Chapter 14

Overview and Outlook

Modern vertebrates display an immense variety of inner-ear structures and functions. While it is necessary to take the huge structural variety into account, it is also important to attempt to describe some unifying principles underlying the facts and concepts that have emerged from 20 years of research on the anatomy and the electrophysiology of the hearing organs of birds and reptiles, and to suggest which aspects are deserving of our attention in the near future. It is also important to consider the ways in which these comparative studies have modified our concepts of the function of the mammalian hearing organ. I will attempt to do this as concisely as possible in this chapter.

One of the central questions to be considered in comparative auditory physiology is that of the relationship between structure and function, especially in view of the fact that, despite large structural variations, the variation in function revealed to date is surprisingly small. What can the data tell us about the function of the diverse structures in the various parts of the ear?

I shall discuss the following conclusions:

1. The middle ear is partially responsible for the relatively low upper limit of hearing in non-mammals.
2. The hearing range of reptiles is almost independent of the development of the hearing organ.
3. There are different patterns in the spontaneous activity that are partly related to tuning mechanisms.
4. The tectorial membrane plays a role in the sharpening of frequency selectivity and in suppression.
5. There is a specialization of hair-cell populations across the papilla in the archosaur lineage but not in other reptile lines.
6. The functional consequences of variations in hair-cell polarity and innervational pattern in lizards are not yet clear.
7. All vertebrate hair-cell systems are frequency selective.
8. All vertebrate hearing organs show tonotopic organization.
9. There are four different mechanisms of hair-cell frequency selectivity, appearing in different combinations in the various groups.
10. There is a strong tendency towards a division of the hearing range into roughly ‘below 1 kHz’ and ‘above 1 kHz’. In lizards, this division has an anatomical substrate and manifests itself in several characteristics of the physiological response patterns. It is also observable in the physiological data from both birds and, to a lesser extent, mammals.
14.1 The Middle Ear and the Hearing Range

As discussed in Chapter 3, land vertebrates have one of two fundamental types of middle ear, namely the single- or the three-ossicle type. The reptiles and birds do show significant variability in the details of their middle-ear structure and in the ossification of columella and extracolumella, but can still be described as possessing the single-ossicle, second-order lever system.

The joint between the extracolumella and the columella cannot be at the position where the greatest articulation takes place to transform the swinging motion of the inferior process into the piston-like motion of the columella, but is some way down the shaft towards the footplate. Thus the transformation to a piston-like motion must take place within the extracolumella itself, for which the extracolumella must be made of a flexible substance. This fact prohibits a full ossification of the extracolumella. In many reptiles, such an ossification is out of the question, as the extracolumella-columella complex is highly exposed to mechanical disturbance both on the body surface and within the buccal cavity. Anyone who has seen small lizards ingesting very large insect prey can understand the necessity of these animals retaining a flexible, non-rigid, middle-ear transmission system. Birds have isolated their middle ear from the buccal cavity to a much greater extent and have, on average, a deeper external auditory meatus than the reptiles. Thus in birds, the middle-ear ossicle is more highly ossified than in reptiles. A degree of flexibility must, however, be retained by the extracolumella in order to translate the rotary motion of the inferior process into a piston-like motion of the columella shaft. In general, all of these non-mammalian middle ears have, as far as their transfer function for displacement is concerned, a low-pass characteristic. The upper limits of this characteristic are significantly lower than in mammals (Ch. 3; Manley, 1981).

The upper frequency limit of the non-mammalian ear is strongly influenced by the flexibility of the middle ear (Manley, 1972 a,b,c, 1973). At high frequencies (>4 kHz), much of the acoustic energy is lost in a flexing motion within the inferior process and the efficiency of the middle ear deteriorates rapidly. A higher degree of ossification in birds has extended the limit of efficient transmission only slightly. In addition, however, the inner ear itself influences middle-ear transmission, especially at low levels. This fact has largely been ignored until it recently became possible to measure motion at much lower SPLs. Destruction of the basilar papilla and round window uncouples the middle ear from significant damping even at high sound levels (Manley, 1972 c).

14.2 The Hearing Range and Papillar Development

A glance at Fig. 14.1 makes the following fact obvious: regardless of whether a lizard has a very well-developed hearing organ with over a 1000 hair cells on a relatively long papilla (e.g. geckos and skinks) or 100 or 200 hair cells on a very