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Evolution of Sensory Hair Cells

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1. Introduction

The ears of all vertebrate species use sensory hair cells (Fig. 3.1) to convert mechanical energy to electrical signals compatible with the nervous system. However, although the basic structure of hair cells is ubiquitous among the vertebrates and hair cells are also found in the lateral line of fishes and aquatic amphibians, a growing body of literature has demonstrated considerable heterogeneity in morphology and physiology in different taxa and even within different end organs of the same species. Although far less is known about the functional diversity that accompanies the differences in structure and physiology, it is increasingly likely that these differences reflect the ability to respond to different types of signals and/or to process signals in different ways before a neurotransmitter is released and a signal is sent to the brain.

What is also clear is that the vertebrate sensory hair cell is likely to be very ancient, at least in terms of the origins of the vertebrates (see Manley and Clack, Chapter 1, for a discussion of vertebrate phylogeny). Although soft tissues such as sensory hair cells do not survive in the fossil record, several lines of evidence support an origin of hair cells at least as far back as the very earliest vertebrates and perhaps even in vertebrate (chordate) ancestors (Burighel et al. 2003). Such evidence includes the presence of hair cells in both modern lamprey (jawless fishes that represent a sister group to jawed vertebrates) and modern gnathostomes (jawed vertebrates), suggesting an origin in a common ancestor at least 430 million years ago (Fig. 3.2 for a phylogeny highlighting the taxonomic groups discussed here). The existence of an inner ear with hair cells in *Myxine* (hagfishes), craniates that are considered the sister taxa to vertebrates, is further evidence for the early evolution of inner-ear structures (Löwenstein and Thornhill 1970; Forey and Janvier 1993), as is the finding of very similar cells in tunicates (Burighel et al. 2003). Ears similar to those of the hagfishes, with only a single semicircular canal, were probably present at the dawn of vertebrate evolution (Jarvik 1980). Although there is no direct evidence of hair cells, one would imagine that the presence of a distinct ear means the presence of mechanosensory cells within that ear.

At the same time, ciliated mechanosensory cells are not unique to vertebrates,

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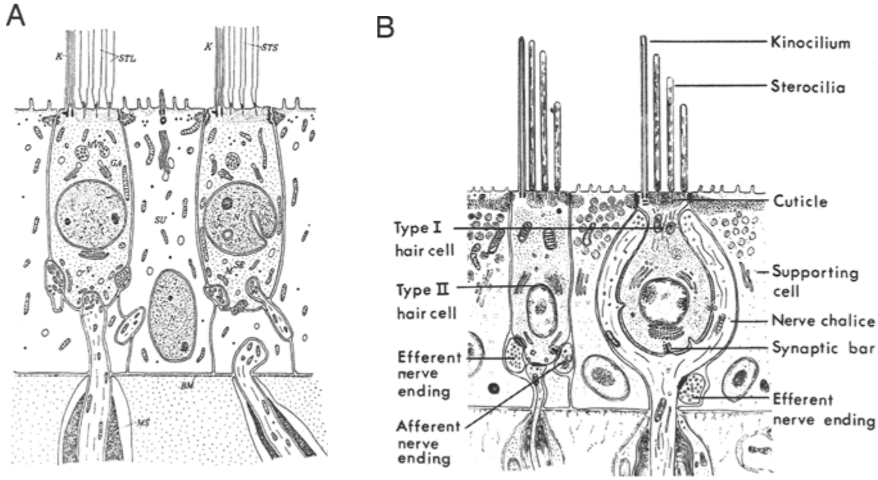

FIGURE 3.1. **A**: Schematic drawing of hair cells from the ear of the ray, *Raja clavata*. BM, basement membrane; CR, ciliary rod; CU, cuticular plate; GA, Golgi apparatus; K, kinocilium; M, mitochondria; MS, myelin sheath, MR, membrana reticularis; MV, microvillus; MVB, multivesicular body; N, nucleus; NE, nerve ending; Se, sensory cell; STL, "large" diameter stereocilia; STS, "small" diameter stereocilia; SU, supporting cell; V, vesicle. (From Löwenstein et al. 1964, with permission.) **B**: Drawing of type I and type II vestibular hair cells from the mammalian ear. (From Wersäll and Bagger-Sjöbäck 1974, with permission.)

and derivatives of vertebrate sensory hair cells are used in other detection paradigms such as electroreception (Jørgensen 1989). Mechanosensory "hair cells" in invertebrates have many features in common with those of vertebrates (Jørgensen 1989), although these similarities do not necessarily imply homology. Secondary sensory cells occur in tunicates (Bone and Ryan 1978; Burighel et al. 2003) and in a fossil organism that may be a vertebrate ancestor (Conway Morris 2000). Consequently, there has been discussion as to whether the vertebrate sensory hair cell arose de novo in the early evolution of the vertebrates (or chordates) or whether vertebrate hair cells and one or more of the even more ancient invertebrate mechanoreceptor cells share a common ancestry. This discussion has been amplified recently with the introduction of molecular techniques to study gene expression in specific cells in different taxa. As a result,

FIGURE 3.2. Phylogeny of species discussed in this chapter. **A**: The vertebrates. **B**: The phylogeny of the anamniote chordates discussed herein. The phylogeny shown here is closely allied with that for the vertebrates found in Manley and Clack (Chapter 1). **C**: Details of the ancestral invertebrates discussed in this chapter.