1. Introduction

The scope of this chapter is to review what is currently known about the workings of the two types of auditory hair cells in the mammalian cochlea, the inner hair cells (IHCs) and outer hair cells (OHCs). Mammalian hair cells have for a long time been impenetrable to the electrophysiologist’s microelectrodes, necessitating the extrapolation of results from more easily accessible and less vulnerable hair cells of nonmammalian vertebrate preparations to explain mammalian cochlear physiology. To assess the validity of this approach, we need to consider first whether there are common elements shared by all vertebrate hair cells.

1.1 The Minimal Hair Cell

Hair cells are sensory receptors used by all vertebrates to transduce mechanical stimuli into electrical responses. The organ in which the hair cells are situated determines to which type of mechanical stimulus they respond best: for example, hair cells in the lateral line organ of fishes and amphibians signal motion of fluid around the animal, vestibular hair cells are most sensitive to linear acceleration or rotational velocity, and auditory hair cells detect sound. Moreover, taking the hearing organs as an example, there is an enormous variation in structure among different classes of vertebrates, and even among different species. This variation is matched by large differences in sensitivity and frequency range, and both intensity and frequency discrimination (Stebbins 1983; Fay 1992). As judged by behavioral audiograms, mammals as a group are on average more sensitive than other classes of vertebrates, although some individual nonmammalian species approach the performance of the most sensitive mammals. The most salient distinguishing feature of mammalian auditory function is a considerably increased limit of high-frequency hearing (11–150 kHz, depending on...
the species) compared with birds (6–12 kHz) and other nonmammalian vertebrates (0.2–4 kHz). The architecture of the mammalian inner ear is quite unlike that of other vertebrates, with a coiled cochlea containing a longer basilar membrane, and two distinct types of hair cells with different afferent and efferent innervation patterns (Slepecky, Chapter 2). The mammalian basilar membrane acts as a sharply tuned frequency analyzer (Patuzzi, Chapter 4). The cochlea anatomy of birds and Crocidilia is more or less intermediate between that of other nonmammalian vertebrates and mammals, with tall hair cells comparable to IHCs, and short hair cells comparable to OHCs, also in their innervation. There is, however, a gradual transition from tall to short hair cells across the width of the cochlea, rather than two very distinct cell types. Basilar membrane tuning in birds is also apparently considerably less sharp than in mammals (Gummer, Smolders, and Klinke 1987).

Despite these differences in the anatomical environment in which the hair cells are situated and the functional requirements made on them, the hair cells themselves appear morphologically quite similar. This raises the question how many of the functional differences that exist among the organs containing hair cells can be attributed to the accessory structures, and how many to physiological differences in the hair cells themselves. This is an important question, because much information about hair cell physiology is derived from experiments on the sacculus, a vestibular organ responding to linear acceleration, of the bullfrog, *Rana catesbeiana*, and the basilar papilla, a primitive hearing organ, of the red-eared turtle, *Pseudemys scripta*. Likely differences between cochlear hair cells in mammals and those of other vertebrates are associated with the extended high-frequency limit of the mammalian cochlea.

The common elements expected for all hair cells are illustrated in Figure 6.1. First, displacements of the stereociliary bundle need to be transduced into a change in the electrical current flowing through mechanosensitive ion channels. By flowing across the electrical resistance \( R \) of the basolateral cell membrane, this transducer current \( I_T \) brings about a receptor potential. The size and shape of the receptor potential are determined by the properties of the transducer current itself, by the low-pass filter of the cell's membrane capacitance \( C \) and input resistance, and by any time- and voltage-dependent or ligand-gated ion channels that may be present in the basolateral cell membrane, provided they are activated over the relevant range of potentials. As a minimum, a \( K^+ \) current \( I_K \) is required to help set the resting potential and input conductance \( g, \) the inverse of resistance \( R \) of the cell. Such a role could, in principle, also be played by a \( Cl^- \) conductance, but it will become clear that this would not be appropriate for a hair cell (Section 3.2.). Finally, the cell needs to exert an effect on its environment. The most common effect is excitation of the afferent nerve fibers by release of neurotransmitter. As in nerve fibers, a \( Ca^{2+} \) current