. *Vision Res,* **15,** 1037–1038.

Karten, H. J., and Hodos, W. (1967). "A Stereotaxic Atlas of the Brain of the Pigeon (*Columba livia*)." The Johns Hopkins Press, Baltimore.

Karten, H. J., Keyser, K. T., and Brecha, N. C. (1990). Biochemical and morphological heterogeneity of retinal ganglion cells. *In* "Vision and the Brain" (B. Cohen and I. Bodis-Wollner, eds.), pp. 19–33. New York, Raven.

Katayama, Y., Kiyama, H., Avai, Y., and Tohyama, M. (1984). Immunoreactive avian pancreatic polypeptide in the chicken retina: Overall distribution. *Brain Res.* **310,** 164–167.

Keyser, K. T., Britto, L. R. G., Woo, J.-I., Park, D. H., and Ioh, T. H. (1990). Presumtive catecholaminergic ganglion cells in the pigeon retina. *Vis. Neurosci.* **4,** 225–235.

Keyser, K. T., Karten, H. J., and Ehrlich, D. (1988). "Bullwhip" association amacrine cells in the pigeon retina: morphology and histochemical heterogeneity. *Invest. Ophtalmol. Vis. Sci. (Suppl.)* **29,** 196.

Kimberly, R. P., Holden, A. L., and Bamborough, P. (1971). Response characteristics of pigeon forebrain cells to visualstimulation. *Vision Res.* **11,** 475–478.

Kirmse, W. (1990). Kritische Übersicht zur selektiven Sensomotorik des Blickens und multifoveales Spähen bei Vögeln. *Zoologisch. Jahrbuch Physiol.* **94,** 217–228.

Kiyama, H., Katayama-Kumoi, Y., Steinbusch, H., Powell, J. F., Smith, A. D., and Tohyama, M. (1985). Three dimensional analysis of retina neuropeptides and amines in the chick. *Brain Res. Bull.* **15,** 155–165.

Knipling, R. R. (1978). No deficit in near-field visual acuity of pigeons after transection of the isthmo-optic tract. *Brain Res.* **22,** 813–816.

Knudsen, E. I. (1982). Auditory and visual maps of space in the optic tectum of the owl. *J. Neurosci.* **2,** 1177–1194.

Kusmic, C., Musumeci, D., and Spinelli, R. (1991). Binocular probability summation in a choice reaction-time task in pigeons. *NeuroReport* **2,** 615–618.

Leresche, N., Hardy, O., and Jassik-Gerschenfeld, D. (1983). Receptive field properties of single cells in the pigeon's optic tectum during cooling of the "visual Wulst." *Brain Res.* **267,** 225–236.

Letelier, J. (1983). Respuestas cromáticas en el tectum óptico de la paloma. Tesis de Licenciatura, Fakultad de Ciencias, Universitad de Chile, Santiago, Chile.

Lockhart, M. (1979). Quantitative morphological investigations of retinal cells in the pigeon: a golgi, light microscopic study. *In* "Neural Mechanisms of Behavior in the Pigeon" (A. M. Granda, and J. H. Maxwell, eds.), pp. 371–394. Plenum, New York.

Lubinski, D., and MacCorquodale, K. (1984). "Symbolic communication" between two pigeons (Columba livia) without unconditioned reinforcement. *J. Comp. Psychol.* **98,** 372–380.

Macko, K. A., and Hodos, W. (1984). Near-field acuity after visual system lesions in pigeons I. Thalamus. *Behav. Brain Res.* **13,** 1–14.

Mallin, H. D., and Delius, J. D. (1983). Inter- and intraocular transfer of colour discriminations with mandibulation as an operant in the head-fixed pigeon. *Behav. Anal. Lett.* **3,** 297–309.

Mariani, A. P. (1983). A morphological basis for verticality detectors in the pigeon retina: asymmetric amacrine cells. *Naturwissenschaften* **70,** 368–369.

Mariani, A. P. (1987). Neuronal and synaptic organization of the outer plexiform layer of the pigeon retina. *Am. J. Anat.* **179,** 25–39.

Mariani, A. P., and Leure-du Pree, A. E. (1978). Photoreceptors and oildroplet colors in the red area of the pigeon retina. *J. Comp. Neurol.* **182,** 821–838.

Martin, G. R. (1993). Producing the Image. *In* "Vision, Brain and Behavior in Birds" (H. P. Zeigler and H.-J. Bischof, eds.), pp. 5–24, MIT Press, Cambridge.

Martin, G. R. (1994). Form and Function in the Optical Structure of Bird Eyes. *In* "Perception and Motor Control in Birds" (M. N. O. Davies and P. R. Green, eds.), pp. 5–34, Springer-Verlag, Berlin.

Martinez-de-la-Torre, M., Martinez, S., and Puelles, L. (1990). Acetylcholinesterase–histochemical differential staining of subdivisions within the nucleus rotundus in the chick. *Anat. Embryol.* **181,** 129–135.

Maturana, H. R., and Frenk, S. (1963). Directional movement and horizontal edge detctors in the pigeon retina. *Science* **142,** 977.

Maturana, H. R., and Frenk, S. (1965). Synaptic connections of the centrifugal fibers in the pigeon retina. *Science* **150,** 359–361.

McGill, J. I., Powell, T. P. S., and Cowan, W. M. (1966a). The retinal representation upon the optic tectum and isthmo-otpic nucleus in the pigeon. *J. Anat.* **100,** 5–34.

McGill, J. I., Powell, T. P. S., and Cowan, W. M. (1966b). The organisation of the projection of the centrifugal fibers to the retina in the pigeon. *J. Anat.* **100,** 35–40.

Miceli, D., Gioanni, H., Repérant, J., and Peyrichoux, J. (1979). The avian visual Wulst. I. An anatomical study of afferent and efferent pathways; II. An electrophysiological study of the functional properties of single neurons. *In* "Neural Mechanisms of Behavior in Birds" (A. M. Granda, and Maxwell, J. H. eds.). Plenum, New York.

Miceli, D., Marchand, L., Repérant, J., and Rio, J.-P. (1990). Projections of the dorsolateral anterior complex and adjacent thalamic nuclei upon the visual Wulst in the pigeon. *Brain Res.* **518,** 317–323.

Miceli, D., Repérant, J., Rio, J.-R. and Medina, M. (1995). GABA immunoreactivity in the nucleus isthmo-opticus of the centrifugal visual system in the pigeon: A light and electron microscopic study. *Vis. Neurosci.* **12,** 425–441.

Miceli, D., Repérant, J., Villalobos, J., and Dionne, L. (1987). Extratelencephalic projections of the avian visual Wulst: A quantitative autoradiographic study in the pigeon *Columba livia. J. Hirnforsch.* **28,** 45–57.

Miles, F. A. (1972a). Centrifugal control of the avian retina. I. Receptive field properties of retinal ganglion cells. *Brain Res.* **48,** 65–92.

Miles, F. A. (1972b). Centrifugal control of the avian retina. II. Receptive field properties of cells in the isthmo-optic nucleus. *Brain Res.* **48,** 93–113.

Miles, F. A. (1972c). Centrifugal control of the avian retina. III. Effects of electrical stimulation of the isthmo-optic tract on the receptive field properties of reinal ganglion cells. *Brain Res.* **48,** 115–129.

Millar, T. J., Ishimoto, I., Boelen, M., Epstein, M. L., Johnson, C. D., and Morgan, I. G. (1987). The toxic effects of ethylcoline mustard aziridinium ion on cholinergic cells in the chicken retina. *J. Neurosci.* **7,** 343–356.

Morgan, I. G., Oliver, J., and Chubb, I. W. (1983). The development of amacrine cells containing somatostatin-like immunoreactivity in chicken retina. *Dev. Brain Res.* **8,** 71–76.

Morino, P., Bahro, M., Cuénod, M., and Streit, P. (1991). Glutamate-like immunoreactivity in the pigeon optic tectum and effects of retinal ablation. *Eur. J. Neurosci.* **3,** 366–378.

Murphy, C. J., Howland, M., and Howland, H. C. (1995). Raptors lack lower field myopia. *Vision Res.* **35,** 1153–1155.

Nalbach, H.-O., Wolf-Oberhollenzer, F., and Remy, M. (1993). Exploring the Image, *In* "Vision, Brain and Behavior in Birds" (H. P. Zeigler and H.-J. Bischof, eds.), pp. 25–46. MIT Press, Cambridge.

Neuenschwander, S., and Varela, F. J. (1993). Visually triggered neuronal oscillations in the pigeon: An autocorrelation of tectal activity. *Eur. J. Neurosci.* **5,** 870–881.

Oehme, H. (1962). Das Auge von Mauersegler, Star und Amsel. *J. Ornithol.* **103,** 187–212.

Pateromichelakis, S. (1981). Response properties of visual units in the anterior dorsolateral thalamus of the chick (*Gallus domesticus*). *Experientia* **37,** 279–280.

Perry, V. H., and Cowey, A. (1985). The ganglion cell and cone distributions in the monkey's retina: implications for central magnification factors. *Vision Res.* **25,** 1795–1810.

Pettigrew, J. D. (1978). Comparison of the retinotopic organization of the visual Wulst in nocturnal and diurnal raptors, with a note on the evolution of frontal vision. *In* "Frontiers of Visual Science" (S. J. Cool. and E. L. Smith, eds.), pp. 328–335. Springer-Verlag, New York.

Pettigrew, J. D. (1979). Binocular visual processing in the owl's telencephalon. *Proc. R. Soc. London* **204,** 435–455.

Pettigrew, J. D. (1993). Two ears and two eyes. *Nature* **364,** 756–757.

Pettigrew, J. D., and Konishi, M. (1976a). Neurons selective for orientation and binocular disparity in the visual Wulst of the barn owl (*Tyto alba*). *Science* **193,** 675–678.

Pettigrew, J. D., and Konishi, M. (1976b). Effects of monocular deprivation on binocular neurons in the owl's visual Wulst. *Nature* **264,** 753–754.

Pettigrew, J. D., Wallman, J., and Wildsoet, C. F. (1990). Saccadic oscillations facilitate ocular perfusion from the avian pecten. *Nature* **343,** 362–363.

Pirenne, M. H. (1943). Binocular and uniocular thresholds in vision. *Nature* **152,** 698–699.

Porciatti, V., Fontanesi, G., Rafaelli, A., and Bagnoli, P. (1990). Binocularity in the little owl, *Athene noctua.* II. Properties of visually evoked potentials from the Wulst in response to monocular and binocular stimulation with sine wave gratings. *Brain Behav. Evol.* **35,** 40–48.

Prada, F. A., Chmielewski, C. E., Dorado, M. E., Prada, C., and Génis-Gálvez, J. M. (1989). Displaced ganglion cells in the chick retina. *Neurosci. Res.* **6,** 329–339.

Prada, C., Medina, J. I., López, R., Génis-Gálvez, J. M., and Prada, F. A. (1992). Development of retinal displaced ganglion cells in the chick: Neurogenesis and morphogenesis. *J. Neurosci.* **12,** 3781–3788.

Quesada, A., Prada, F. A., and Génis-Gálvez, J. M. (1988). Bipolar cells in the chicken retina. *J. Morphol.* **197,** 337–351.

Rager, G., and Rager, U. (1978). Systems-matching by degeneration. I. A quantitaive electron microscopic study of the generation and degeneration of retinal ganglion cells in the chicken. *Exp. Brain Res.* **33,** 65–78.

Reiner, A. (1992). The neurotensin-related hexapeptide LANT6 is found in retinal ganglion cells and in their central projections in pigeons. *Vis. Neurosci.* **9,** 217–223.

Remy, M., and Emmerton, J. (1989). Behavioral spectral sensitivities of different retinal areas in pigeons. *Behav. Neurosci.* **103,** 170–177.

Remy, M., and Güntürkün, O. (1991). Retinal afferents to the tectum opticum and the n. opticus principalis thalami in the pigeon. *J. Comp. Neurol.* **305,** 57–70.

Reymond, L. (1985). Spatial visual acuity of the eagle *Aquila audax*: A behavioral, optical and anatomical investigation. *Vision Res.* **25,** 1477–1491.

Reymond, L. (1987). Spatial visual acuity of the falcon, *Falco berigora*: A behavioural, optical and anatomical investigation. *Vision Res.* **27,** 1859–1874.

Revzin, A. M. (1969). A specific visual projection area in the hyperstriatum of the pigeon. *Brain Res.* **15,** 246–249.

Revzin, A. M. (1979). Functional localization in the nucleus rotundus. *In* "Neural Mechanisms of Behavior in Birds" (A. M. Granda and J. H. Maxwell, eds.), pp. 165–175. Plenum, New York.

Ritchie, T. L. C. (1979). Intratelencephlic visual connections and their relationship to the archistriatum in the pigeon (*Columba livia*). Unpubished Ph.D. Thesis, University of Virginia.

Rochon-Duvigneaud, A. (1943). Les yeux et la vision des vertebrés, Paris: Masson.

Roberts, W. A., and Mazmanian, D. S. (1988). Concept learning at different levels of abstraction by pigeons, monkeys, and people. *J. Exp. Psychol. Anim. Behav. Process* **14,** 247–260.

Rogers, J. J., and Miles, F. A. (1972). Centrifugal control of the avian retina. V. Effects of lesions of the isthmo-optic nucleus on visual behaviour. *Brain Res.* **48,** 147–156.

Shimizu, T., and Karten, H. J. (1990). Immunohistochemical analysis of the visual Wulst of the pigeon (*Columba livia*). *J. Comp. Neurol.* **300,** 346–369.

Shimizu, T., and Karten, H. J. (1993). The avian visual system and the evolution of the neocortex. *In* "Vision, Brain and Behavior in Birds" (H. P. Zeigler and H.-J. Bischof, eds.). MIT Press, Cambridge.

Shortess, G. K., and Klose, E. F. (1977). Effects of lesions involving efferent fibers to the retina in pigeon (*Columba livia*). *Physiol. Behav.* **18,** 409–414.

Singer, W. (1993). Synchronization of cortical activity and its putative role in information processing and learning. *Annu. Rev. Physiol.* **55,** 349–374.

Snyder, A. W., Laughlin, S. B., and Stavenga, D. G. (1977). Information capacity of eyes. *Vision Res.* **17,** 1163–1175.

Thin, N. D., Egedy, G., and Tömböl, T. (1992). Golgi study on neurons and fibers in nucleus rotundus of the thalamus in chicks. *J. Hirnforsch.* **33,** 203–214.

Thompson, I. (1991). Considering the evolution of vertebrate neural retina. *In* "Vision and Visual Dysfunction" (J. R. Cronly-Dillon and R. L. Gregory, eds.), Vol. 2, pp. 136–151. Macmillan, New York.

Tömböl, T., Ngo, T. D., and Egedy, G. (1992). EM and EM golgi study on structure of nucleus rotundus in chicks. *J. Hirnforsch.* **33,** 215–234.

Uchiyama, H. (1989). Centrifugal pathways to the retina: Influence of the optic tectum. *Vis. Neurosci.* **3,** 183–206.

Uchiyama, H., and Ito, H. (1993). Target cells for the isthmo-optic fibers in the retina of the Japanese quail. *Neurosci. Lett.* **154,** 35–38.

Uchiyama, H., Ito, H., and Tauchi, M. (1995). Retinal neurones specific for centrifugal modulation of vision. *NeuroReport* **6,** 889–892.

Uchiyama, H., and Watanabe, M. (1985). Tectal neurons projecting to the isthmo-optic nucleus in the japanese quail. *Neurosci. Lett.* **58,** 381–385.

Uchiyama, H., Matsutani, S., and Watanabe, M. (1987) Activation of the isthmo-optic neurons by the visual Wulst stimulation. *Brain Res.* **406,** 322–325.

Vander Wall, S. B., and Balda, R. P. (1977). Coadaptation of the Clark's nutcracker and the pinyon pine for efficient seed harvest and dispersal. *Ecol. Mon.* **47,** 89–111.

Varela, F. J., Palacios, A. G., and Goldsmith, T. H. (1993). Color Vision of Birds. *In* "Vision, Brain and Behavior in Birds" (H. P. Zeigler and H.-J. Bischof, eds.), pp. 77–98. MIT Press, Cambridge.

Verstappen, A., Van Reeter, O., Vaudry, H., and Pelletier, G. (1986). Demonstration of a neuropeptide Y (NPY)-like immunoreactivity in the pigeon retina. *Neurosci. Lett.* **70,** 193–197.

von Fersen, L., Wynne, C. D. L., Delius, J. D., and Staddon, J. E. R. (1992). Transitive inference formation in pigeons. *J. Exp. Psychol. Anim. Behav. Process* **17,** 334–341.

Wagner, H., and Frost, B. (1993). Disparity-sensitive cells in the owl have a characteristic disparity. *Nature* **364,** 796–798.

Wagner, H., and Frost, B. (1994). Binocular responses of neurons in the barn owl's visual Wulst. *J. Comp. Physiol. A* **174,** 661–670.

Walls, G. L. (1942). "The Vertebrate Eye and Its Adaptive Radiations." Cranbook Institute of Science, Bloomfield Hills, MI.

Wang, Y., and Frost, B. J. (1992). Time to collision is signalled by neurons in the nucleus rotundus of pigeons. *Nature* **356,** 236–238.

Wang, Y., Jiang, S., and Frost, B. J. (1993). Visual processing in pigeon nucleus rotundus: Luminance, color, motion, and looming subdivisions. *Vis. Neurosci.* **10,** 21–30.

Watanabe, M. (1987). Synaptic organization of the nucleus dorsolateralis anterior thalami in the Japanese quail (*Coturnix coturnix japonica*). *Brain Res.* **401,** 279–291.

Watanabe, M., Ito, H., and Masai, H. (1983). Cytoarchitecture and visual receptive neurons in the Wulst of the Japanese quail (*Coturnix coturnix japonica*). *J. Comp. Neurol.* **213,** 188–198.

Wathey, J. C., and Pettigrew, J. D. (1989). Quantitative analysis of the retinal ganglion cell layer and optic nerve of the barn owl, *Tyto alba. Brain Behav. Evol.* **33,** 279–292.

Weidner, C., Repérant, J., Desroches, A. M., Miceli, D., and Vesselkin, N. P. (1987). Nuclear origin of the centrifugal visual pathway in birds of prey. *Brain Res.* **436,** 153–160.

Wilson, P. (1980). The organization of the visual hyperstriatum in the domestic chick. II. Receptive field properties of single units. *Brain Res.* **188,** 333–345.

Wolf-Oberhollenzer, F. (1987). A study of the centrifugal projections to the pigeon retina using two fluorescent markers. *Neurosci. Lett.* **73,** 16–20.

Woodson, W., Reiner, A., Anderson, K., and Karten, H. J. (1991). Distribution, laminar location, and morphology of tectal neurons projecting to the isthmo-optic nucleus and the nucleus isthmi, pars parvocellularis in the pigeon (*Columba livia*) and chick (*Gallus domesticus*): A retrograde labelling study. *J. Comp. Neurol.* **305,** 470–488.

Wright, A. A., Cook, R. G., Rivera, J. J., Sands, S. F., and Delius, J. D. (1988). Concept learning by pigeons: Matching-to-sample with trial-unique video picture stimuli. *Anim. Learn. Behav.* **16,** 436–444.

Yang, G., Millar, T. J., and Morgan, I. G. (1989) Co-lamination of cholinergic amacrine cell and displaced ganglion cell dendrites in the chicken retina. *Neurosci. Lett.* **103,** 151–156.

Yazulla, S. (1974). Intraretinal differentiation in the synaptic organization of the inner plexiform layer of the pigeon retina. *J. Comp. Neurol.* **153,** 309–324.

Young, S. R., and Martin, G. R. (1984). Optics of retinal oil droplets: a model of light collection and polarization detction in the avian retina. *Vision Res.* **24,** 129–137.