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The Evolutionary Biology of Hearing

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Evolution and Specialization of Function in the Avian Auditory Periphery

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1. Introduction

Birds, particularly passerines, are generally highly vocal animals. In view of the importance of these vocal communication signals, it would be reasonable to expect that strong selection pressures have influenced the evolution of the inner ear and auditory pathway. In this chapter, we shall discuss the structure and physiology of the hearing system peripheral to and including the auditory nerve. The features of auditory sensitivity, frequency discrimination, and time resolution abilities should be appropriate to the communication tasks at hand, as well as to normal environmental acoustic awareness.

Information concerning the evolution of structure and function can be derived from a number of sources. Data relevant to the present discussion can be obtained from palaeontological, comparative morphological, comparative physiological, and behavioral studies. In practice, however, our main sources of data on the evolution of the soft structures of the hearing organ are comparative anatomical and neurophysiological studies, which will be described below. The discussion is made much more difficult by the fact that birds do not fossilize well, so the course of evolution within the Class Aves is poorly understood (Carroll 1987).

It is of considerable importance to recognize the great similarity of the hearing organs of Aves and Crocodilia (Manley 1990): this fact suggests that the hearing organ has not changed substantially since the divergence of these two groups and that the ancestral avian hearing organ was probably similar in many respects to that of modern birds. One point we shall emphasize is that despite the structural similarities between the crocodilian-avian hearing organ and that of mammals, the available evidence indicates that the resemblance between these two hearing-organ types is due to the *independent* development of specialized groups of sensory cells (Manley et al. 1989).

2. The Middle Ear and the Hearing Range

Although reptiles and birds show significant variability in the details of their middle-ear structure and in the ossification of columella and extracolumella, all have the single-ossicle, *second-order-lever* middle-ear system (Fig. 27.1; Manley 1981; Manley 1990). Proximally, the columella forms a simple footplate in the oval window and connects distally with the tympanic membrane via a set of radiating, flexible processes of the extracolumella (Fig. 27.1). The long inferior process swings in and out when the tympanic membrane moves; its fulcrum is at the edge of the tympanum and the shaft of the extracolumella is attached somewhere near the middle. This generates a lever system. The transformation from the radial swinging of the inferior process to a piston-like motion takes place within the extracolumella itself, which prohibits a full ossification of the extracolumella. In birds, the middle ear is mechanically more protected than it generally is in reptiles, in being isolated from the buccal cavity and having, on average, a deeper external auditory meatus than the reptiles. Thus, in birds, the middle-ear ossicle is generally more ossified than in reptiles.

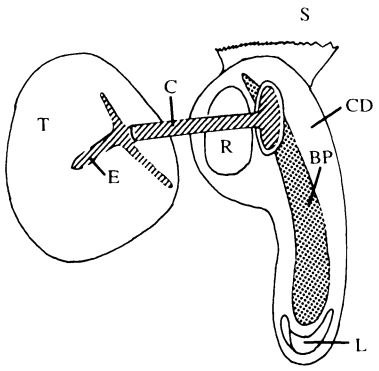

FIGURE 27.1. Schematic diagram of the middle ear and membranous labyrinth of the cochlear duct of a bird. The cochlear duct (CD) is connected to the sacculus (S), not shown here. Within the cochlear duct lies the basilar papilla (BP); the lagena macula (L) is at the apex. The tympanum (T) connects to various processes of the extracolumella (E) and via the columella (C) to the footplate in the oval window adjacent to the round window (R). The basilar papilla is typically 3 to 5 mm long.

All of these nonmammalian middle ears have a "low-pass" characteristic in the displacement transfer function. Although there are no systematic differences in the sensitivity and lever ratio to the mammalian ear, the upper frequency limit of the transfer characteristic is significantly lower than it is in mammals (Manley 1973; Manley 1981) and is strongly influenced by the flexibility of the middle ear (Manley 1972a,b). At high frequencies (>4 kHz), the efficiency of the middle ear deteriorates (Manley 1981), because an increasing amount of the acoustic energy is lost in a flexing motion *within* the inferior process. In addition, however, the inner ear itself ceases to absorb energy and thus dampens high-frequency middle-ear transmission, especially at low levels. Even if we look at the barn owl and at very small passerines, which have the highest high-frequency limits of nonmammals, the absolute limit of avian hearing at physiological sound levels is seen to be near 12 kHz. This value is very low when compared to a "typical" mammal, which has an upper limit near 50 to 70 kHz. Especially in such species as barn owls, oil birds, and cave swiftlets, whose existence depends on the fine analysis of relatively high-frequency sounds, selection pressures must have pushed the inner ear and middle ear to operate at the physiological limit. In the face of only small differences in the frequency response compared to "normal" birds, however, we conclude that the single-ossicle middle ear really is limited by its basic structure. The inability of the middle ear to transmit high frequencies, even though it does contain a lever system, has strongly limited the evolution of function in the reptiles and birds.

It is highly unlikely that synapsid reptiles at the reptilian-mammalian transition were able to process high-frequency sounds (Manley 1973; Manley 1990). A recent study of such transition mammals confirms this, indicating that they possessed only a very short hearing organ grossly resembling that of modern advanced reptiles (Graybeal et al. 1989). It was thus a fortuitous predisposition of structure in the three-ossicle ear which allowed the modern descendants of the mammals to modify their inner ear for the processing of very high frequencies.

3. Phylogenetic Considerations

3.1 The Phylogenetic Relationships of Extant Reptiles, Birds and Mammals

The vertebrate fossil record is so complete that there remains little doubt concerning the time of origin and the relationships of the major groups that concern us in this chapter. This information is essential for the discussion below and will be outlined briefly. Further detail can be found in textbooks of palaeontology, such as that of Carroll (1987). Although both birds and mammals are derived from reptiles, the times of the divergence of their direct ancestors from the other reptile groups are very different. The *synapsid* mammal-like reptiles are considered to have diverged from the stem reptiles about 300 million years (MY) ago, in the Pennsylvanian period (Fig. 27.2). True mammals originated over 200 MY before the present. The archosaur ancestors of birds and Crocodilia, in contrast, derive much later (and quite independently of mammals) from *diapsid* reptiles of the early triassic period (about 230 MY), with ancient birds emerging at the border of the upper jurassic and early cretaceous periods (140 MY; Carroll 1987; Fig. 27.2).

Thus the nearest common ancestors of birds and mammals are the stem reptiles older than 300 MY,

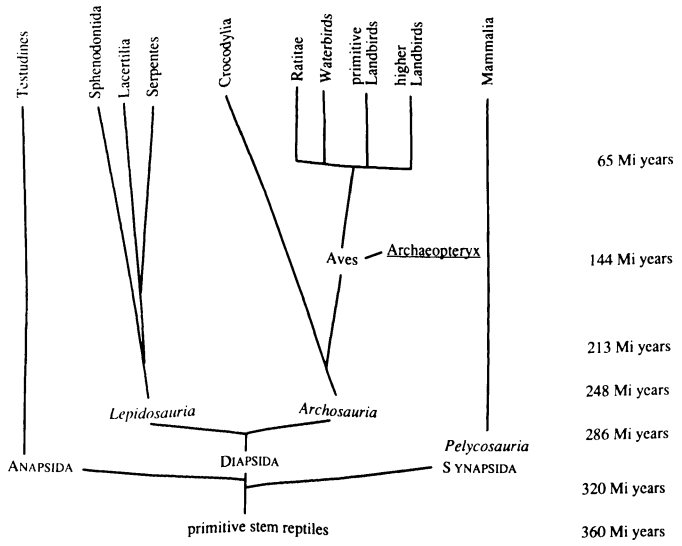

FIGURE 27.2. Highly simplified "family tree" of recent land vertebrates of interest to the discussion in this chapter, showing the approximate geological time scale of the various adaptive radiations. (After various authors.)

about whose hearing organ we have no direct information. We can, however, propose that modern chelonians, such as turtles, possess an inner ear whose structure has not fundamentally changed over this time period. This notion is supported by its structural similarities to the hearing organ of primitive diapsids such as Sphenodon (see the Chapter 23, Miller). If this is true, then the early mammal-like reptile hearing organ did not show the differentiation seen in the mammalian inner ear today. More specifically, the sensory cells and their innervations were not specialized into two groups placed neurally (that is, on the side where the nerve fibers enter the papilla) and abneurally (that is, on the side opposite the nerve) on the papilla. The similar specialization of the hair-cell populations of birds and Crocodilia is also a later development, with a probable origin soon after their common ancestor diverged from the ancestors of the lepidosaurs such as lizards and snakes (which show a different kind of hair-cell specialization). We thus observe the parallel and convergent acquisition by mammals and birds of auditory papillae having two or more groups of sensory hair cells organized across the papilla and of a specialized innervation pattern. We have discussed new evidence for important functional parallels between these auditory specializations in a recent paper (Manley et al. 1989).

3.2 Relationships Between Extant Families of Birds

Unfortunately, the fossil record of birds is relatively poor, so that there are substantial uncertainties with regard to the details of relationships between different avian groups. As we have no information at all about the hearing of the ratites (flightless birds retaining the ancient palaeognathous palate), we do not need to concern ourselves with the ongoing discussion as to whether this group is monophyletic or not. All other birds are neognathous (have a more modern palate) and can be divided into a water-bird assemblage and a land-bird assemblage (Feduccia 1980; Carroll 1987). The duck and seagull referred to below belong in the water-bird assemblage. The pigeon and chick belong to a primitive subdivision of the land-bird assemblage, whereas the starling and the barn owl belong to a more derived group of land birds (cf. Figs. 27.2 and 27.10).

4. The Starling as a Model of Bird Hearing

As there is more information available on the hearing of starlings than for any other avian species, we shall use its basilar papilla to briefly describe the structural arrangement and the physiology. This is

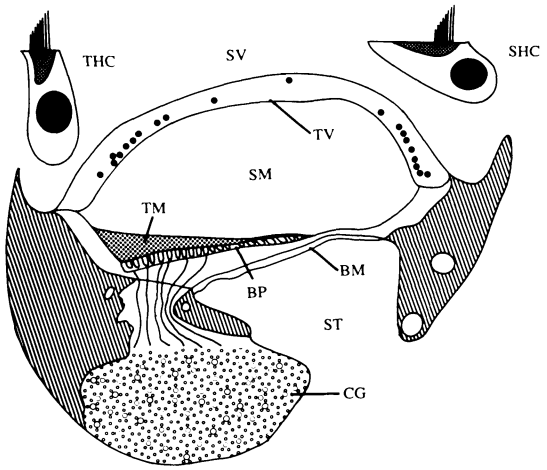

FIGURE 27.3. Schematic drawing of a cross-section through the cochlear duct near the apex of a typical avian basilar papilla. Scala vestibuli (SV) is separated from scala media (SM) by the tegmentum vasculosum (TV) which is equivalent to the mammalian stria vascularis. Above scala tympani (ST) lies the basilar membrane (BM) supporting the abneural part of the basilar papilla (BP), which is covered by the tectorial membrane (dotted pattern, TM). Nerve fibers (very few are illustrated) from the basilar papilla run to the cochlear ganglion (CG). Cut limbic material is shown shaded. The enlarged insets show (top left) a tall hair cell (THC) from the neural side of the papilla and (top right) a short hair cell (SHC) from the abneural side.

not intended to imply that the starling is in any way primitive or that this pattern indicates a kind of ancestral condition for birds.

4.1 The Avian Cochlear Duct

There is a strong similarity to be found in the structural arrangement of the cochlear ducts of birds and Crocodilia, with their lagenar macula and basilar papilla receptor areas (Fig. 27.1). The duct is not coiled, but twisted; this twisting is quite complex in the long ducts of owls (Schwartzkopff and Winter 1960; Fischer, Köppl, and Manley 1988). In general, the average avian auditory sensory epithelium is shorter (mostly less than 4 to 5 mm) and wider than that of a typical mammal. A thick tectorial membrane covers the entire papilla (Fig. 27.3). Almost all authors recognize two to four intergrading hair-cell types, i.e., the tall (THC), intermediate (INHC), short (SHC), and lenticular hair cells (Fig. 27.3; Smith 1985). Not all types have been recognized in all species and they are, unlike in the papilla of Caiman, frequently difficult to distinguish in a surface view (Fig. 27.4). The hair cells are surrounded by supporting cells. THC are the least specialized and most strongly resemble the typical hair cell of more primitive groups of vertebrates (Takasaka and Smith 1971; Chandler 1984). They are distinguished from SHC by their columnar shape (Fig. 27.3) and different innervation pattern. Except near the apical end, THC are found predominantly supported by the neural limbus and *do not lie over the free basilar membrane*. They can be entirely absent from the basal end. In contrast, the SHC are wider than they are tall (Fig. 27.3). These cells occupy most of the space over the free basilar membrane. INHC are intermediate in both shape and position, but have not been described in all species. A few hair cells at the basal end of the chick papilla and many hair cells of the basal 3 mm of the barn owl papilla have been called lenticular hair cells. They are flattened, with a large apical surface area, only part of which has a cuticular plate (Smith 1985). In the barn owl papilla, short hair cells grade into the lenticular type; at any one location, these cell types can be neighbors (Fischer, Köppl, and Manley 1988). The actual distribution of these hair-cell types is species-specific, the most striking differences being found at the apical end (Smith 1985). In all avian species investigated so far, the orientation of the hair cell bundles changes systematically according to the position across the papilla (Fig. 27.5; Fischer et al., 1988; Gleich and Manley, 1988; Tilney et al., 1987). The innervation of hair-cell types also differs (Takasaka and Smith 1971; Chandler 1984; von Düring, Andres, and Simon 1985; Smith 1985; Singer, Fischer, and Manley 1989).

The total number of sensory hair cells is comparable to that of the mammalian cochlea and ranges from a few thousand in some song birds (e.g., starling; 5,800 hair cells in a 3 mm long papilla) to about 10,000 in the pigeon and chicken papilla (Gleich and Manley 1988). In the papilla of barn owls, which exceed 11 mm in length and is thus more than twice the length of the papillae of starling, chick, or pigeon, there are more than 16,000 hair cells (Schwartzkopff 1968; Fischer, Köppl, and Manley 1988). The avian papilla being short, there can be over 50 hair cells in a single cross section of its widest area (apical), compared to 4 to 6 in mammals.

4.2 Structure of the Starling's Hearing Organ

We (Gleich and Manley 1988) have previously described quantitatively the morphological patterns of the basilar papilla of the starling. It is roughly five times wider at the apical end than at the basal end (190 to 40 μm), reaching its widest point about 80 to 90% of the length from the basal end (cf. Fig. 27.9). The number of hair cells in any one cross section roughly parallels the change in width, rising from 8 basally to 30 apically. The number of stereovilli per hair-cell bundle falls from near 200 at the basal end to near 50 at the apical end, the form of the bundle changing from elongated basally to rounded apically. The height of the tallest stereovilli in the bundles (in the fixed, embedded state) varies from about 2.7 μm basally to 9.4 μm apically, the increase in height being much faster in the apical third. There is no consistent difference between the height of the neural and abneural bundles in each transect, although hair-cell bundles tend to be shortest on centrally lying cells. Hair cells lying at the extreme neural and abneural positions on the papilla have their stereovillar bundles all oriented nearly perpendicularly (±20°) to the edge of the papilla ("abneural"), similar to that seen in mammalian hair cells. Cells in the center of the papilla, however, tend to have their bundles turned towards the apex, the orientation gradually changing in any cross section from either edge towards the middle of the papilla. Although this tendency is hardly noticeable at the base, the orientation angle increases towards the apex to such an extent that the bundles of centrally located apical cells are rotated up to 90° towards the apex (Figs. 27.4 and 27.5).

Relatively little is known about the innervation of the avian auditory papilla. In new studies of the starling and chick papillae using serial ultrastructural sections, Fischer et al. (1991) and Singer et al. (1989) found greater differences between the innervation patterns of THC and SHC than would be predicted from the data of von Düring et al. (1985), especially in the basal half of the papilla. There, whereas THC receive both afferent and efferent innervation, the SHC studied had no afferent synapses at all and thus no afferent connection to the brain. Their synaptic areas were dominated by large efferent endings. These data indicate an unexpectedly high degree of functional separation of THC and SHC in these species.

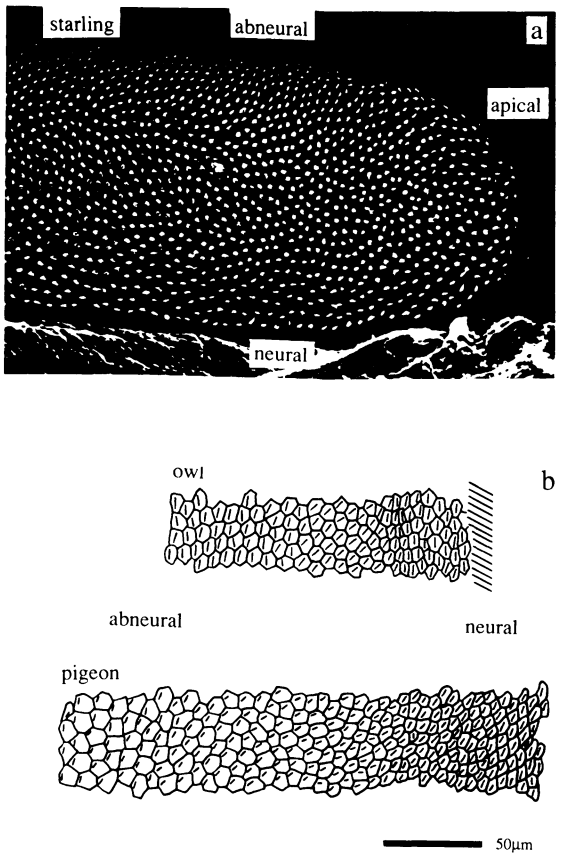

FIGURE 27.4. (a) Scanning electron micrograph of the apical hair-cell mosaic of the starling's basilar papilla. There are no clear rows of hair cells and THC and SHC are not distinguishable in surface view. (b) Schematic drawings of the surfaces of strips of hair cells across near-apical regions of the barn owl's and pigeon's basilar papillae, with the longer axis of the stereovillar bundles represented as bars. Whereas both neural and abneural hair-cell bundles are oriented more-or-less parallel to the neural papillar edge, hair cells lying medially on the papillae have their bundles rotated towards the cochlear apex. In the owl, the transition between differently oriented areas is abrupt. The shaded area of the owl papilla was covered in limbic material and not visible.

4.3 Physiology of the Auditory Papilla of the Starling

As there are very few data on the electrical activity of avian basilar-papilla hair cells stimulated by sound, we will briefly describe the activity

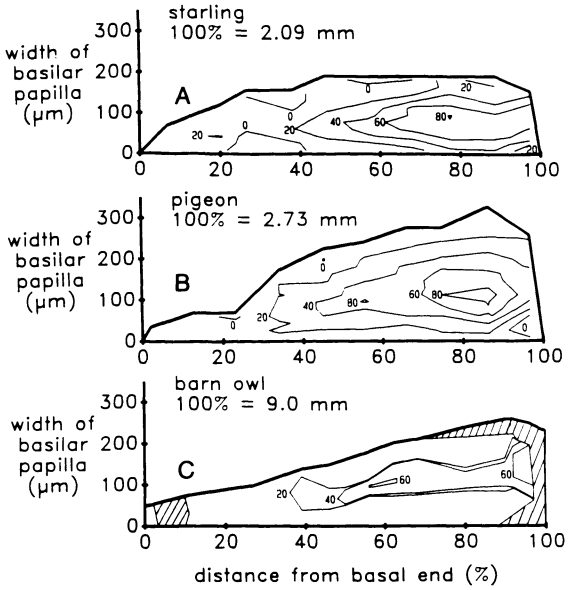

FIGURE 27.5. Highly schematic outlines of the basilar papillae of (A) the starling, (B) the pigeon, and (C) the barn owl, all normalized in length. The lengths given for the three papillae are those measured from SEM micrographs (fixed, dried). Within each papilla are shown a number of iso-orientation contours for the the orientation of the hair-cell stereovillar bundles, in degrees of bundle rotation towards the apex. Shaded areas in the owl could not be analyzed. (From Manley 1990.)

patterns of primary auditory nerve fibers. In this section, we review briefly the starling data as an example of the sensory responses originating in the avian papilla (Manley and Leppelsack 1977; Manley 1979; Manley and Gleich 1984; Manley et al. 1985, 1989; Gleich and Narins 1988; Gleich 1989).

4.3.1 Spontaneous Activity of Single Auditory Nerve Fibers

All primary auditory nerve fibers of the starling are irregularly spontaneously active, with a mean rate of 48 spikes/sec. The distribution of spontaneous rates is unimodal, whereas it is bimodal in mammals (Sachs, Lewis, and Young 1974; Sachs, Woolf, and Sinnott 1980; Manley et al. 1985). However, the overall interval distribution in time-interval histograms (TIH) in the spontaneous activity of nerve fibers in birds generally resembles that in mammals. The pseudo-Poisson interval distribution (Fig. 27.6B) is attributed to stochastic processes either in the hair cell or in the nerve fiber terminal. At short intervals, these processes are modified by the absolute and relative refractory periods of the fiber and, possibly, limiting factors in the hair cell synapse. The modes (most frequent interval) of the TIH in the starling data are very short, typically 1 to 2 ms (Manley et al. 1985).

The distribution of intervals in spontaneous data is, in many cells, strongly modified by the presence of more or less prominent preferred intervals (Manley 1979; Manley and Gleich 1984; Manley et al. 1985). In such cells, the activity is quasi-periodic, such that certain numerically related intervals occur more often and others less often than expected (Fig. 27.6A). They are not due to inadvertent stimulation or to background noise (Manley et al. 1985; Temchin 1988). The characteristic properties of these preferred intervals are:

1. They are found only in about half of the cells and with a best, or characteristic response frequency (CF) to acoustic stimuli below about 1.7 kHz. The limit in frequency could be related to the fact that the nerve fibers rapidly lose their ability to phase lock and/or the hair cells' AC receptor potentials become very small above 1 kHz (Gleich and Narins 1988).

2. The variations between interpeak intervals within each histogram are almost all $<5\%$ (Manley et al. 1985). The mean interpeak intervals are inversely related to the CF of the cell, but the mode of their distribution in the starling is on average 15% longer than the CF-period. This fact also indicates that they do not result from inadvertent noise stimulation (Manley et al. 1985). Even in those low-CF cells that do not show preferred intervals, the mode of the TIH of spontaneous activity is itself correlated with the CF. Here also, the interval of the mode is on average slightly longer than the CF-period (see above); the mode is thus a special case of a preferred interval. Gleich (1987) also found evidence of electrical tuning in the phase-response characteristics of primary auditory fibers of the starling, a tuning whose best frequency was, on average, 20% lower than the acoustic CF of the cell. This percentage difference corresponds extremely well to the discrepancy noted between the basic interval in preferred intervals and the period of the CF.

The most probable explanation of these details is that the spontaneous activity of all low-CF fibers

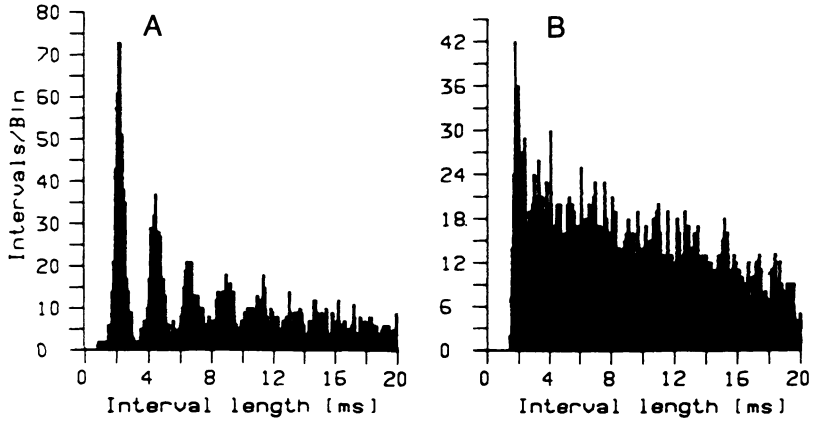

FIGURE 27.6. Typical time-interval histograms of spontaneous activity of single auditory nerve fibers of the starling. These histograms show the relative frequency of occurrence of intervals of various lengths between action potentials. (A) a low-frequency fiber showing very obvious preferred intervals (fiber CF: 0.45 kHz). (B) a low-CF fiber not showing preferred intervals, but whose mode was 1/CF (fiber CF: 0.5 kHz). (From Manley et al. 1985.)

is influenced by rhythmical electrical potentials of the individual hair cells they innervate. In the red-eared turtle, voltage oscillations are observed due to the properties of the ion channels of individual hair cells (Fettiplace 1987). Preferred intervals are thus manifestations of an *electrical tuning mechanism* in hair cells (summary in Manley 1986). Under certain conditions, isolated tall hair cells from the apex of the chick cochlea show electrical resonances to injected current, resembling those previously demonstrated in the turtle basilar papilla and frog sacculus (Fuchs and Mann 1986; Fuchs, Magai, and Evans 1988). The frequencies of these oscillations depended on the original location of the hair cell and were estimated by Fuchs, Nagai, and Evans (1988) to be up to 1 kHz for hair cells from the middle third of the chick papilla when corrected to the temperature of the living animal. Preferred intervals would be most easily seen in nerve fibers that only innervate one single hair cell, as is the case in starling low-CF THC (see above).

4.3.2 Frequency-Response Characteristics of Single Nerve Fibers

In common with all other vertebrate auditory fibers, starling eighth-nerve afferents each have a best, or characteristic frequency (CF) to which they respond at the lowest sound-pressure level (SPL). Responses to sounds of other frequencies can only be evoked by applying a greater SPL, the tuning curves being highly frequency selective (Fig. 27.7A). This characteristic was certainly inherited by birds from their reptilian ancestors. The CFs range from very low frequencies (below 100 Hz) to an upper limit of about 6 kHz. As noted by Sachs, Woolf, and Sinnott (1980), avian tuning curves are, if anything, more sharply tuned than those of mammals in the equivalent frequency range (Manley et al. 1985), at least when measured as the sharpness of the tip region ($Q_{10\ dB}$). However, starling nerve fiber tuning curves have a different symmetry from those of the mammals (Manley et al. 1985).

4.3.3 Tonotopicity and the Localization of Active Afferents

The various CFs of the nerve or cochlear ganglion of the starling are distributed nonrandomly in space, indicating a tonotopic organization of the papilla. Tonotopicity is also a primitive characteristic of vertebrate hearing organs (Manley 1990). Recently, single-fiber staining techniques permitted tracing the origin of responses in different frequency ranges to specific locations in the papilla of the starling and the chick (Manley, Brix, and Kaiser 1987; Gleich 1989; Manley et al. 1989). Using cobalt stains in the starling and HRP

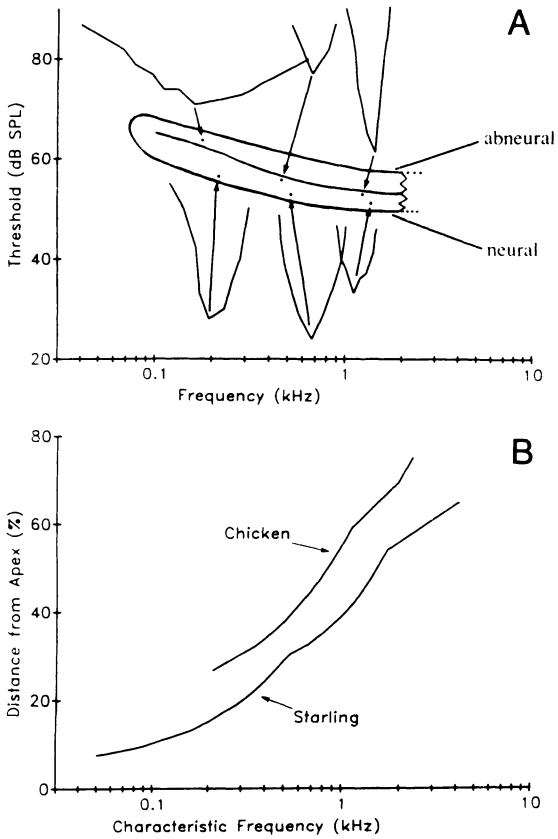

FIGURE 27.7. Diagram illustrating the systematic distribution of starling nerve-fiber response parameters according to the location of the hair cell they innervate. (A) Frequency tuning curves for six fibers traced to hair cells located at the locations shown on the schematic apical half of the papilla (arrows). The three sensitive tuning curves belonged to fibers that each innervated one neurally lying hair cell. In contrast, the three insensitive fibers innervated more abneurally lying hair cells. The continuous line along the middle of the papilla separates THC from SHC. (B) Best-fit functions illustrating the tonotopic organization of the basilar papillae of the chick and starling (CF of afferent fiber-hair cell connections vs the distance of their innervation site from the apex of the papilla, the papillar lengths being normalized to 100%). For references see text.

in the chick, fibers that had been physiologically characterized were traced to their synaptic contacts. Almost all fibers only contacted THC, and a tonotopic organization was obvious (Fig. 27.7A,B), the apical end of the papilla responding to the lowest frequencies and the basal end to the highest. The arrangement of CFs is unequal, the CF distribution in the low-frequency range being about 0.1 mm/octave, whereas at high frequencies it is near 0.6 mm/octave (Manley et al. 1988, 1989; Gleich 1989). This phenomenon is also known, but is not so pronounced, in the cat cochlea (Liberman 1982) and is also typical of lizard papillae (Manley et al. 1988; Manley, Köppl, and Yates 1989; Manley 1990).

Of the traced fibers in the starling, 24 were also successfully localized in transverse sections. This made it possible to describe the relative positions of innervated hair cells in both dimensions of the sensory mosaic. Hair cells were classified as THC (height/width ratio > 1) or SHC (ratio < 1). In virtually all cases, each stained fiber only contacted one single THC (Fig. 27.7A). The locations of these hair cells were described by using their relative position (= rank) across the row of hair cells in the cross sections, calling the neuralmost hair cell number 1. Virtually all hair cells innervated by the stained fibers had a rank of less than 15, even though up to 35 hair cells were found in any one cross-section (Gleich 1989; Manley et al. 1989).

Only two out of 34 stained fibers innervating abneurally lying hair cells were found (Fig. 27.7A); both were in the apical part of the papilla (Gleich 1989; Manley et al. 1989). One of these fibers innervated about 6 hair cells and was the only branched fiber found. In the apical area of the starling papilla, SHC receive very few afferent terminals (Miltz et al. 1990); this might explain why so few stained fibers to SHC were encountered. These two fibers did, however, have unusual response properties–they not only had high thresholds (>70 dB SPL) but also extremely flat, low-frequency tuning curves for which it was hardly possible to define a characteristic frequency (Fig. 27.7A). They resemble the infrasound fibers stained by Schermuly and Klinke (1988) in the apical abneural area of the pigeon's papilla. In the pigeon, these fibers apparently belong to a group of apical fibers not forming part of the large group representing the "normal" frequency map of the avian papilla.

As the THC area of birds is much larger than the equivalent area for mammals, which have only a single row of IHC, we tested the starling for differences in the physiological properties of fibers innervating hair cells at different positions *across*

the papilla (Gleich 1989; Manley et al. 1989). Neither the sharpness of tuning nor the spontaneous activity of the fibers correlated with position. However, there was a surprisingly strong relationship between the rank of the innervated hair cell and the rate-response threshold of fibers (Fig. 27.7A), such that the most neurally lying cells were more sensitive to sound. According to a linear correlation of the data ($n = 12$, $r = 0.764$, $P < 0.01$), there is a threshold shift of almost 6 dB/hair cell across the papilla (to exclude threshold differences due, for example, to the middle-ear transmission characteristic, we selected the CF range between 0.6 and 1.8 kHz, where the starling audiogram is relatively flat; Kuhn et al. 1982). Considering the morphological variability between different avian groups, it will be necessary to investigate additional species, to see whether this threshold gradient is a general phenomenon in birds. Large threshold differences between neural and medial fibers would explain why it is not unusual in auditory nerve recordings in birds to find threshold ranges for any one frequency region which exceed 50 dB (Manley et al. 1985).

In birds, almost all of the THC are supported by the neural limbus (superior cartilaginous plate) and do not lie over the free basilar membrane. Traditional concepts in auditory physiology suggest that hair cells lying over the free basilar membrane (with the largest displacement amplitudes to sound) should be more sensitive. The highest sensitivity of THC furthest from the basilar membrane is contrary to intuition based on these traditional concepts. However, very little is known about the mechanics of hair-cell stimulation in birds. The pattern of hair-bundle orientation across all avian papillae (see Sections 4.1 and 4.2) suggests a complex pattern of hair-cell stimulation. Assuming a simple radial pattern of stimulation, the change of hair-cell bundle orientation across the starling papilla (in which medial, apical hair cell bundles in the frequency region we analyzed are rotated up to 70° towards the apex, Fig. 27.5) would certainly reduce the effectiveness of stimulation on rotated cells. The maximal threshold effect would, however, be < 1 dB per hair cell. Thus the pattern of hair-cell bundle orientation alone cannot explain the range of sensitivity differences we found in the starling. There is evidence in some species that the tectorial membrane

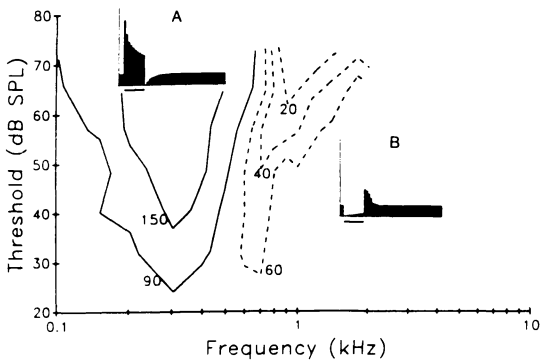

FIGURE 27.8. Tuning curve of a single auditory nerve afferent fiber showing the excitatory area (continuous lines, different response criteria in spikes/sec) and areas of primary suppression (dashed lines). The insets show idealized forms of poststimulus time histograms to short excitatory (A, upper left) and suppressive (B, lower right) pure-tone bursts (bar = stimulus duration).

contributes its mass to a resonance system (bobtail lizard, Manley et al. 1988; Manley, Köppl, and Yates 1989; guinea pig, Zwislocki et al. 1988). If the stimulus to the hair cells depends mainly on a resonance of the tectorial membrane and less or only indirectly on the vibrational amplitude of the basilar membrane, there is no reason why hair cells over the basilar membrane should be more sensitive.

4.3.4 Discharge Patterns of Auditory Nerve Fibers to Pure Tones

4.3.4.1 Discharge Patterns to Single-Tone Stimuli

Avian auditory nerve fibers can respond to a sound stimulus in one of three ways: an increased firing rate above the spontaneous level, a decrease below spontaneous level, or a phase locking with or without a change in discharge rate (Manley 1990). The second of these phenomena, also known as primary or single-tone suppression, has not been observed in mammals and is described in Section 4.3.4.3. The most common response to a tonal stimulus is a tonic increase in discharge rate (Fig. 27.8a; Manley et al. 1985). With increasing sound-pressure level, the response includes an increasingly large phasic component, whose time course may exceed that of the stimulus, that is, a steady state is not reached before the stimulus (50 ms

duration) is turned off. Except for near-threshold stimuli, the tonal response is followed at offset by a period of reduced spontaneous activity, the magnitude and duration of the reduction depending on the strength and duration of the stimulus (Fig. 27.8A). The discharge rate increases monotonically with increasing sound pressure, often exceeding 300 spikes/s (averaged over the entire 50 ms stimulus; the instantaneous rates at onset are higher). Such discharge rates are higher than those reported for various mammals and correlate with the higher spontaneous rates in birds (Manley 1983; 1990).

4.3.4.2 Phase Locking to Tonal Stimuli

In the starling, significant phase locking occurs in most low-CF cells at sound pressures below the mean rate threshold (Gleich and Narins 1988). The difference between phase locking threshold and mean rate threshold decreased with increasing frequency, suggesting that for low-frequency cells, phase locking is more important than a rate increase. No phase locking was observed above a few kHz. In general, the rate of change in the phase of the response towards higher frequencies was faster in lower-CF cells, indicating a greater delay in their responses than those of higher-CF cells. A plot of response phase versus stimulus frequency for single primary nerve fibers of the starling did not, however, always result in a straight line. Below CF, the phase lag was less than expected and was greater than expected for frequencies above CF. The overall phase response could be modelled by the combination of a constant delay plus the phase shift introduced by a standard LRC filter (made up of an inductance, resistance, and capacitance). Gleich (1988) used an iterative procedure to calculate the center frequency and sharpness of the putative LRC filter functions from the curves which resulted from subtracting a straight line response-phase characteristic from the individual phase function. The resonance frequency of the best-fit LRC filter and the fibers' acoustic CFs were correlated. As in the case of the preferred intervals in spontaneous activity (Section 4.3.1), however, individual fibers had a best-filter match in which the center frequency was on average 20% lower than that of the acoustic CF of the fiber. This also indicates that the tuning of the hair-cells' electrical filters is, in most cases, mismatched to the acoustic CF.

4.3.4.3 Primary and Two-Tone Suppression

Not only can some tones suppress responses to other tones (two-tone suppression or TTRS; a phenomenon well known in the mammalian auditory nerve), but spontaneous activity can often be suppressed by single tones which do not themselves excite the cell (single-tone or primary suppression). Primary suppression has only begun to be studied systematically. Although in the case of very sensitive cells the possibility that the spontaneous activity of some fibers is partly a response to uncontrolled, low-level noise cannot be excluded, many fibers showing this phenomenon are quite insensitive. The observation of such nonclassical responses to sound from avian single fibers has been reported by Gross and Anderson (1976); Temchin (1982); Manley et al. (1985); Temchin (1988); and Hill, Mo, and Stange (1989a,b). Experimental procedures for examining fiber responses to a large matrix of frequencies and SPLs readily reveal the presence of such suppressive side bands on avian tuning curves. In the starling (Fig. 27.8B; Manley et al. 1985), the discharge rate of the cell to single suppressive tones often falls well below the spontaneous rate – sometimes even to zero. Such suppression is often accompanied by an "off" response (Fig. 27.8B). Of course, such effects can only be seen in cells with a significant spontaneous activity.

In both mammals and nonmammals, the phenomenon of two-tone suppression (TTRS) has similar properties to those described here for primary suppression, except of course that the suppressed activity is in response to the first tone (Sachs and Kiang 1968; Manley 1983). The threshold for suppression of a CF tone (10 dB above threshold) by a second tone may be lower for frequencies of the second tone which lie above or below the CF. TTRS areas in the chick and the starling have characteristics similar to those of the primary suppression areas (Manley 1990). That the suppression is not a synaptic (inhibitory) phenomenon is indicated by the fact that it has essentially no latency. In addition, Temchin (1988) observed primary suppression in the pigeon even after severance of the eighth nerve.

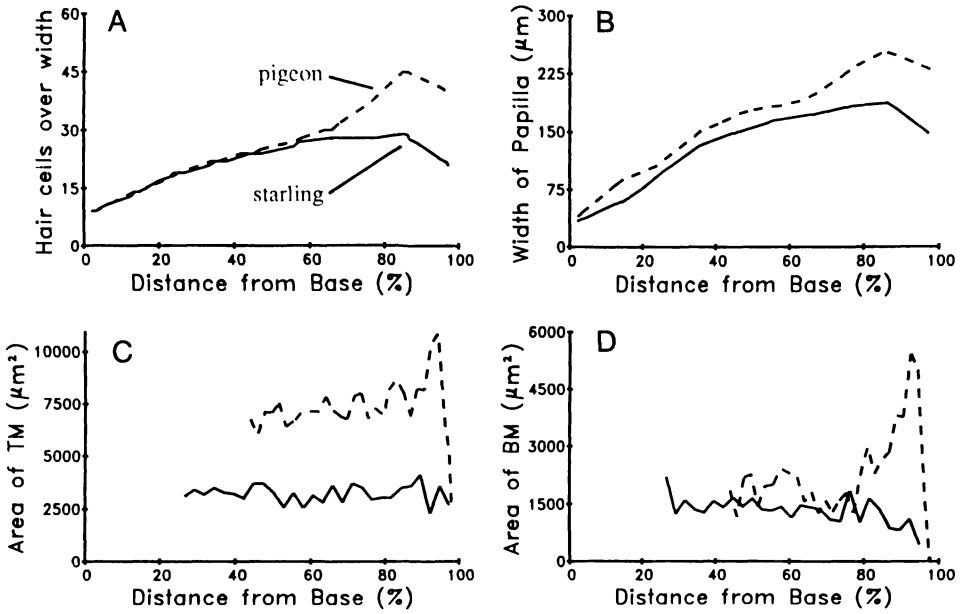

FIGURE 27.9. Four morphological criteria measured along the papillae, to illustrate the apical specialization of the pigeon's papilla compared to that of the starling. (A) number of hair cells across the papilla; (B) papillar width; (C) area of the tectorial membrane in cross section and (D) area of the basilar membrane in cross section. In each case, the pigeon data are drawn as dashed lines.

5. A Comparison of Structural and Functional Data From Other Avian Species

Comparative data on hearing-organ structure are available from the pigeon (Takasaka and Smith 1971; Gleich and Manley 1988), chick (Tanaka and Smith 1978; Tilney and Saunders 1983; Tilney, Tilney, and DeRosier 1987; Manley et al. unpublished data), barn owl (Smith, Konishi, and Schull 1985; Fischer, Köppl, and Manley 1988), duck (Chandler 1984) and seagull (Counter and Tsao 1986). Single-fiber physiological data are available for the pigeon (Sachs, Lewis, and Young 1974; Gross and Anderson 1976; Temchin 1982; Schermuly and Klinke 1985; Schermuly and Klinke 1988; Temchin 1988; Hill, Mo, and Stange 1989a,b) redwing blackbird (Sachs, Woolf, and Sinnott 1980) and chicken (Manley, Brix, and Kaiser 1987 and in preparation; Warchol and Dallos 1989a). There are a large number of structural similarities between the different avian papillae. Here, we shall only refer to data that show significant deviations from the basic patterns described for the starling.

1. In the pigeon, the basilar papilla does not increase steadily in width from base to apex. The width increases gradually from 40 μm basally to 190 μm at 60% of the length from the basal end and then becomes disproportionately wider to 250 μm at 85%, before tapering somewhat to the apical end (Fig. 27.9B). The apical third of the pigeon papilla has more hair cells than expected even from this disproportionate width increase (Fig. 27.9A). Between 65% and 88% of the length, the number of hair cells in a transect rises from 30 to almost 50. This is accompanied by a dramatic reduction in the surface area of the hair cells of the abneural side of the papilla, which falls from near 120 μm² at 60% of the length from the basal end to <40 μm² at 85% of the length. A smaller size reduction is seen in hair cells in the middle area of the papilla. The patterns in the areas of the stereovillar bundles in the pigeon papilla differ from those seen in the starling, the abneural cells showing more dramatic changes. In the basal region, such abneural hair cells have almost 50% of their surface covered by

the stereovillar bundle. This percentage falls to only about 10% for cells near the middle of the papilla and remains constant to the apical end, the cells and their bundles both getting progressively smaller. This change in the relative surface area of cell and bundle occurs in spite of the fact that the number of stereovilli per cell falls quite steadily from base to apex. In addition, the apical area of the pigeon cochlea shows large increases in the dimensions of the basilar and tectorial membranes. Such dramatic dimensional changes are not seen in the starling (Fig. 27.9C,D). The pigeon specializations are found in the apical area described by Klinke and Schermuly (1986) as giving rise to responses to infrasound stimuli (see Section 6.2).

2. In the chick, the anatomy of the most apical region of the papilla apparently differs from that seen in other species of birds. Lavigne-Rebillard, Cousillas, and Pujol (1985) describe a crescent-shaped apical region they termed "very distal part," in which the hair cells show a greater resemblance to vestibular than to auditory receptors. There is evidence that this area also mediates very low-frequency hearing (see Section 6.2). In a comparative 2-deoxyglucose study of the auditory forebrain of a variety of avian species, Müller and Scheich (1985) found evidence in both the pigeon and the chicken of an area specialized for the processing of infrasound frequencies.

3. A partial tonotopic map is also available for the chick basilar papilla, obtained using horseradish-peroxidase staining of single fibers (21 single afferents or groups of afferents). It differs from that obtained from the starling, in that the curve lies at lower frequencies for equivalent locations on the hearing organ (Fig. 27.7B; Manley, Brix, and Kaiser 1987). This suggests that both the upper and lower frequency limits are lower in the chick.

4. The basilar papilla of the barn own *Tyto alba* is the longest so far described in birds, being over 11 mm in length in the unfixed state and containing over 16,000 hair cells. In the fixed, dried state, it is roughly 9 mm long, being 250 μm wide at the apical end and gradually reducing to 50 μm at the basal end. Whereas the data from the pigeon and the chick are relatively consistent with those from the starling in regard to the height and orientation of the stereovilli, (Tilney and Saunders 1983; Tilney, Tilney, and DeRosier 1987; Gleich and Manley 1988), the change in hair-cell orientation in the owl papilla is very abrupt. In the apical two-thirds, both the neurally placed and abneurally placed hair cells are oriented parallel to the edge of the papilla (0°). In the center of the papilla, however, is a region where the orientation suddenly changes to at least 50° and up to 90° (apical orientation), and, further over the papilla, just as suddenly back again to 0°. On the neural side of middle and apical areas of the barn-owl papilla, the sudden change in orientation occurs at the place where Smith, Konishi, and Schull (1985) indicate a border between the tall, intermediate, and short hair cells. The sudden change in hair-cell orientation is often accompanied by a sharp rise in the number of stereovilli per hair-cell bundle at exactly the same place, so that a change in orientation angle from 0° to 50° may be correlated with a rise in the number of stereovilli from 120 to 180 per hair cell. Similarly, a return to 0° orientation is accompanied by a fall in the number of stereovilli. In the barn owl, the height of the tallest stereovilli in any one bundle changes from near 5 μm apically to 1 μm basally. Most of the height reduction occurs, however, in the apical half of the papilla, so that by 4.5 mm towards the base, it has already dropped to about 1.5 μm, remaining remarkably constant over the basal half of the papilla. Smith, Konishi, and Schull (1985) found that in the barn owl, this basal end has a marked thickening of the basilar membrane, a feature that has been found in specialized areas of some mammalian (e.g., bat) cochleae. As the basal area also differs in some other respects from that of other birds (Fischer, Köppl, and Manley 1988), it can be regarded as a specialization for high-frequency hearing (Section 6.2).

5. Unlike birds and despite the very similar cochlear anatomy, spontaneous activity rates in Caiman are bimodally distributed, as in mammals (Klinke and Pause 1980). The population of mammal and Caiman units that have spontaneous rates near zero does not exist in birds. Even within the avian data on spontaneous rates of nerve fibers, there are discordances, even for different studies of the same species. Whereas Sachs, Woolf, and Sinnott (1980) report a mean rate of 90 spikes/sec for the pigeon, Temchin (1988) found a mean rate of 78 spikes/sec in the 26 pigeon units he studied and Hill, Mo, and Stange (1989a) report a mean rate of only 35 spikes/sec. However, we will not

discuss this further, as the origin of these discrepancies is not yet understood.

6. Primary suppressive areas in the chick (Manley et al., in preparation) were not, as in the pigeon (Temchin 1988), only found in cells that showed preferred intervals in their spontaneous activity. Although TTRS has also been described for the pigeon by Sachs, Lewis, and Young (1974), it is curious that they report that in the pigeon nerve, "spontaneous activity was never inhibited by acoustic simuli," that is, primary suppression did not occur. This difference may be explained if these authors only refer to single stimuli within the excitatory tuning curve or through the use of threshold-tracking paradigms, which do not detect a reduced discharge rate. In the same species, Hill, Mo, and Stange (1989a) report clear cases of primary suppression.

TABLE 27.1. Inherited and derived features of avian basilar papillae

Inherited

- The good frequency selectivity of auditory nerve fibers
- The presence of a tonotopic organization and its direction
- Electrical tuning at low frequencies (e.g., preferred intervals in spontaneous activity)
- A basalward extension of the papilla to higher frequency responses (at least partially mechanical tuning)
- Tonic responses to tones; single- and two-tone suppression

Derived

- Specialization of hair-cell types *across* the papilla
- Specialization of afferent and efferent innervations to different hair-cell populations
- Macromechanics (e.g., nonuniform hair-cell bundle orientation)
- Specific adaptations of some apical (infrasound reception) and basal (extended higher-frequency range) papillar areas

6. The Evolution of the Avian Hearing Organ

6.1 General Trends in the Early Evolution of the Avian Papilla

Certain features of the avian papilla are regarded as being relatively unchanged from the stem reptiles (i.e., "primitive"; see also Table 27.1). These include the presence and the direction of the tonotopic organization, the presence of a high frequency selectivity (sharp tuning) in the responses of auditory nerve fibers and their general response patterns, including that of the spontaneous activity (irregularity of the spontaneous discharge and the presence of preferred intervals).

As shown in Fig. 27.10, one of the earliest trends in papillar evolution following the divergence of several evolutionary lines from the stem reptiles was an elongation of the papilla. This elongation was accompanied by the extension of the hearing range above the presumed upper limit of the stem reptiles (about 1 kHz). It is not known definitively whether this event occurred independently in the three lines leading to the mammal-like reptiles, to the archosaurs and to the lepidosaurs. At some stage, it is apparent that at the highest frequencies, a mechanical frequency selectivity mechanism became dominant over an electrical mechanism. This change was associated with a change in the space constant of frequency distribution on the papilla (Manley et al. 1988). Also accompanying the elongation of the papilla in the archosaurs was a differentiation and specialization of the hair cells into recognizable, but intergrading, types and the establishment of clear differences in their innervation patterns. The spontaneous and sound-driven activity patterns of the nerve fibers innervating apical hair cells in the avian papilla probably did not change significantly compared to those inherited from the stem reptiles. The above changes were most likely essentially complete before the ancestors of the Crocodilia and Aves diverged. Later changes in the avian line involved the orientation patterns of the hair-cell bundles, the specialization of the abneural area of the apical papilla for encoding extremely low frequencies, and, at least in owls, changes in the basal papilla to facilitate high-frequency hearing. Some of these later specializations are described in more detail below.

Thus we assess these other features of the avian papilla as being specialized (see also Table 27.1). These include the presence of different types of hair cells across the width of the papilla and their very different afferent and efferent innervation patterns, the elongation of the papilla and probable dominance of mechanical frequency selectivity at higher frequencies, and the changes in hair-cell bundle orientation along and across the papilla, which also implies a new pattern of mechanical stimulation.

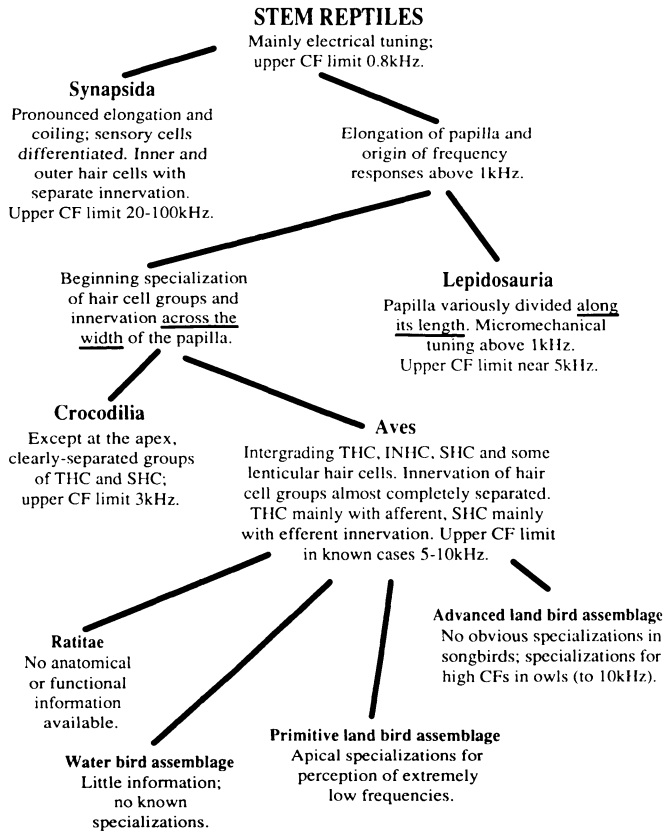

FIGURE 27.10. Schematic diagram to illustrate (top to bottom) our current understanding of the changes in morphology and function of the hearing organ, observed during the evolution of different lines of land vertebrates from stem reptiles.

6.2 Functional Implications of Variations in Avian Papillar Anatomy

Our understanding of the function of the avian basilar papilla is still relatively poor. It is thus difficult to realize the full implications of the anatomical variability discussed above. It should, however, be noted that each of the bird papillae investigated to date is unique. We thus expect that there will be species-specificities in the response patterns of the hair cells and their associated nerve fibers. To date, the following specializations are known:

a: *The mechanics of stimulation of the avian papilla probably differ from those of mammals.* In the chick, the change of hair-cell bundle orientation across the papilla led Tilney, Tilney, and DeRosier (1987) to suggest that there is an unexpected pattern of hair-cell stimulation—unexpected that is, when we consider the essentially radial shear pattern thought to be present in the mammalian cochlea. Since we found similar morphological patterns in the starling, pigeon, and the barn owl (Fischer, Köppl, and Manley 1988; Gleich and Manley 1988), they can probably be considered as typical of birds. It should also be borne in mind that in all birds, a high proportion of THC do not lie over the free basilar membrane, and thus require their mechanical stimulus to come from the tectorial membrane.

b: *The barn owl (an "advanced land bird") has exceptional high-frequency hearing and a specialized basal papillar area.* Major differences are not seen in the hearing ranges (measured behaviorally or as the range of CFs of the tuning curves) of most avian species studied so far (100 Hz to about 6 to 8 kHz; Konishi 1970). However, Sullivan and Konishi (1984) report recordings in the brainstem of the barn owl which, together with the behavioral audiogram (Konishi 1973) indicate that in this large bird, the CFs in the nerve reach 9 to 10 kHz. The morphological data indicate that, whereas the apical half of the barn owl papilla shows structural patterns that resemble those of the entire papillae of other birds, the basal half is exceptional

(Fischer, Köppl, and Manley 1988). This is presumably a specific adaptation for processing of the high frequencies (5 to 10 kHz) used by the barn owl for sound localization. Also in the barn owl, the abruptness of the change in the orientation of hair-cell bundles across the papilla is striking and appears to correlate in position both with a change in the number of stereovilli on the hair cells and, at least in the neural half of the papilla, with the edge of the neural limbus. That is, hair cells on the two sides of the outer edge of the superior cartilaginous plate have quite different stereovillar-bundle orientation.

c: *The pigeon and the chick ("primitive land birds") have differently specialized apical papillar areas sensitive to very low sound frequencies.* The low-frequency sensitivity of the pigeon disappears upon removal of the cochlear duct (Kreithen and Quine 1979), proving that the receptors lie in the basilar papilla or the lagena macula. Klinke and Schermuly (1986) report finding extremely low-frequency, phase-locked responses in pigeon auditory nerve fibers. When stained, these fibers were found to innervate hair cells in the abneural area of the apical part of the basilar papilla. This area (see Section 5) is specialized in the pigeon, being unusually wide and having an exceptionally large number of sensory cells (Gleich and Manley 1988).

In the chick, Warchol and Dallos (1989a) report finding cochlear nucleus cells that responded to low-frequency sound (10 to 500 Hz). About half of the cells responded with equal sensitivity to frequencies between 10 and 100 Hz, the other half having broad, but more classical, auditory tuning curves with CF near 100 Hz. Many of these cells responded to sound only with a modulation of their spontaneous discharge and had more Gaussian than Poisson distributions of intervals in the spontaneous activity. Warchol and Dallos (1989b) later traced low-CF fibers in the chicken to the apical papillar area, suggesting that the "very distal part" might be specialized in a functionally similar way to the pigeon. As the anatomical patterns are very different, however, it is probable that the pigeon and chick have independently developed a low-frequency specialization. In this respect it is important to note that both the pigeon and the chicken belong to a more primitive group of land birds than the other species described here (Feduccia 1980; Carroll 1987). In most previous experiments with other species, however, the sound systems were often unable to stimulate adequately below 100 Hz and phase-locking responses were neglected, so it is difficult to estimate the relative occurrence of very low-frequency responses in other avian species.

6.3 Mechanisms of Frequency Selectivity in the Avian Basilar Papilla

It has been suggested for some years now that there is more than one mechanism of frequency analysis in the vertebrate inner ear (Klinke 1979; Manley 1979). More recently, fundamentally different mechanisms of frequency selectivity have been recognized in terrestrial vertebrates, which frequently coexist (Manley 1986, 1990). Although it is not yet possible in any individual case to cleanly separate the different mechanisms, for descriptive purposes they will be treated separately.

There are two fundamental foundations upon which frequency-selectivity mechanisms can operate:

(a) Frequency selectivity resulting from the *electrical* characteristics of the hair-cell membrane, which may operate in addition to:
(b) Frequency selectivity resulting from *mechanical* factors. These factors can be one or a combination of the following:
  b1: mechanical properties of the hair-cell stereovillar bundle if not coupled to a tectorial membrane,
  b2: mechanical interaction between hair-cell bundles and the tectorial membrane, and
  b3: active movement processes in a large number of hair cells, resulting in mechanical interactions between the hair cells and the basilar (and tectorial?) membrane(s). This last mechanism is inextricably mixed with the passive selectivity of the accessory structures (e.g., basilar and tectorial membranes) themselves.

Which of the above selectivity mechanisms have been retained by or have evolved in birds? Electrical tuning is most likely a primordial property of hair cells (Manley 1986, 1990). The presence of both a voltage-sensitive Ca^{2+} conductance and a Ca^{2+}-sensitive K^+ conductance in hair cells can

under stimulation produce a resonance whose properties can explain a good deal of the frequency selectivity of certain hair cells. In the frog sacculus and the turtle basilar papilla, the variations in the number and the kinetics of these channels are thought to be responsible for the different CFs of hair cells (Crawford and Fettiplace 1981; Ashmore and Atwell 1985; Hudspeth 1985; Art, Crawford, and Fettiplace 1986; Hudspeth 1986; Fettiplace 1987). Recently, it has also been show that such channels are found in low-CF hair cells of the alligator (Evans and Fuchs 1987) and the chicken (Fuchs, Nagai, and Evans 1988). In the latter, the properties of the channel kinetics also suggest a role of electrical tuning in the frequency selectivity of low-frequency avian THC. Three other factors, the presence of preferred intervals in the spontaneous activity of primary auditory nerve fibers, the finding of specific deviations from expected phase responses and of a temperature sensitivity in the frequency tuning also provide strong evidence that birds have retained electrical tuning in their hair cells, at least at low CF (Klinke 1979; Manley 1979, 1981, 1986; Manley and Gleich 1984; Schermuly and Klinke 1985; Gleich 1987). Thus a major part of the peripheral tuning mechanism in low-CF avian THC resides in the properties of individual cell membranes of the sensory cells. We do not yet know how high in frequency this mechanisms can operate at the high body temperatures of birds. Indeed, one important feature of electrical tuning to be investigated in future research concerns the factors that limit its frequency response. The highest limits found for indicators of electrical tuning in preferred intervals in the spontaneous activity of primary auditory nerve fibers in birds are between 1.5 kHz (Manley et al. 1985) and 2.5 kHz (Temchin 1988). These limits are, however, influenced by the decreasing ability of the nerve fibers or their synapses to follow higher-frequency oscillations of the hair-cell membrane potential. The question of frequency limitations has not been exhaustively analyzed at the hair-cell level. Above the limit of function of electrical tuning, it would be necessary for higher CFs to be analyzed using other, presumably predominantly micromechanical, mechanisms.

The situation with regard to mechanical tuning is much more complex than with electrical tuning, for there is a variety of mechanical structures that can play a role in tuning, the basilar and tectorial membranes and the hair-cell stereovillar bundles being the most obvious candidates. The presence of obvious gradients in the structural parameters of the hair-cell stereovillar bundles in all species examined in this respect has led to the expectation that in all hair cells, the mechanical properties of the stereovillar bundle will play an important role in frequency selectivity. This would be true irrespective of the presence or absence of, for example, a tectorial membrane. Although such gradients certainly influence the tuning, it is at present not possible to quantify the contribution of individual parameters in avian species. In order to gain an impression of the frequency-response parameters of the different cells, it is not enough to know the height of the stereovillar bundles, for this parameter is constant in the basal half of the owl papilla. At low frequencies, even a knowledge of all bundle parameters will not suffice where electrical tuning also plays a role.

In the avian hearing organ, all hair cells are rather firmly connected to the tectorial membrane. This makes it unlikely that the resonance properties of individual stereovillar bundles alone play an important role in frequency selectivity. We would rather expect that larger numbers of hair cells and an area of tectorial membrane would form some sort of resonant unit, as in b2 above.

With regard to possibility b3 above, it now seems virtually certain that in mammals, the macromechanical resonance of the organ of Corti depends at low levels to a very large extent on active mechanical motions of the outer hair cells. These cells respond actively to specific stimuli, which locally greatly increases the motion of the entire cochlear partition. This increased motion influences the inner hair cells, which thus respond to the "net result" of the passive and active motion of the organ of Corti. The active motions of hair cells result under certain conditions in the generation of otoacoustic emissions, sounds that emerge from the cochlea and are often present spontaneously. These emissions, which are currently being studied extensively in mammals, are also present at higher frequencies in the external meatus of the starling (Manley, Schulze, and Oeckinghaus 1987), suggesting that similar patterns of mechanical activity of hair cells are present in birds, at least at higher CFs. The only available evidence on the

macromechanics of the avian basilar membrane is from the pigeon (Gummer, Smolders, and Klinke 1986) and suggest that there is a crude equivalent of the travelling wave of mammals. However, there are no equivalent measurements of relatively low-frequency regions in the mammalian cochlea and the difficulties associated with such investigations are very large. In the pigeon, Smolders (personal communication) found a pattern of tonotopic organization very similar to that which we reported for the starling and chick, the frequency map for the basal third strongly resembling that derived from the macromechanical measurements. Our recent experiments marking single avian nerve fibers (Manley, Brix, and Kaiser 1987; Gleich 1989) indicate that it is not unreasonable to speculate that there are substantial functional differences between THC and SHC, which may manifest themselves in a similar functional separation of hair-cell populations in birds as in mammals. There is a large number of hair cells across the papilla in birds, so that if avian hair cells can produce active movement there would be enough cells to drive the papilla. However, the amount of space along the papilla devoted to one octave is less than in mammals and the basilar papilla is thick, both factors that would reduce the selectivity of any active process. In addition, most THC do not sit over the free basilar membrane, so it would be important to take the motion of the tectorial membrane into account. Perhaps an interaction between hair-cell populations through the tectorial membrane would be a more appropriate postulate for the avian situation.

In the hair-cell populations recognized in Crocodilia and in birds, the differences in the position of the cells (neural and abneural part of the papilla, over the limbs or on the free basilar membrane), in their structure (e.g., form of the cell body, form and position of the stereovillar bundle), and in the pattern of the afferent and efferent innervation are substantial and comparable to the differences between inner and outer hair cells of mammals. This raises the important question of the evolutionary origin of separate hair-cell populations. We hypothesize that the specific abilities of primitive vertebrate hair cells (both sensory transduction and active motility of some sort; Crawford and Fettiplace 1985) predispose large arrays of such cells to specialization. It is conceivable that the selection pressures acting on a large uniform population of hair cells in different vertebrate classes could produce sense organs of similar structure and function based on a "division of labor" between hair-cell groups. Depending on the differences in their stimulus input, hair cells could specialize by emphasizing certain functions above others (e.g., mechanical response to the stimulus rather than accurate transmission through afferent synapses). The development of functionally similar hair-cell populations in birds and mammals is a remarkable case of the independent and convergent evolution of a complex interactive process in a sense organ resulting in specific improvements in the function of their hearing organs.

6.4 Is the Avian Basilar Papilla a Multifunction Sense Organ?

Our finding (Manley, Brix, and Kaiser 1987; Gleich 1989) both in the starling and the young chick, that afferent fibers of the auditory nerve primarily contact tall hair cells indicates that there is a division of labor among the different hair-cell populations of the avian papilla (Manley et al. 1989). That primary afferents primarily contact THC over the neural limbus has recently also been confirmed in the pigeon (Smolders, personal communication). The fibers of the pigeon which responded to infrasound, and which were stained by Klinke and Schermuly (1986), innervate an abneural area of the pigeon papilla which, as the tonotopic organization of the pigeon resembles that of the starling (Smolders, personal communication), lies adjacent to an area of neural cells responding to a few hundred Hz. Fibers innervating abneural hair cells in the starling were also quite different in their properties. It is possible that the fact that THC of birds, at least the lower-frequency THC, show some electrical tuning, allowed the THC of the apical part of the hearing organ to fulfill the function of a frequency-selective organ without necessitating any mechanical interaction between hair-cell populations. In this sense, the apical, abneural hair cells would then be unnecessary for "hearing" of normal acoustical frequencies and could be involved in a different function. The very different structure and innervation of SHC, and their proliferation in the pigeon in an area responding to infrasound

suggest this also. One can thus speculate that the avian papilla consists of three functional areas:

a: Apical THC responding selectively and at least partly via electrical tuning to sound up to frequencies of about 1.5 kHz,
b: Apical abneural hair cells (INHC or SHC) encoding very low frequency and infrasound, predominantly via phase locking in their afferents,
c: The basal end of the papilla responding to sound frequencies above 1.5 kHz mainly by mechanical frequency selectivity involving both THC and SHC.

As flying animals, it is certainly important for birds to collect information about their position in space. The infrasound receptors described are in a position to respond to the slow air-pressure changes of winds and of slightly different flight altitudes. Such a function would be best fulfilled by hair cells over the free basilar membrane. Further study of the specializations of hair-cell populations will show whether these speculations have any real substance. Indeed, the investigation of the functional significance of distinct hair-cell populations – those factors accompanying the evolution of complex hearing organs – will be one of the most fruitful future areas of avian auditory research.

7. Summary

Birds have retained the single-ossicle middle ear, which limits their upper frequency of hearing to 12 kHz. In the course of the evolution of the archosaurs from the stem reptiles, the sensory hair cells have become specialized into several intergrading types, the extremes of which have profoundly different structure and innervation patterns. Present evidence suggests a specialization of function during this evolution parallel to that seen in the mammalian organ of Corti. However, the anatomy of the basilar papilla varies between representatives of the different avian groups, suggesting that there may be significant differences in functional patterns. THC are generally not on the free basilar membrane and may be stimulated in a different way than mammalian inner hair cells. Apically, THC also show electrical tuning and analyze low-frequency sound. In some primitive land birds, this abneural, apical end is specialized, transducing low- and very-low-frequency stimuli which are then coded primarily via phase locking in the afferent fibers. In the basal area, present evidence indicates that high frequencies are analyzed by a mechanical tuning mechanism which may involve interaction between hair-cell types. Barn owls have evolved a specialized basal cochlear area.

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