Chapter 16

SPECIAL SENSE ORGANS

EYE

Nearly all birds are intensely visual animals. A simple indication of this fact is the size of the eye which is extremely large in relation to the rest of the head. Indeed some owls and hawks have eyes which are absolutely as large or even larger than those of a man. The head accounts for about 10 per cent of the total body weight in both a man and a starling, but the weight of the eyes forms less than 1 per cent of the weight of the human head; in the starling it forms about 15 per cent. The eye of the Ostrich is about 50 mm in diameter and is absolutely the largest among the contemporary terrestrial vertebrates. In many birds the two eyes together outweigh the brain, but the weight ratio between the eyes and the brain in the domestic fowl is about 1:1. The relatively large eye in birds as a group permits a correspondingly large image to be projected on the retina, thus contributing to the acuity of avian vision.

In species with narrow heads such as pigeons the position of the eyes is lateral in the skull, while birds with broader heads such as falcons have eyes which are directed more frontally. Thus in pigeons the angle between the right and left bulbar axes is about 145° (the bulbar axis being a line passing through the centre of the cornea and lens to the retina). In predators like the Common Kestrel the angle may be reduced to 90° or less. Species with laterally placed eyes have a larger visual field (300° in pigeons) than those with frontally directed eyes (150° in the Barn Owl). On the other hand, the binocular field of vision in pigeons (24°) is correspondingly less than that of owls (60–70°). In binocular vision both eyes are focused on the same object, and the movement of the two eyes becomes coordinated. Monocular vision occurs when only one eye is focused on one object at any particular moment. Most birds can use binocular vision, but some (e.g. penguins) cannot.

The eyeball consists of a small anterior region covered by the cornea, a much larger and almost hemispherical posterior region covered on the outside by the sclera, and a variably shaped intermediate region based on the scleral ossicles and uniting the other two regions. In the 'flat' eyeball (Fig 16–1A) found in the majority of diurnal birds with narrow heads like the domestic fowl, the intermediate region is a flat disc almost parallel with the surface of the body and the bulbar axis is relatively short. Because of the shortness of the axis in this type of eye the image thrown on the retina is relatively small, so visual acuity is correspondingly low in these species. In diurnal birds with wider heads, like passeriforms and birds of prey, the intermediate region is cone-shaped producing a 'globular' eye (Fig 16–1B) and relatively greater visual acuity. Nocturnal birds of prey, e.g. owls, have a 'tubular' eye (Fig 16–1C), in which the intermediate region is relatively elongated. Fig 16–1 shows that in all these different forms of avian eye the shape of the retina resembles a parabolic reflector (like the dish aerial of a radio telescope). Consequently, the

Fig 16–1 The ventral half of the left eyeball of A a 'flat' eye as in swans, B a 'globular' eye as in eagles, and C a 'tubular' eye as in owls. In all three forms the eyeball consists of a relatively small corneal region, a variable intermediate region supported by the scleral ossicles (dark shading), and a more or less hemispherical 'posterior' region. In all birds the eyeball is somewhat asymmetrical, in that the bulbar axis begins slightly towards the nasal side of the midline (to the right in these diagrams). From Walls (1942), with kind permission of the Cranbrook Institute of Science, Michigan.
Fibrous tunic

The fibrous tunic is a tough layer which maintains the shape of the eyeball and protects the deeper layers within it. The cornea in most birds has a relatively small area compared to the rest of the eyeball. Its area is particularly small in underwater swimmers, but it tends to be relatively more extensive and more strongly curved in species such as eagles and owls with globular or tubular eyes (Fig 16-1B and -1C). As in mammals it consists of an anterior (outer) stratified squamous epithelium, an anterior (outer) limiting lamina (Bowman's membrane), a substantia propria which forms the great bulk of the corneal wall and consists of bundles of collagen fibres, a posterior (inner) limiting lamina (Descemet's membrane), and a posterior (inner) layer of simple cuboidal epithelium. In the domestic fowl all these layers are present, but in some species the anterior limiting lamina is not differentiated. The thickness of the cornea is about 450 μm in the domestic fowl, which is about midway in the range of thickness in the various species. The difference between the refractive indices of the cornea and of air is relatively great, and therefore the cornea is very important in refracting light in air. Under water, however, the cornea has no power to act like a lens since its refractive index is practically the same as that of water.

In birds generally, as in many reptiles, the whole of the sclera is reinforced by a continuous layer of hyaline cartilage, except in the region of the scleral ossicles (Fig 16-3). In the zone which is nearest to the cornea the wall of the sclera is modified into a ring of small, roughly quadrilateral, overlapping bones, the scleral ossicles, which strengthen the eyeball and provide attachments for the ciliary muscles. The number of ossicles varies from 10 to 18, but in most species including the domestic fowl there are usually 14 or 15. In many species, including falconiforms, hummingbirds, woodpeckers and passerines, the scleral cartilage round the optic nerve is ossified forming a U-shaped bone, the os nervi optici. The scleral venous sinus (canal of Schlemm) is quite conspicuous in some species but in others is small or almost invisible. It lies at the limbus, i.e. at the junction between the cornea and sclera (Fig 16-3). In this region a wide meshed plexus of connective tissue fibres, the trabecular reticulum (pectinate ligament), joins the limbus to the iris and to the ciliary body. The spaces between these fibres form the spaces of the irido-corneal angle (spaces of Fontana) through which the aqueous humour drains into the scleral venous sinus.

Vascular tunic

The vascular tunic consists of the choroid, the ciliary body and the iris (Fig 16-3). The choroid is the thick, highly vascular and darkly pigmented layer which coats the retina and contributes nutrition to the tissues of the eyeball. It is particularly vascular in many divers. A tapetum lucidum, the brilliantly coloured area which reflects light in many nocturnal vertebrates, has been found in only a few birds (e.g. the nocturnal goatsuckers). The choroid is continued by the ciliary body and iris. The ciliary body suspends the lens by the zonular fibres, and also forms small folds, the ciliary processes, which...
produce the aqueous humour. The ciliary processes are firmly pressed against the rim of the lens by the posterior sclerocorneal muscle, which suspends the lens by the zonular fibres and thus allowing the elastic lens passively to assume a more spherical shape. In many birds the posterior sclerocorneal muscle brings about accommodation directly by forcing the ciliary body against the lens so that the curvature of the lens is increased. In nocturnal birds including owls, but also in hawks, this muscle is weak, but accommodation in this group is achieved by the anterior sclerocorneal muscle. The attachments of this muscle from the cornea to the sclera (Fig 16-3) enable it to distort the cornea by pulling the corneoscleral junction posteriorly, thus increasing the curvature of the cornea at its centre. In diving birds this mechanism would be ineffective while the bird is under water, since the cornea is then no longer a significant refracting surface; as would therefore be expected, the anterior muscle is very much reduced in diving birds. Diving creates problems in focusing, because of the sudden need for an additional 20 diopters of refraction to compensate for the loss of corneal refraction. Some diving birds such as terns seem to lack the means to overcome this difficulty and are consequently long-sighted (hypermetropic) while in the water; they detect their fish from above, but often miss them in the water. Penguins, on the other hand, can see accurately in the water but are somewhat short-sighted (myopic) on land. However, many other diving birds, including cormorants, diving ducks and dippers, have truly amphibious vision. In these birds the lens is particularly soft and the two sclerocorneal muscles are enormously powerful. Even so, additional accommodation is probably produced by compression of the anterior part of the lens by the strongly developed sphincter muscle of the iris. Furthermore, it has been suggested that the coordinated action of the sclerocorneal muscles and the iris sphincter could force the soft lens against the iris and hence cause the centre of the lens to bulge through the pupil (Fig 16-2b) thus greatly increasing its curvature at the bulbar axis. The power of accommodation of the cormorant has been shown to be four to five times greater than that of the young human adult. As mentioned below under Retina, kingfishers seem to have adopted yet another device, i.e. a second fovea, to obtain sharp vision under water. To sum up, three mechanisms of accommodation occur in birds: (1) compression of the whole lens by the posterior sclerocorneal muscle, in many diurnal birds; (2) distortion of the centre of the cornea by the anterior sclerocorneal muscle, in nocturnal birds and hawks; and (3) compression of the front of the lens by the combined action of the sclerocorneal muscles and the sphincter muscle of the iris perhaps forcing the lens to bulge through the pupil.

Fig 16-3 Diagram of the wall of the avian eyeball in the region of the corneoscleral junction and ciliary body. The scleral wall is supported by cartilage and, near the rim of the lens by the ciliary muscles (the muscles of accommodation), and are directly attached to the lens capsule (Fig 16-3). There are two ciliary muscles (sclerocorneal muscles) in birds (Fig 16-3), i.e. the anterior sclerocorneal muscle (Crampton's muscle) and the posterior sclerocorneal muscle (Brücke's muscle). These muscles are striated in birds, in contrast to the smooth muscle of the ciliary muscle in mammals. Two other possible
in many diving birds. To these can be added the possible utilization of a fovea
for underwater vision, in kingfishers.

The iris in most birds is dark in colour, ranging from brown to black, but in
some species it is highly coloured (e.g. yellow in most owls, green in cormor-
ants, red in night-herons and pale blue in the Gannet). Refractive cells
(iriocyctes) form a tapetum lucidum of the iris in several columbiform species,
and are responsible for the rapid changes in colour of the iris which occur in
these species when excited. The shape of the pupil is round in almost all birds,
but it forms a horizontal oval when dilated in some species (e.g. thick-knees);
in skimmers, but no other known species of bird, it is a vertical slit. 
Measurements of the area of the skimmer's pupil when constricted and dilated
suggest that the vertical shape in bright light achieves a greater reduction in
pupillary area than would a constricted circular pupil; on the other hand when
the bird is in almost complete darkness the pupil is circular and relatively
wide in relation to the diameter of the eye. These characteristics may enhance
the skimmer's ability to feed even during the darkest nights, and yet protect
the retina when the bird is active in brilliant sunlight. In the domestic fowl the
iris can become mis-shaped in ocular leucosis. In contrast to mammals the
sphincter and dilator muscles of the pupil are again striated. The movements of
the avian pupil can be very extensive and much faster than in mammals, and
yet the pupil seems unexpectedly unresponsive to light possibly because of
inhibition by the brainstem. In birds (and also in teleost fish and frogs, but not
in mammals) the amount of light reaching the visual cells of the retina can
also be regulated by photomechanical changes in the cells of the pigment
epithelium of the retina. The processes of the pigment cells extend between the
photosensitive tips of the receptor cells (Fig 16-5). In light adaptation the
pigment migrates inwards within these processes, shielding the outer seg-
ments of the receptor cells.

Lens

The lens of birds is much softer than that of mammals. A lens vesicle, filled
with fluid, lies between the annular pad and the body of the lens (Fig 16-3),
contributing to the general softness of the lens. This softness facilitates the
rapid accommodation which typifies the avian eye. The anterior surface of the
lens is generally much flatter in diurnal species than in nocturnal and aquatic
birds. In all birds the lens includes the annular pad (Ringwulst) round its
equator, adjacent to the ciliary processes. The pad is particularly well
developed in diurnal predators, but is reduced in nocturnal species, diving
birds and flightless birds. In primates the lens acts as a yellow filter which cuts
off light of wavelengths below 400 nm and therefore renders ultraviolet
radiation invisible: the cornea and lens of diurnal birds are optically clear and
appear to transmit wavelengths down to about 350 nm, thus rendering near
ultraviolet radiation visible and absorbing only those ultraviolet wavelengths
which are not physiologically destructive.

Retina

In contrast to the retina of mammals, that of birds is relatively thick and has
no blood vessels. It resembles the mammalian retina, however, in consisting of
a non-nervous pigment epithelium and a nervous layer formed essentially
from rods and cones, bipolar cells and ganglion cells (Fig 16-5). The ganglion
cells form the axons of the optic nerve. Cones (Fig 16-4) are responsible for
visual acuity and colour vision. Diurnal birds have far more cones than rods
over the entire retina, the cone density being greater than in man. In diurnal
predators and passerines the few rods are confined to the periphery. Rods (Fig
16-4) are sensitive to the intensity of light; nocturnal birds such as owls have
some cones but mostly rods. Although it has not been directly demonstrated, it
As in mammals, a part of the retina of birds is thickened into a mound where there is a relatively high concentration of cones and other nervous elements but no rods thus forming a special region of maximum optical resolution known as the central area (Fig 16-6). Some birds have a laterally-placed special region, which is then known as the temporal area. The central area may have a fovea, which in principle resembles that of primates in being a shallow bowl with its concavity facing the vitreous body (Fig 16-6); at the bottom of the fovea the cones are extremely closely packed, and since the non-receptor elements are displaced peripherally the light can pass almost directly to the receptors in this part of the retina. Compared to the fovea of primates, however, that of birds is much deeper. It has been suggested that the deep fovea of birds may increase their visual acuity. The two steeply convex lips of the fovea could act like the edges of two adjacent convex lenses, refracting the rays of light so that they diverge and thereby magnify the area of the image by as much as 30 per cent (Fig 16-6). It has also been proposed that the fovea of the round central area fixes the eye on an object by refraction from its steep sides and increases the sensitivity to movement of the object. The temporal area of maximum optical resolution may also have a fovea.

There are three main types of arrangement of the fovea and area (or areas) of maximum optical resolution. (a) The great majority of species have a single round central area (in each eye) close to the optic axis, with a fovea. The domestic fowl and a few other species have a round central area but no fovea. (b) Two foveate areas, comprising a central area close to the optic axis and a laterally situated temporal area, occur in each eye in a number of species. Examples are terns, swallows and falconiforms, all of which pursue fast-moving prey or feed on the wing and therefore require a very accurate perception of distance and relative speed. The temporal fovea is so positioned that the image of the object is formed on the temporal fovea of both the left and the right eye simultaneously, indicating that they function in stereoscopic binocular vision. Kingfishers also have two foveae in each eye. These birds see well under water despite having no power of accommodation. It is suggested
that in kingfishers one fovea is adapted for aerial and the other for aquatic vision. (c) Owls are unique among birds in possessing a single foveate temporal area in each eye. (d) Water birds and birds which live in open plains have a horizontal central area which is expanded into a ribbonlike band. This type of area can occur regardless of whether the retina is avoveate, monoveoveate or bifoveate. The eye of these birds is held in such a position that the long axis of the horizontal central area lies close to the horizontal plane. The ribbonlike area could then fix the horizon accurately as a reference point.

There has been much discussion of the popular idea that diurnal birds have far greater visual acuity than mammals. Visual acuity is the sharpness with which detail is perceived, i.e. the resolving power of the eye. Factors which influence visual acuity include (1) the relative size of the eye, (2) the accuracy of focus on the various regions of the retina, (3) the possible magnifying capacity of the fovea, (4) the absence of blood vessels in the retina, (5) the fineness of 'grain' of the retina, (6) the degree of convergence of receptor cells on the ganglion cells, and (7) the amount of contrast between an object and its background. Of these factors, 1, 2, 3 and 6 have already been discussed, and all of them favour greater visual acuity in birds; 7 is considered below under colour vision. Factor 4 again indicates greater acuity in birds. In mammals the floor of the fovea is devoid of blood vessels and can be used for acute vision, but the rest of the retina suffers from optical interference by the retinal vessels. The complete absence of retinal vessels in birds means that the whole of the retina is free of such interference. Factor 5, retinal grain, is important for the same reason as the fineness of grain in photographic film is a factor in photographic detail. In diurnal birds the retina is heavily dominated by cones. In the fovea of the hawk there are about 300 000 cones per mm², whereas the human fovea contains only about 147 000 cones per mm². Furthermore, nearly every cone may be individually represented in the optic nerve of a diurnal bird, whereas in the human eye there are 6 to 7 million cones but only a million axons in the entire optic nerve. Moreover, diurnal birds seem to be able to detect a rapidly flickering stimulus better than man; thus the pigeon's retina can distinguish between individual flashes at a rate of 140 per second, while the maximum rate for man is about 70 per second. Measurements including counts of cones in the fovea suggest, nevertheless, that the resolving power of passerine and falconiform birds is in fact only about twice to three times greater than that of man or monkey. On the other hand, the anatomical characteristics of the eye make it likely that a diurnal bird could see a whole panorama as accurately as a mammal could see a single detail. Thus both a bird and a man could see a mouse from a height of 250 feet, but the man could only do so if his attention were accurately directed to it: the bird should be able to see it without looking directly at it. Moreover, the bird should be able to see in a single glance all the mice in a field, whereas the man could only do this by scanning the area laboriously with his central area and fovea. In other words, the bird should be able to assimilate detail very much faster than a mammal. Furthermore, because it can follow a faster flickering stimulus, the bird should be better able to detect and follow movement. Very few birds are active at night. Those that are, amount to less than 3 per cent of all the avian species, and the 146 species of owl account for well over half of these. The owls are the only nocturnal birds which are thought to rely at all extensively on vision for feeding. The sensitivity of the owl's eye to small amounts of light has therefore been much debated. The receptor cells of the owl's eye consist predominantly of rods but the ganglion cells are very numerous, indeed more so even than in the human fovea, so there appears to be relatively little convergence. Cones are present, and there is a temporal fovea placed for binocular vision. Measurements suggest that the owl's eye is in fact, only about two-and-a-half times more sensitive than that of a man. This superiority is not a factor of the sensitivity of the rods themselves; it has been suggested that the individual human rod can respond to the absorption of a single quantum of light, thus reaching the theoretical limit of light detection. The difference in absolute sensitivity appears to be due, instead, to the better optics of the owl's eye, which enable it to gather more light than the human eye; thus it loses fewer quanta from absorption, scatter and reflection in the optic media. The f-number of the owl's eye is about 1.30, whereas that of man is about 2.10. This produces a retinal image in the owl which is about two-and-a-half times brighter than that in a man. This optical advantage is, however, too small to explain the extraordinary ability of owls to fly between obstacles and to hunt successfully in what looks to us like pitch darkness. This reason lies much more in the sense of hearing. Owls can locate sounds with sufficient accuracy to catch prey in the total absence of light. However, the Tawny Owl can also see perfectly well in daylight, with colour vision. When food requirements are strong this highly nocturnal species will hunt by day. Its visual acuity is, indeed, equal to that of a pigeon and only slightly inferior to that of a man. The main factor accounting for the visual acuity of the owl is the exceptionally large size of its eye, which therefore produces a very large retinal image. Owls, like man, have a dual purpose eye that is well-adapted for both nocturnal and diurnal vision.

The magnificent plumage of many avian species suggests that birds have colour vision, and this is confirmed by behavioural and electrophysiological observations. Spectrophotometry has demonstrated three visual pigments in birds, and there is perhaps a fourth which is sensitive to wavelengths near the ultraviolet. Thus birds are at least trichromatic, and perhaps tetrachromatic. A complication in the avian cone (and in the cones of many amphibia and reptiles) is the presence of a brightly coloured oil droplet at the base of the photosensitive outer segment (Fig 16-4) and therefore interposed between the incident light and the visual pigment; the rods usually lack the oil droplet. The oil droplets are orange, red, yellow or clear, but five types have been identified by their absorbency spectra. One interpretation of this is that avian cones have only one visual pigment and that colour vision depends entirely on the oil droplets. The more widely held view is that colour vision is a function of several (three or four) visual pigments in the cones, and that the oil droplets simply enhance contrast by acting as intraocular light filters thereby intensifying similar colours by reducing the discrimination of others. Thus the yellow droplets would remove much of the blue from the background, hence increasing the contrast between an object and the blue sky. Similarly, the red
The pecten is a thin black structure projecting from the retina into the vitreous body, towards the lens. Its base is always planted on the optic disc, which is functionally the best place for it to be since the optic disc is the blind spot and the pecten is non-sensory. In general, it is small and simple in nocturnal birds, and large and elaborate in diurnal birds, although there are many species variations. Basically, however, there are two main types of pecten (Fig 16–7A). In the pleated type of pecten, which occurs in carinate, the surface of the ridge is thrown into narrow thick vertical corrugations or pleats (a in Fig 16–7A). The tips of the pleats are generally held together distally by a bridge which is strongly adherent to the vitreous body. The number of pleats varies widely between species, the pecten of active diurnal birds tends to be larger and more folded than that of nocturnal species; the pecten of the domestic fowl has 16 to 18 pleats while that of owls has only five to eight pleats. In the vaned type, which occurs in most ratites such as the Ostrich and rheas, the ridge carries 25 to 30 thin vertical vanes projecting all round it (b in Fig 16–7A). The pecten of kiwis differs from the two main types in being a simple conical structure without any pleats or vanes at all. The curvature and length of the pecten also vary greatly (Fig 16–7B). In structure the pecten is extremely vascular, consisting mainly of modified small blood vessels and melanotic pigment cells. Both the luminal and external surfaces of the endothelial cells form large numbers of microfolds, which greatly increases the surface area. It is widely accepted that the main function of the pecten is to provide nutrients to the avascular retina by diffusion through the vitreous body. A similar but smaller and simpler structure, the conus papillaris, occurs at the same site in reptiles which like birds do not have blood vessels within the retina. Numerous other functions have been suggested but not conclusively substantiated. They include a role in accommodation by varying the pressure in the vitreous body; maintaining a high ocular temperature at high altitude where the ambient temperature is extremely low; acting as a dark mirror by decreasing glare and reflecting an image onto the retina of an object approaching from the direction of the sun; protecting the central area from the sun; and providing a fixed point as a navigational aid to fix the position of the sun during migration.

The chambers of the eye and vitreous body

The anterior chamber is bounded by the cornea and the iris and the posterior chamber by the iris and the lens (Fig 16–3), the anatomy of these chambers being essentially the same as in mammals. They contain the aqueous humour, which is formed by the ciliary body and is responsible for the intraocular pressure, thus maintaining the global shape of the eye. The aqueous humour percolates through the spaces of the iridocorneal angle and then drains into the venous circulation via the scleral venous sinus. The vitreous body, as in mammals, is a clear translucent gel which fills the eyeball between the lens and retina.

Eyelids

The cornea is protected by the upper and lower eyelids and the nictitating membrane. In many or most birds the eyelids close only in sleep, and the nictitating membrane alone is responsible for blinking. On the other hand, in the American Dipper there is a regular and frequent blinking of the eyelids. In the domestic fowl the dorsal border of the mobile part of the upper eyelid forms a deep groove housing several species of lice and fleas; the comparable groove...
on the lower lid is much shallower. The lower eyelid is thinner, more extensive and more movable than the upper eyelid being mainly responsible for closing the eyes. It is devoid of glands. When the eyelids are open their edges form a circle round the edge of the iris so that very little of the white of the eye (the sclera) is visible. In altricial birds the lids remain closed for a short period after hatching. Rows of small overlapping bristle feathers take the place of eyelashes. At least three striated muscles act on the eyelids. The levator of the upper lid is innervated by the oculomotor nerve, and the depressor of the lower lid by the mandibular nerve. Two other muscles have been named as eyelid muscles, the m. tensor periorbitae and the m. orbicularis palpebrarum.

**Fig 16-8** Diagrammatic horizontal section through the eye to show the positions of the gland of the nictitating membrane and lacrimal gland, and the direction taken by their secretions (arrows). From Slonaker (1918).

but it is not clear whether or not these are one and the same muscle. However, it seems certain that sphincter-like striated muscle fibres encircle the eyelids and are innervated by the mandibular nerve. It is also probable that smooth muscle fibres are present in the avian, as in the mammalian, eyelid.

The nictitating membrane (third eyelid) lies beneath the eyelids on the nasal side of the orbit, and can be freely moved transversely across the front of the eye (Fig 16–8). It darts across the eye about 30 to 35 times a minute in the domestic fowl, and also moves in response to objects approaching the eye, suddenly or striking the comb, wattles or ear lobes. The free edge of the membrane is stiffened by a connective tissue band, and on its outer surface it has an anteriorly-directed scooplilke projection, the marginal fold (Fig 16–8). In contrast to mammals, two striated muscles, namely the quadratus and pyramidalis muscles (Fig 16–9), are responsible for movements of the nictitating membrane. These muscles are under the control of the sixth cranial nerve. At its insertion on the back of the eyeball the quadratus muscle forms a fibrous pulleylike sheath just dorsal to the optic nerve; the tendon of the pyramidalis muscle passes mediolaterally through the pulley and inserts on the ventral part of the free edge of the membrane (Figs 16–9 and 16–10). Since the dorsal part of the free edge of the membrane is fixed to the eyeball, the membrane makes a pendulumlike movement as it passes to and fro across the eye. As the nictitating membrane travels across the eye from the nasal to the temporal side it sweeps the surface of the cornea distributing the secretion of the gland of the nictitating membrane over the cornea, but the marginal fold is flattened so that excess fluid can flow onto the anterior surface of the membrane (Fig 16–8). As the membrane makes its return journey medially across the eye the marginal fold swings outwards to become scooplilke, and thus sweeps the excess of fluid into the nasal commissure of the eyelids where it drains into the lacrimal apparatus (Fig 16–8). In a few species, including the American Robin, American Dipper, and owls, the membrane is cloudy. In most birds, however, vision is not severely impaired when the eye is covered by the nictitating
membrane because the membrane is usually transparent in diurnal species. Indeed it has even been suggested that some birds may fly with the membrane covering the cornea, thus protecting it from desiccation. In a number of diving birds, including auks, divers and some diving ducks, the central part of the membrane has a transparent window. In other diving birds, including cormorants and certain diving ducks such as pochards, mergansers and goldeneyes, the membrane is transparent all over. It has long been held that in diving birds the transparent region of the membrane is highly refractive and bends light under water thus compensating for the loss of corneal refraction when submerged. It has now been shown, however, that the refractive index and curvature of the membrane are virtually the same as those of the cornea, so the membrane does not after all possess a refractive function under water.

**Lacrimal apparatus**

The gland of the nictitating membrane (Harderian gland). In birds generally, this relatively large compound tubular or tubuloalveolar gland is tongue-shaped and has a pink or yellow colour which is very similar to that of the muscles of the eyeball. In the domestic fowl and the Rook it is about $18 \times 8 \times 2\text{ mm}$ in size. It lies on the ventral and caudomedial surface of the eyeball (Figs 16–9 and 16–10), but often remains in the orbit when the eyeball is removed. Its position in the orbit is much deeper than that of the lacrimal gland. The mucoid secretion of the gland discharges through a single duct into the conjunctival pouch between the nictitating membrane and the eyeball, and cleans and moistens the cornea. In birds generally, the gland becomes infiltrated by plasma cells which are derived from the cloacal bursa. These cells produce specific antibody in response primarily to local antigenic stimulation of the eye, thereby protecting the eye against microbial invasion.

The **lacrimal gland**. In birds generally, the lacrimal gland is much smaller ($7 \times 2 \times 1.5\text{ mm}$ in the domestic fowl) than the gland of the nictitating membrane, this relationship being the reverse of that in mammals. It is usually reddish-brown in colour. It lies in the region of the temporal (caudal or lateral) commissure of the eyelids and is firmly attached to the orbital rim (Figs 16–9 and 16–10). In contrast to the gland in mammals, it drains by a single duct which opens into the conjunctival sac on the bulbar surface of the lower lid. The gland is absent in a few species including penguins.

The **drainage system**. The lacrimal secretions drain by the lacrimal ostia of the upper and lower eyelids. The ostium of the upper lid is a large opening about $3\text{ mm}$ in diameter in the domestic fowl, that of the lower lid being only about one-third of this diameter. In this species the two ostia are close together within about $1-2\text{ mm}$ of the medial commissure of the eyelids. Each ostium leads into a lacrimal canaliculus (Fig 16–8). After a few millimetres the two canaliculi join to form the spacious nasolacrimal duct (Fig 7–1B) which passes through the dorsal and medial wall of the infraorbital sinus and opens into the nasal cavity through an elongated slit. This opening lies dorsal to the rostral end of the choanal opening and ventral to the middle nasal concha (Fig 7–1B).

**Extraocular muscles**

Eye movements in birds are generally limited since the eyeball almost completely fills the orbit. The eyes of many species, however, are capable of forward convergence towards the tip of the beak, this being demonstrated in an extreme form by the Eurasian Bittern which can direct its gaze forwards and horizontally over the surface of the ground even while its beak is pointing vertically upwards in the typical cryptic posture. There is relatively great mobility of the eyes in toucans and hornbills. The small eye movements of the majority of birds, however, are compensated by the great mobility of the head and neck. In contrast to mammals, movements of both eyes are quite independent. They are controlled by the dorsal and ventral oblique muscles and by the dorsal, medial, ventral and lateral rectus muscles (Figs 15–9 and 16–9) resembling those of mammals. (See Chapter 15 for their innervation by the oculomotor, trochlear and abducens nerves.) However, unlike many mammals and reptiles the retractor bulbi muscle is absent. Although the extraocular muscles in owls are fairly well developed, the enormous tubular eyes in these species are only capable of small movements.
**EAR**

**External ear**

The external ear is a relatively short canal extending ventrally and caudally from the external acoustic meatus to the tympanic membrane. The external acoustic meatus is a small aperture, nearly always circular, which opens externally on the side of the head. In the domestic fowl it is 4–5 mm in diameter. In most birds the meatus is covered by specialized contour feathers, the ear coverts (Fig 14–2), and only rarely is it naked as in vultures and the ostrich. The coverts lying on the rostral aspect of the meatus reduce the drag caused by turbulence in flight and thus diminish the masking of sound by noise generated from turbulence in the external ear; since the barbs of these coverts lack barbules the sound waves are not obstructed. On the caudal aspect of the meatus the specialized feathers combine into a tight funnel which is particularly enlarged in songbirds, parrots and falconiform species such as the Osprey. In many species of owl the rostral border of the external meatus has a vertical skin flap, the operculum (Fig 16–11), bearing a row of feathers along and at right angles to its edge. The operculum (also commonly known as the concha) can be erected by striated muscle to assist in locating sounds. In the Barn Owl the facial ruff, which consists of small, curved, stiff feathers supporting the lower feathers of the facial disc, is an effective sound reflector, similar to a man cupping his hands behind his ears. If the operculum swings rostrally (like a door on a hinge) its feathers form, in conjunction with the peripheral feathers of the disc, a vertical slitlike aperture resembling the semi-tubular concha of many mammals. Acoustic location is apparently improved still further in owls by asymmetry of the external ear (Figs 16–11

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**Fig 16–11** Facial disc, facial ruff and operculum of the Barn Owl. In the drawing on the left the facial disc is intact. In the drawing on the right the facial disc has been removed to show the facial ruff and the operculum on each side. The left and right opercula are asymmetrical. The external acoustic meatus lies between the operculum and the facial ruff. Redrawn from Knudsen and Konishi (1979), with kind permission of the editor of *Journal of Comparative Physiology.*

**Fig 16–12** Left and right lateral views of the external aperture of the ear in the Long-eared Owl. The operculum (also known as the pre-aural flap) is a flap of feathered skin which can be moved to aid localization of sound sources. In both drawings it has been moved rostrally to expose the external acoustic meatus. The meatus is asymmetrical in shape in this species of owl. Also the skull bones are asymmetrical, the meatus being more dorsal on the left side. Redrawn from Pycraft (1910).

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The middle ear (Fig 16–14) is the air-filled cavity between the tympanic membrane and the inner ear. Unlike that of mammals, the tympanic membrane projects outwards rather than inwards. In owls the membrane is exceptionally large in diameter. The tension in the tympanic membrane is altered by the columnellar muscle, which attaches to the extracolumellar cartilage and to the tympanic membrane itself. Since this muscle arises from...
the second embryonic pharyngeal arch and has a motor nerve supply from the facial nerve, it is presumably homologous to the mammalian stapedius muscle, although its action resembles that of the mammalian tensor tympani muscle. Vibrations of the tympanic membrane are carried to the perilymph of the inner ear by the extracolumellar cartilage which is in contact with the tympanic membrane, and the rodlike bony columella which is implanted medially in the

vestibular window. The columella is homologous to the mammalian stapes, the mammalian incus and malleus are homologous to the avian quadrate and articular bones respectively. The columella has taxonomic significance. The typical avian columella is reptilian with a flat footplate and a straight bony shaft arising from the centre of the footplate. In a few groups, for example storks, the columella is tubular and its shaft has many perforations, especially near the footplate. Medially the base (footplate) of the columella is attached to the margin of the vestibular window, and its medial surface is therefore in direct contact with the perilymph of the vestibule of the inner ear (Fig 16-14).

Fig 16-14 Diagrammatic transverse section through the right middle ear of the domestic fowl. In the diagram, dorsal is upwards and lateral is to the right. Ossicular conduction from the tympanic membrane to the vestibular window is achieved by the columellar complex, consisting of the extracolumellar cartilage laterally and the bony columella medially. The columellar muscle attaches to the tympanic membrane rather than to the columella, but is innervated by the facial nerve. The vestibular and cochlear windows have both been partly transected by the plane of the section. Redrawn from Pohlan (1921).

probably it is also in direct contact with perilymph in the cistern of the vestigial scala vestibuli (Fig 16-15). In most birds the footplate of the columella is flat and moves in and out of the window like a piston, but in owls the footplate is hemispherical and the columella is oblique to the window so that rocking movements must occur (the mammalian stapes also undergoes rocking movements). The cochlear (round) window lies near the vestibular window and is in contact with the scala tympani of the inner ear (Fig 16-15). The membrane which covers the cochlear window is particularly thin and transparent in passerine species and owls. The compression of the perilymph of the inner ear, which occurs when the columella pushes the vestibular window inwards, is accompanied by an outward movement of the membrane of the cochlear window. The pharyngotympanic tube (Eustachian tube) connects the cavity of the middle ear to the oropharynx via the infundibular cleft (Fig 6-1), thereby equalizing the pressure on either side of the tympanic membrane.

Inner ear

The inner ear consists of bony and membranous labyrinths. The bony labyrinth, comprising the vestibule, semicircular canals and the cochlea, encloses the membranous labyrinth. The space between the bony and membranous labyrinths is filled with a fluid, the perilymph. The cavities of the membranous labyrinth are occupied by endolymph. Of the membranous labyrinth, the utricle, saccule and semicircular ducts are concerned with the position and movement of the head in space, whereas the cochlear duct is involved in hearing. The function of the lagena is not clear.

Auditory organ. The avian cochlea differs from the spiral cochlea of most mammals in being a relatively short and only slightly curved tube (about 6 mm in length in the domestic fowl). The cochlea of the owl is relatively long compared to that of other birds. Extending throughout the length of the cochlea is the cochlear duct (scala media) which is filled with endolymph, but because of the shortness of the cochlea the avian cochlear duct is only about one-tenth the length of that of a mammal of comparable body size. The scala vestibuli is vestigial, being reduced to a small space adjacent to the vestibular window, namely the cistern of the scala vestibuli (Fig 16-15), and another small space near the lagena known as the fossa of the scala vestibuli (Fig 16-15). The cochlear duct is separated from the vestigial scala vestibuli by the thick folded tegmentum vasculosum (corresponding to the vestibular membrane of Reissner in mammals), and from the well-developed scala tympani by the basilar membrane (Fig 16-15). The scala tympani and the remnants of the scala vestibuli connect with each other at the apical end of the cochlea via the apical interstrial canal which thus corresponds to the mammalian helicotrema; the two scalae also connect at the base of the cochlea by the basal interstrial canal (ductus brevis) (Fig 16-15). The scala tympani, and presumably also the vestiges of the scala vestibuli, contain perilymph. The blind apex of the cochlear duct is formed by the lagena (absent in mammals apart from the egg-laying monotremes) which contains the macula lagena, a group of
sensory cells with otoconia. Afferent nerve fibres from this macula appear to end in auditory centres of the medulla, and presumably have an auditory function.

As in mammals the basilar membrane carries the neuroepithelial receptor cells which constitute the organ of hearing. The basilar membrane of birds is considered to be relatively shorter than that of mammals (for instance 3 mm long in the pigeon, 35 mm long in man) because of the relative shortness of the avian cochlea, but it is much wider in birds thus making it possible for a relatively large number of receptor cells to be carried per unit length; indeed,

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positions of the ears, which cause the left ear to be more sensitive to regions below the horizontal plane, and vice versa for the right ear; thus as sound frequency increases, the plane of equal sensitivity for the two ears rotates from vertical to horizontal. A possible alternative, or perhaps additional mechanism for localization in birds, and especially in owls, depends on acoustic coupling of the two ears across the pneumatic cavities of the skull bones. The principle would be the sensing of pressure differences on either side of the tympanic membrane. If sound strikes both surfaces of the membrane, a net cancelling effect would occur when intensity and phase are closely matched. Such a system relies on null detection, as in radio navigation, and is an extremely accurate method for direction finding.

The necessary neuronal equipment for all this elaborate central analysis appears to be present, since the nocturnal hunting owls (e.g. the Barn Owl) which have asymmetrical ears, also possess an extraordinary number of neurons in the auditory nuclei of the medulla oblongata exceeding by three- or four-fold the number in a passerine bird (e.g. the Common Crow) of about twice the body weight. Midbrain auditory components are also very well developed in owls. On the other hand the Little Owl, which hunts at dawn, shows no special development of the auditory areas of the medulla oblongata.

Although birds as a group do not hear ultrasonic vibrations, a few nocturnal species (the Oilbird and cave swiftlets, which live in caverns) do use echo location. By this means they avoid obstacles in the dark, but cannot catch moving targets as bats do. These nocturnal species produce short pulses at a frequency of about 4–8 kHz, which are fully audible to man (i.e. not ultrasonic). The pulses emitted by bats have frequencies up to 100 kHz (inaudible to man). For birds flying in the dark the silent period between each signal is very short (about 2–3 ms), showing a similar time resolution to that of bats. However, the lower frequency used by birds enables them only to avoid bars over 6 mm in diameter, whereas bats using the highest frequencies avoid wires of 0.6 mm diameter and can catch prey of this diameter. Apparently, penguins are able to hunt in the water by echo location, although once again the signals are not ultrasonic.

**Balance organ.** The (membranous) semicircular ducts (Fig 16–16) occupy the (bony) semicircular canals; the (membranous) utricle and saccule lie within the (bony) vestibule. The three semicircular ducts (and of course the three semicircular canals that enclose them) are in roughly orthogonal planes. In all birds, the horizontal semicircular duct has a constant orientation, being parallel to the geophysical plane when the head is in the alert position. The rostral and caudal ducts are vertical in position, approximately at right angles to each other and at 45° to the sagittal plane; thus the rostral duct on one side is parallel to the caudal duct on the other side. The semicircular canals of birds generally are long in comparison with those of other vertebrates (averaging about 10 mm in length in the domestic fowl, compared to 15 mm in man). In the strongest fliers such as the falconiform species the canals are long and thin and have pronounced osseous ampullae, whereas weaker fliers, including the domestic fowl, have short wide canals. These and other avian elaborations of the canals and their ducts probably reflect their relatively great functional importance to life in three dimensions. The semicircular ducts arise from the saccule (utricle). At the origin from the utricle each duct has a dilation known as the membranous ampulla (Fig 16–16). The utricle connects by a small opening in its floor with the saccule. The saccule in turn connects to the cochlear duct by the sacculcochlear duct (ductus reuniens). The endolymphatic duct arises from the saccule and ends blindly in the cranial cavity under the dura mater.

**Zones of neuroepithelial mechanoreceptor cells are present in the ampulla of each of the three semicircular ducts and in the utricle, saccule and lagena. Those in the ampullae take the form of a ridge, the ampullary crista (Fig 16–16). The crista of the horizontal duct is a simple ridge, but the cristae of the rostral and caudal ampullae have an additional transverse ridge, the cruciate septum, which has no receptor cells and divides the sensory epithelium of the crista into two regions. The mechanoreceptor zones of the utricle, saccule and
lagena consists of patches of receptor cells, each patch being known as a macula (Fig 16-16). The zone in the utricle, the macula of the utricule, is strictly horizontal in its orientation; the macula of the saccule is orientated obliquely, and the macula of the lagena is vertical in position. The utricle has another smaller zone, the crista neglecta, which is a ridge rather than a macula.

The cristae and the maculae have an essentially similar structure. Each receptor cell carries a single kinocilium and a cluster of about 50 stereocilia. The cilia of the cristae are inserted into a gelatinous cap, the cupula, which is secreted by the supporting cells of the crista. The cupula almost fills the membranous ampulla. The cilia of the maculae are inserted into the gelatinous statoconial membrane which covers each macula. The statoconial membrane resembles the cupula, except that it contains numerous crystals of calcium carbonate, the statoconia. The cupulae and statoconial membranes are shifted by appropriate movements of the head, thus applying shearing stresses to the cilia. As in the crista basilaris of the cochlear duct, it is the bending of the cilia which induces the receptor (generator) potential in the receptor cell. Bending the cilia towards the kinocilium excites the receptor cell, but bending them away inhibits the receptor cell. The receptor cells make synaptic contacts with axons of the vestibular part of the vestibulocochlear nerve.

The receptor cells of the maculae tend to be tonically active, responding to the effects of gravity. Their patterns of activity vary, however, with the position of the head, since the shearing stresses in the maculae on each side of the head will vary when the head is tilted. Thus the maculae continuously inform the brain about the position of the head in space. The cristae, on the other hand, signal on and off discharges in response to changes in the rate of movement of the head, that is to acceleration or deceleration, but are silent when the head is still. Thus essentially, the cristae inform the brain about movement of the head in space.

**OLFACTORY ORGANS**

The visual life-style of the great majority of birds, coupled with the likelihood that odours would be quickly dispersed high above the surface of the land or water, probably account for the popular assumption that birds have very little sense of smell. Indeed, in both of the two great groups of flying vertebrates, the pterosaurs and birds, the visual region of the midbrain (the mesencephalic tectum, commonly called the optic lobe) became greatly enlarged, and the olfactory lobes were proportionately reduced. Nevertheless there is abundant evidence (anatomical, physiological and behavioural) that birds do perceive olfactory stimuli; what is not yet established, however, is the full role of olfaction in avian life.

Anatomically the olfactory region of the nasal cavity lies in the region of the domelike caudal nasal concha. The outer (nasal) surface of the concha is lined by an olfactory epithelium, which also extends over the adjoining walls of the nasal cavity (Fig 7-1C and -1D). The small septal concha, which is unique to

petrels, is also covered with olfactory epithelium. In most birds the caudal concha is a simple dome, but in a few species its surface area is much increased by scroll-formation as in vultures or several very extensive transverse folds as in kiwis. In birds such as swifts in which the caudal concha is absent, the olfactory epithelium covers the roof and lateral walls of the nasal cavity, as well as the dorsal part of the nasal septum. In birds generally the anatomy of the nasal cavity is adapted for effective airflow over the olfactory region.

As in other vertebrates the olfactory cell is a bipolar ciliated neuron supported by sustentacular and basal cells. Its terminal cilia and microvilli project from the epithelial surface. The unmyelinated axonal processes of the receptor cells form the olfactory nerve and end in the olfactory bulb of the brain. The size of the olfactory bulb relative to the cerebral hemispheres varies greatly. The smallest size occurs in passerines, and also in parrots and woodpeckers. Pigeons, galliforms, falconiforms, waders and gulls form an intermediate group. Larger bulbs have been found in a group of water birds including anseriforms, the Common Loon, American Coot, Horned Grebe and especially in some oceanic procellariiforms (albatrosses, storm petrels); however, there are others with larger olfactory bulbs that are not aquatic, such as the Yellow-billed Cuckoo which lives in trees and the whip-poor-wills which catch insects on the wing. The olfactory bulb reaches its largest relative size in the Brown Kiwi.

Electrical activity comparable to that of macromastic reptiles and mammals has been observed in the olfactory pathways of numerous avian species, in response to various odorous stimuli. It is known from behavioural studies that pigeons possess excellent olfactory perception. The nocturnal Brown Kiwi, which is a deplorably noisy sniffer, has no difficulty in finding buried delicacies.

Vultures have been shown to congregate rapidly over odiferous up-drafts, and are therefore presumed to use olfaction for locating the position of carrion. Leach's Storm Petrel and other oceanic procellariiforms have been found to navigate, at least partly, by olfaction, their own nesting material attracting them to their own island in the dark and leading them correctly through a maze to their burrows. However, if their nostrils were plugged or their olfactory nerves were cut the birds failed to return to their burrows within one week. Furthermore, experiments also show that procellariiform species use olfaction to find food at sea. Other examples of specific olfactory functions may occur in African honeyguides which appear to locate beehives by the smell of the beeswax on which they feed, and in pigeons which possibly utilize olfaction in homing. Although the exact contribution of olfaction to the biology of birds remains uncertain it must be assumed that birds do perceive odours to a greater or lesser degree.

**TASTE**

In the past it has been widely believed that the sense of taste is poorly developed in birds. However, recent work has shown that taste buds are much
more numerous than had previously been supposed, at least in the chicken, pigeon and duck. In most of the species which have been investigated, including the domestic fowl, pigeon, swift, falconiforms and several songbirds, the taste buds lie on the base of the tongue. In the Mallard there are no taste buds on the tongue, but groups occur at five other sites as follows: the internal aspect of the tip of the lower bill just caudal to the mandibular nail; the corresponding region at the tip of the upper bill just caudal to the maxillary nail; two sites on the caudal part of the roof of the oropharynx on either side of the midline; and the region of the roof immediately rostral to the choanal opening. The total number of taste buds in the Mallard is less than 500, whereas 10000 have been reported in man and 17000 in the rabbit. In the flamingo and oystercatcher areas of taste buds have been found on the floor of the caudal region of the oropharynx just cranial to the laryngeal mound. In parrots they occur on the roof of the oropharynx on either side of the choanal opening, and on the floor of the oropharynx at the rostral end of the laryngeal mound. In general, taste buds are confined to regions where the epithelium is soft, non-cornified and glandular; typically, they have a strong topographical affinity for the ducts of the salivary glands.

Histologically the taste buds of birds are often ovoid with a funnel-shaped outer pore. No distinction can be made between receptor cells and supporting cells. The so-called 'taste hairs' at the apical ends of the receptor cells are apparently artefacts. About 20 to 30 axons enter a typical taste bud. The axons from the taste buds on the tongue and palate travel in the glossopharyngeal nerve; axons from the taste buds in the upper and lower bill of the Mallard travel peripherally in the trigeminal nerve but probably belong to the facial nerve.

Electrophysiological observations show that salts and acids are generally effective stimuli, but sweet substances are not. Strong responses are obtained to distilled water. Behavioural studies confirm that birds can distinguish certain tastes, but in general the acuity of taste is less than that of mammals. There are indications that pigeons have relatively high acuity, and that the Mallard may be intermediate between the pigeon and the domestic fowl. Bitter-tasting substances are rejected fairly uniformly. Salt is also commonly rejected. Sour substances are rejected by several species including the domestic fowl, but quail prefer them. Sweet solutions produce the most unpredictable responses; for example domestic fowl vary individually in their reaction to sugars but consistently reject saccharine.

Although the total number of taste buds is probably much less in birds than in mammals there can no longer be any doubt that many birds do have a sense of taste, but very little is known about the role of taste in the biology of birds. In the Mallard the position of the taste buds does agree, however, with the pathway which the food is believed to take in its journey through the oropharynx. The taste buds at the bill tip enable unpleasant food particles to be rejected immediately; the remaining taste buds are distributed so that the palatability of food can be monitored almost continuously until it is swallowed.
APPENDIX

A list of the English common names of the birds cited in the text along with their Latin scientific names. The birds are cited alphabetically according to their common names.

Anhinga anhinga
Avocet
Bananaquit
Blackbird
Budgerigar
Bustard, Great
Chaffinch
Condor, Andean
Coot, American
Cormorant, Great
Crossbill, Red
Crow, Common
Cuckoo
Cuckoo, Yellow-billed
Dipper, American
Dove, Rock
Duck, Muscovy
Duck, Musk
Duck, Ruddy
Duck, Tufted
Eagle, Steller's Sea
Eagle, White-tailed Sea
Emu
Finch, Zebra
Flamingo, Greater