Sturkie's **Avian Physiology**

FIFTH EDITION

AP

Edited by

G. Causey Whittow

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FIFTH EDITION

To Paul D. Sturkie,
Emeritus Professor of Physiology,
Rutgers University.
Author of the first edition
of Avian Physiology, editor
of the second, third, and fourth editions.

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Preface to the Fifth Edition

When the first edition of *Avian Physiology* appeared in 1954, it broke new ground—it was the first book on avian physiology ever published. The next three editions sustained the book's distinctiveness; it remained the only comprehensive, single-volume textbook on the physiology of birds. The present edition recognizes the retirement of the original author and editor, Dr. Paul D. Sturkie, by being titled *Sturkie's Avian Physiology*. The volume continues to break new ground. The treatment of the nervous system has been greatly expanded. A new chapter on flight has been added, occupying a central place in the book, as befits the most conspicuous feature of birds. There are new chapters also on incubation and growth and development, reflecting the characteristic development of the avian egg outside the body and the great deal of information now available. Most of the authors of this edition are new. However, the book retains the unique feature of earlier editions; it covers wild and domestic birds within the compass of one volume, making it suitable for use as a text.

G.C.W.

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Sensory Physiology: Vision

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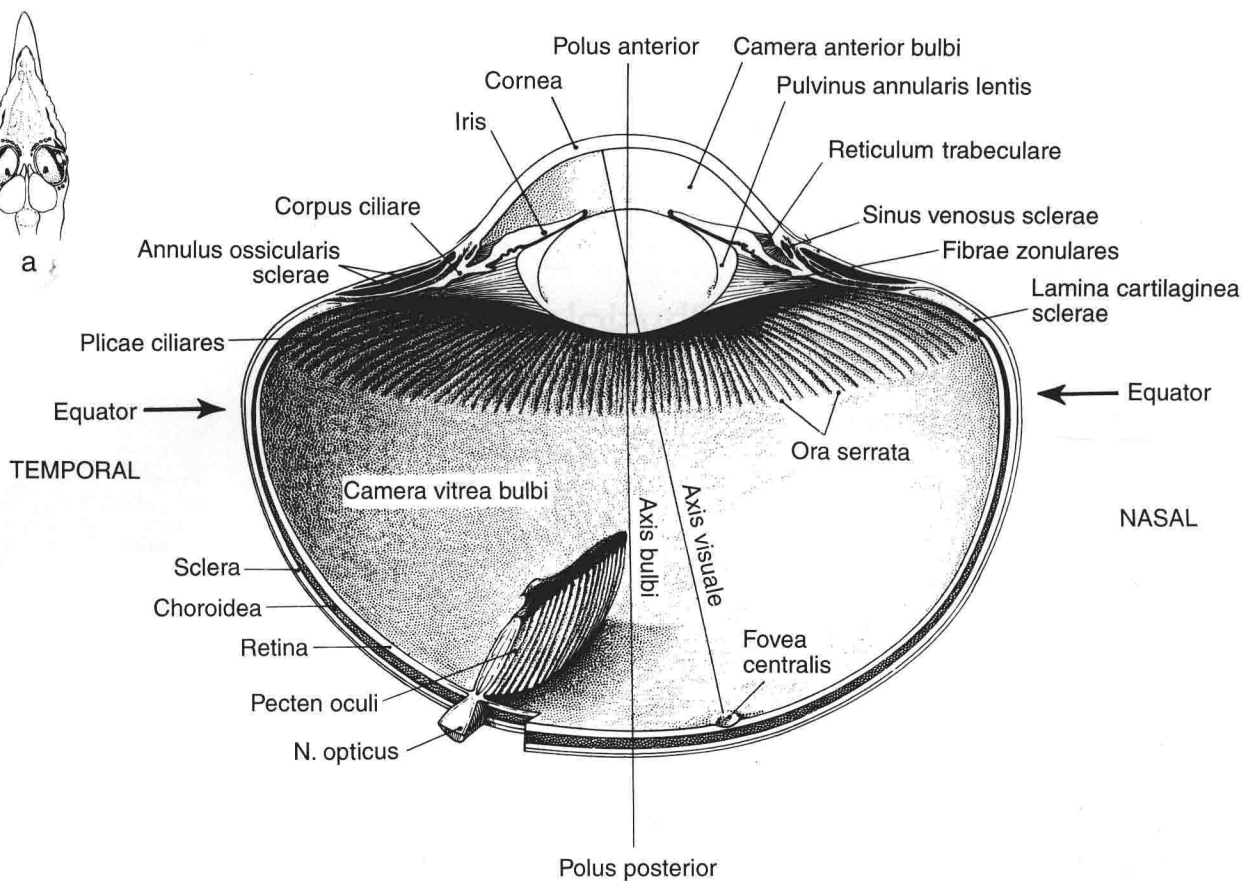
FIGURE 1 Drawing of a horizontal section of the chicken eye showing the position of the eyes within the head. (From H. Evans, 1996.)

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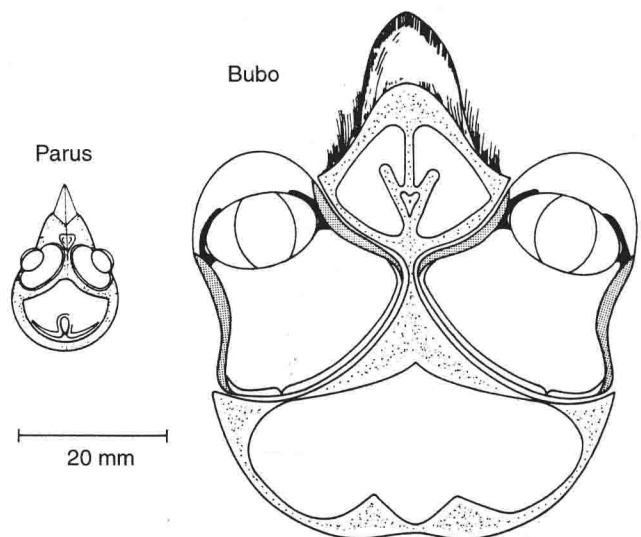
FIGURE 2 Horizontal section through the head of the black-capped chickedee (*Parus atricapillus*) and the great owl (*Bubo virginianus*). (From *Perception and Motor Control in Birds,* Form and function in the optical structure of bird eyes, G. R. Martin, pp. 5–34, Fig. 1.2, 1994, © Springer-Verlag.)

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
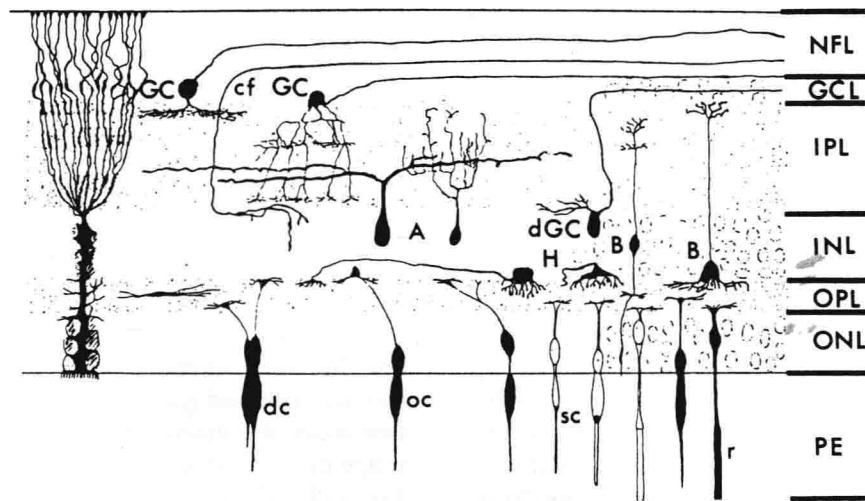
FIGURE 3 Schematic drawing of the avian retina. A, amacrine cell; B, bipolar cell; cf, centrifugal fiber; dc, double cone; dGC, displaced ganglion cell; GC, ganglion cell; GCL, ganglion cell layer; H, horizontal cell; INL, inner nuclear layer; IPL, inner plexiform layer; oc, oblique cone; ONL, outer 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