SENSORY CELLS OF THE FISH EAR — A HAIRY ENIGMA

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Analysis of the structure of the ears in teleost fishes has led to the tentative suggestion that otolithic endorgans may function differently in different species. Recently, evidence has demonstrated different "types" of sensory hair cells can be found in the ears of teleost fishes, and individual hair cell types are found in discrete regions of individual sensory epithelia. The presence of multiple hair cell types in fishes provides strong support to the hypothesis of regional differences in the responses of individual otolithic sensory epithelia. The finding of hair cell types in fishes that closely resemble those found in amniote vestibular endorgans also suggests that hair cell heterogeneity arose earlier in the evolution of the vertebrate ear than previously thought.

INTRODUCTION

Although reports of fish responding to sound have been around since the time of Aristotle, the experimental history of fish audition only began in the early part of the twentieth century (e.g., [1]). As reviewed in a number of studies, the biological role of sound detection by fish still remains, for the most part, unknown (see [2, 3], for reviews). In particular, despite an "in depth" analysis of the structure of the fish ear (e.g., [4 – 7]) and the structure of the eighth nerve pathway in the central nervous system of fishes (e.g., [8]), the functions of the ear and the mechanisms of information processing within the central nervous system of fishes [9] remain poorly known.

Even the most basic assumptions about the fish auditory system, that different sensory endorgans in fishes specifically respond to acoustic or to vestibular stimuli [10], is now subject to question. Indeed, analysis of the ear structure of fish over the past decade have led us to the idea that each of the otolithic endorgans of fish ears may be involved with both senses.

Adding to the problem of understanding the function of the ear in fishes is the more than 25,000 extant species of teleost fish [11] with all the striking inter-specific variation in ear structure among many related genera and families [7]. Variation in structure has led us to suggest that mechanisms of fish hearing, at least at the level of detection and processing of sounds in the ear, may have evolved in different directions among the various species (e.g., [6, 12]).

The purpose of this paper is to examine different aspects of the gross and ultrastructural variations within fish ears and to consider the significance of this variation in terms of the function of the ear. Since a number of recent papers have considered inter-specific variation of the ear in some depth (see [3, 5, 6, 12]), we will principally focus on the evidence for variation in receptor cell structure within single endorgans of the ear. Our discussion of intraepithelial variation suggests that the differences in anatomy of receptor cells in different regions of a single otolithic endorgan gives additional validity to the hypothesis of functional variation within a single endorgan of a fish ear.

The idea of regional variations in structure and function within a single endorgan is not unique, nor should it be surprising. The very function of the basilar papilla or the cochlea, the major auditory endorgans in reptiles, birds and mammals (amniotes), depends upon a variation in structure along the length of the endorgan. Differences such as stiffness, thickness of the basilar membrane, and other such features were recognized by von Békésy [13] and others as being the basis for regional discrimination of sound frequencies in the mammalian cochlea. More recently, the ultrastructural differences, such as those found in the inner and outer hair cells of the mammalian cochlea, have become recognized as a fundamental aspect of mammalian hearing (reviewed in [14]).

In contrast to the amniote ear, it has long been assumed that regional variation in function in any endorgan of the fish ear had no basis because receptor cells were homogeneous. In actuality, there had been very little direct physiological or anatomical data to support an argument for or against region-

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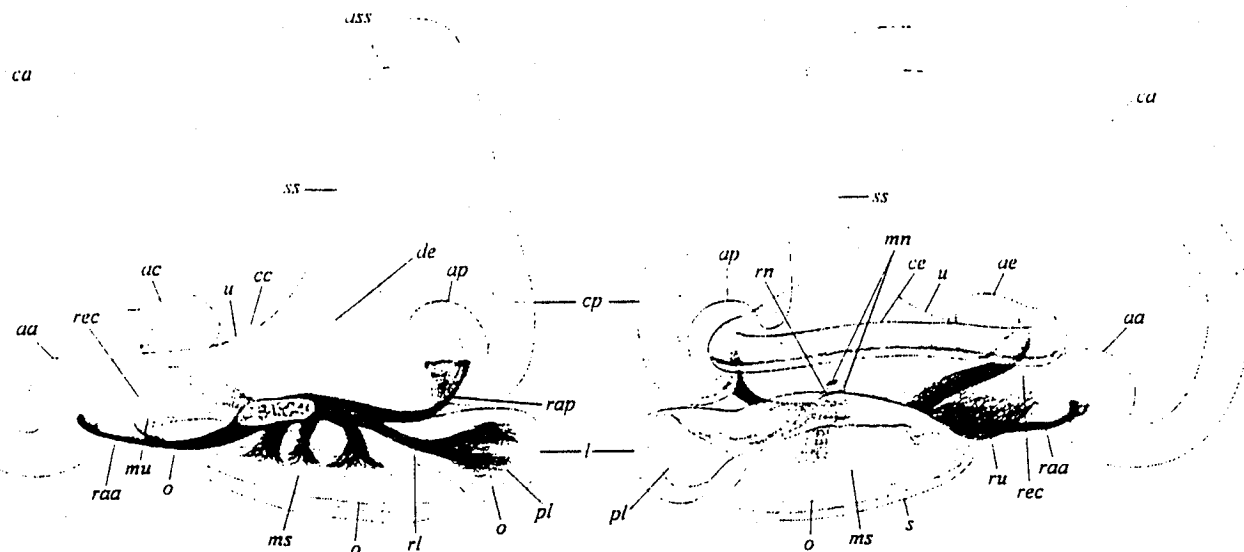[2] Rutgers University, Camden, New Jersey, USA.

Fig. 1. Drawing of the ear of the Atlantic mackerel (*Scomber scomber*) from Retzius (1881). A medial view is shown in the left and a lateral view on the right. *aa, ac, ap*) Cristae of anterior, horizontal and posterior semicircular canals; *ass*) apex of crus commune; *ca, ce, cp*) anterior, horizontal and posterior semicircular canals; *de*) endolymphatic duct; *l*) lagena; *mn*) *macula neglecta*; *ms*) saccular epithelium; *mu*) utricular epithelium; *o*) otolith; *pl*) lagena epithelium; *raa, rap, rl, rn, rec, ru*) rami of eighth nerve to various endorgans; *s*) saccule; *ss*) *crus commune*; *u*) utricle.

alization. However, in the last decade, a sufficient body of data has been developed to support such an argument. To advance the study of eighth nerve sensory systems in fish, a need to understand the relationships between structure and function in the ears of fishes has become imperative.

We begin by examining the basic structure of the ear of fishes and discuss a few gross anatomical findings that support the idea of differences in the function of the ear both inter-specifically and within a single endorgan. We will then consider more recent data, primarily from our laboratory, that further supports the idea of regionalization within single endorgans of the fish ear. Finally, we will briefly consider the functional implications of regionalization

STRUCTURE OF THE EAR

The ear of bony fishes (Fig. 1) is basically similar to the ear of tetrapod with one exception. The fish ear lacks a mechanism for extended hearing as transduced by the cochlea or basilar papilla. The fish ear has three otolithic endorgans (saccule, utricle, lagena) and three semicircular canals with associated sensory regions (cristae). Many species have a seventh endorgan, the *macula neglecta* (see [7]), which appears to function with the cristae in at least some species [15].

Each of the otolithic endorgans has a sensory epithelium containing sensory hair cells and supporting cells. As in amniotic vertebrates, the hair cells have apical ciliary bundles that project into the lumen of the various ear chambers. Each ciliary bundle contains a single kinocilium which is located to one side of a group of stereocilia (e.g., [16]). The ciliary bundles are overlain by a single calcareous otolith which partially, or completely, fills the chamber of the endorgan. The

otolith is considered to be the densest structure in the body of a fish — about three times the density of soft tissues or other calcified structures [17].

As Hudspeth and his colleagues have so clearly shown, the mechanism for stimulating a hair cell is bending of the bundle (e.g., [18]). This is accomplished in fish otolithic endorgans by a shear generated by the relative motion between the sensory epithelium, which moves with the water mass, and the denser otolith which moves at a different amplitude and phase than the soft tissues of the body.

A number of aspects of the gross morphology of the ear vary across fish species. This is perhaps most dramatically seen in the saccule, although utricular structure varies among those species that seem to use that endorgan for hearing (e.g., [19, 20]). Variations in gross structure include the shape and size of the saccular epithelium, the shape of the otolith and the percent of the chamber volume it fills, and the extent of the epithelium actually overlain by the otolith. The shape of the otolith is particularly interesting in that it can be used to taxonomically classify fishes [17].

Perhaps the most extreme differences in epithelial structure are encountered when comparing species of the superorder *Otophysi* (e.g., goldfish, catfish, and relatives) with fishes from almost all other taxonomic groups. In the *Otophysi*, the saccule is long and thin. The lagena is rounded and its total epithelial area is as large, if not larger than, that of the saccule. In contrast, most other species have a diminutive lagena compared with the saccule. This difference may be associated with very different strategies in the manner in which sound detection occurs in the otophysans as compared to other species (see [35], for review). The Weberian ossicles of *Otophysi* appear to enhance the pressure component of a signal by carrying signals directly from the swim-

bladder to the saccule of the inner ear in a manner that may be functionally analogous to the mammalian middle ear bones (e.g., [21]).

Scanning electron microscope examination of the sensory epithelia has revealed distinct variations of ciliary bundle structure. Two aspects of the ciliary bundle in particular appear to hold some importance.

First, the absolute length of the bundle varies in different regions of the epithelium, as well as between different epithelia [22]. For example, the bundles on the cristae of the semicircular canals are generally extremely long (e.g., [23]), whereas those in the otolithic endorgans are generally shorter. Even within an endorgan, the length of ciliary bundles vary. In many species the ciliary bundles on the hair cells at the margins of the saccular epithelia are longer than on the cells towards the center (e.g., [22]) while in otophysans, the ciliary bundles on cells at the rostral end of the saccular otolith are generally shorter than those at the caudal end [24].

The second source of variation lies with the polarization or orientation of the ciliary bundles on the epithelia. Orientation is defined by the position of the kinocilium relative to the rest of the bundle. In fish as in other vertebrates, all of the ciliary bundles in any given region of a sensory epithelium are oriented in the same direction (e.g., [5, 25]). This imparts physiological polarization on the different epithelial regions, and may serve as the basis for sound source localization in fish (e.g., [3, 12]. Popper and Coombs [6] pointed out the particularly extensive inter-specific variation in the hair cell orientation patterns of the saccule. Such variations are not necessarily related to taxonomic position of fishes, but instead, seem to be associated with peripheral specializations relating to biophysical transduction. For example, most species that have swimbladder projections that abut the saccule (considered to be a specialization to enhance hearing) have basically the same type of saccular hair cell orientation pattern [6]. While the functional significance of these different patterns remain unknown, it is reasonable to speculate that the different patterns would have a bearing on the teleostean process of directional detection.

WHAT DO THE OTOLITHIC ENDORGANS DO?

The earliest studies of von Frisch (e.g., [10]) suggested that the saccule, and possibly the lagena, are involved with hearing while the utricle functioned as a vestibular endorgan. More recent evidence (reviewed in [3, 12]) suggests that the different otolithic endorgans may function as both auditory and vestibular receptors. It is important to realize that a distinction between auditory and vestibular stimulation is somewhat difficult to make for aquatic animals since sensory transduction in both sensory domains involves motion of the body with the water mass relative to the denser otoliths in the ears. Whereas vestibular stimulation in terrestrial animals can be readily distinguished from acoustic stimulation, vestibular and auditory stimulation for aquatic vertebrates basically are different frequency functions along a continuum.

HAIR CELL TYPES

One of the most interesting features of the mammalian ear is the presence of sensory hair cells that differ in size, shape, organelles and innervation (see [16, 26, 27]). This variation is encountered in the cochlea with the ultrastructurally distinct inner and outer hair cells, and in vestibular endorgans with their two different types of hair cells (the type I and type II cells). While two hair cell types are found ubiquitously in the different endorgans of amniotes, the functional significance of these receptor cells is only now beginning to be understood (e.g., [28, 29]).

The earliest description of different types of vertebrate hair cells came from the electron microscopic studies of mammalian vestibular endorgans by Wersäll. Wersäll and his colleagues (e.g., [16, 26, 27]) demonstrated two distinct hair cell types found in otolithic endorgans and cristae. They identified a type I hair cell with a vase-like shape that was surrounded by a nerve chalice. A type II hair cell was described as cylindrical in shape with multiple synapses towards the basal end that were made by afferent neurons. More recent studies continue to refer to the type I and type II hair cell, although there is some question as to whether the type I cell may have multiple forms [30] or whether the significant difference between the two cell types is primarily related to innervation. Yet, recent evidence suggests differences in ionic channels between type I and type II hair cells [31, 32].

Wersäll and his colleagues [27], when considering the type I and type II hair cells among the vertebrates, pointed out a taxonomic anomaly. Based upon TEM examination of a number of species ranging from fishes to mammals, they concluded that the type II hair cell is found in the endorgans of all vertebrates, but that the type I hair cell is only found in amniotes. In essence, they proposed that anamniotes (fishes, amphibians, elasmobranchs, agnathans) have a single type of hair cell that is essentially the amniote type II cell.

COULD THERE BE MULTIPLE HAIR CELL TYPES IN FISHES — EARLY EVIDENCE

Wersäll's suggestion that there is but a single hair cell type in fishes was followed by a number of ultrastructural studies that did nothing to dispel this idea (e.g., [33 – 36]). These studies examined only a few of the more than 25,000 extant species, although across a reasonably broad taxonomic range. The basis for questioning homogeneity among fish hair cells arose from a few studies that suggested small variation in the basic hair cell type among fishes. Hoshino [37] pointed out striking differences in the organelle composition of hair cells in different regions of the otolithic endorgans of lampreys. In elasmobranchs, differences in the organelle composition of hair cells in the saccule [38] and macula neglecta [39] were suggested, but these were only passing observations that were not correlated with intraepithelial region. A detailed examination of the hair cells of the lagena of an anabantid fish (Colisa) [40] suggested some variation

in the ultrastructure of different hair cells, but were still interpreted as variations within type II hair cells.

MULTIPLE HAIR CELL TYPES IN FISH — DIRECT EVIDENCE!

A series of investigations in our laboratory have demonstrated distinct physiological and biochemical differences between hair cells found in different epithelial regions of individual otic endorgans in several species of fish. These variations compelled us to reconsider the issue of different types of hair cells within a single epithelium.

In the first of these studies, we focused on the utricle of the oscar, *Astronotus ocellatus* (a cichlid fish), because, like all utriculi, the epithelium has several distinct areas including a striola region and several other regions collectively called the extrastriolar region. We demonstrated that hair cells in the striola region (Fig. 2) exhibited positive immunoreactivity to an antibody to the calcium binding protein S-100, whereas hair cells outside of this region (in an area called the extrastriola) did not exhibit immunoreactivity [42].

This observation led us to test whether regional differences would be seen as a result of treatment with the aminoglycoside drug gentamicin sulphate, an ototoxic drug that selectively damages type I hair cells of mammals [43]. In the oscar, gentamicin caused loss of ciliary bundles on the utricular striolar hair cells and even with significantly greater doses, not to extrastriolar hair cells [44, 45]. Interestingly, individual new hair cells appeared within the striola simultaneously as the more mature hair cells were damaged, and the density of cells in the area damaged by gentamicin also showed complete recovery within 10 days after termination of treatment [44].

Hair cell differentiation in fish was further demonstrated by another type of study. Just as the type I hair cells of amniotes are innervated by calyceal endings of their afferent fibers [16, 26], the striolar hair cells of fishes are innervated by distinct afferents in which spike initiation is located on the postsynaptic membrane [46]. Such is not the case for the extrastriolar hair cells. In addition, the diameter of the fibers innervating the striolar are considerably greater than those innervating the extrastriolar cells.

Additional studies demonstrated similar differential responses to S-100, gentamicin, and/or afferent types in the lagena and saccule of the oscar [42, 46] and the kissing gourami *Helostoma temincki*, [47]), as well as in the saccule and lagena of the goldfish, *Carassius auratus* [48, Saidel et al., submitted]. The taxonomic difference between *As-*
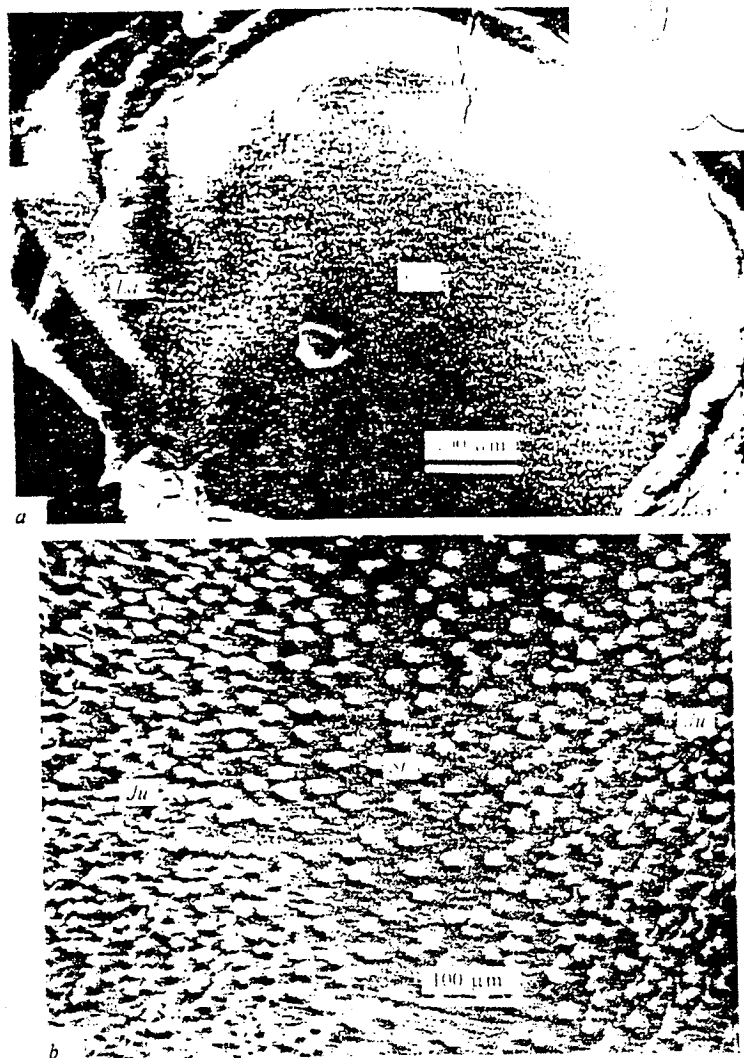

Fig. 2. Scanning electron micrographs of the sensory surface of the utricle from the oscar, *Astronotus ocellatus*. (*a*) Shows the whole surface of the utricle. The striolar region (*St*) has somewhat lower density hair cells (as shown magnified in (*b*)). The extrastriolar region consists of the Rampa (*Ra*), Lacinia (*La*) and Cotillus (*Co*). The inset outlines the striolar region as the stippled area. (from [41]).

tronotus and *Helostoma* compared with *Carassius* is nearly maximal within the euteleostei suggesting that the different classifications of hair cell types may be widely distributed among bony teleost fishes.

STRUCTURAL EVIDENCE FOR CATEGORICAL TYPES OF HAIR CELLS IN FISHES!

While the various studies mentioned above demonstrated a heterogeneity among hair cells in fishes, it was not until we targeted ultrastructural investigations to the above tests that we could relate specific hair cell features to our categorical types. Using serial reconstruction of extrastriolar and striolar hair cells of the oscar utricle, Chang et al. [41] demonstrated

Fig. 3. Transmission electron micrographs of a portion of a striolar (*a*) and extrastriolar (*b*) hair cell. Striolar hair cells have large mitochondria (*M*) and a subnuclear cisternae (*Pc*). Extrastriolar hair cells have small mitochondria and no subnuclear cisternae.

The similarity between the organization of hair cells in the oscar utricle and those in the vestibular endorgans of amniotes becomes compelling. In particular, the extrastriolar hair cells resemble the amniote type II hair cell [27]. Careful examination of the striolar hair cells (including their response to ototoxic drugs and their ultrastructure) suggest a number of important characteristics in common with the amniote type I hair cell. The unique innervation of type I amniote hair cells by a nerve chalice is also paralleled by a unique innervation of striolar hair cells in fishes [42, 47]. Moreover, the type I hair cells and the teleost striolar cells are innervated by the largest diameter eighth nerve fibers (e.g., [50]). In fishes, these hair cells have a higher number of afferent synapses than extrastriolar hair cells [41].

Several alternatives presented themselves for naming teleost striolar hair cells. One would be to give them a distinct name (e.g., fish type I, type III) which would result in the proliferation of names. This procedure would generate confusion as has occurred in the literature on types of hair cell ciliary bundles (see [4]). For both the similarities between the ultrastructure of type I cells and the striolar cells and for this latter reason, we have chosen to call the striolar cells (and similar cells in other fish otic endorgans) type I-like.

ARE TYPE I AND TYPE I-LIKE CELLS HOMOLOGOUS?

The name does not, however, mean to imply homology between type I and type I-like cells. Determination of homology is not something that can be easily done, and we are reluctant to suggest that the two cell types are homologous in the evolutionary sense. However, we do suggest that type I cells could have readily evolved from type I-like cells with minor genetic modifications and the development of a nerve chalice. Ontogenic studies on the developing mouse [51] suggest that a chalice might be a derived characteristic that arises ontogenetically as a multiple-branching axonal termination with multiple afferent terminals on what will become type I hair cells. Thus, it is possible that the nerve chalice found on amniote type I hair cells may represent a simple ontogenetic change evolved after vertebrate adaptation to terrestrial life.

WHY HETEROGENEITY IN FISHES?

Finding multiple hair cell types in fishes leads to a number of interesting and potentially important questions with

clear ultrastructural differences between hair cells in these regions. Striolar hair cells possess smaller synaptic bodies than found in extrastriolar hair cells. They also have larger mitochondria than extrastriolar hair cells as well as a subnuclear cisternae system of smooth and rough endoplasmic reticulum that is not found in extrastriolar hair cells (Fig. 3). These, and a number of other distinct differences between striolar and extrastriolar hair cells can only relate to differences in some, as yet unknown aspect of hair cell physiology. The differences between the two hair cell types are illustrated in Fig. 4.

We raised the question of the ubiquity of ultrastructural differences in hair cell types because the findings in the utricle of the oscar may be unique to that species. Recent examination of the saccule of the oscar also demonstrate the presence of the two cell types in that endorgan [49] as did studies of the saccule and utricle of the goldfish. These latter demonstrated that similar cell types are present in those endorgans of a species that is taxonomically distinct from the oscar [48, Saidel et al., submitted].

WHAT SHALL WE CALL DIFFERENT HAIR CELL TYPES IN FISHES?

The question arose as to what we should call the hair cell types found in the oscar (e.g., [41]), and goldfish [48]. The original suggestion was to call them striolar and extrastriolar hair cells, but that proved to be unrealistic once we discovered that hair cells with the same characteristics were found in different regions of the oscar saccule [49] and now in the goldfish saccule [48, Saidel et al., submitted].
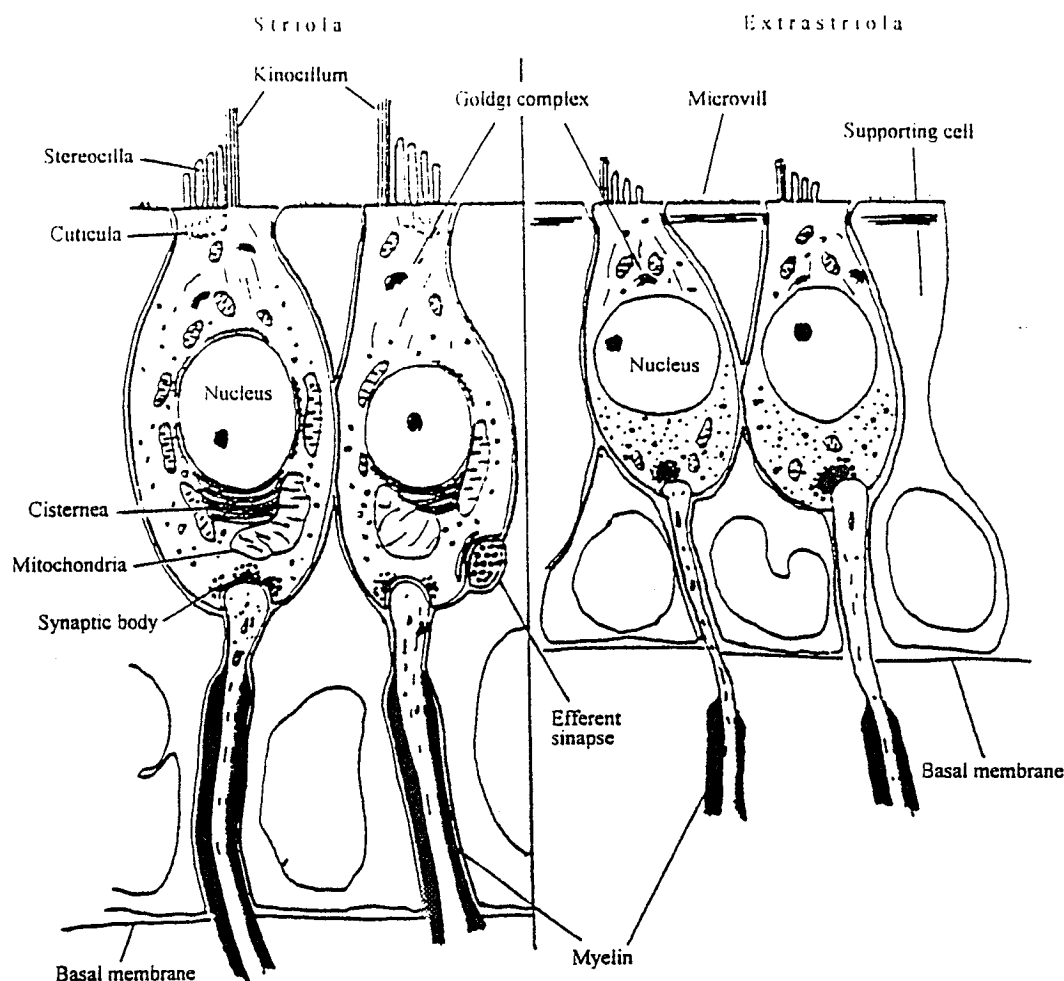
Fig. 4. Schematic drawing of the major features of striolar and extrastriolar hair cells in the oscar. Each sensory hair cell is surrounded by several supporting cells. The major differences between striolar and extrastriolar hair cells illustrated here include the sizes of the mitochondria and synaptic bodies and the presence of sub-nuclear cisternae in the striolar cells. (from [41]).

regard to function of the fish ear and evolution of octavolateralis endorgans, as well as otolithic function in vertebrates. Differences in processing information from different hair cell types to the eighth nerve and then to the CNS is suggested by several factors: the presence of different-sized synaptic bodies and structure of innervating neurons in particular. The presence of large mitochondria and extensive subnuclear cisternae also suggest a significantly higher metabolic activity in type I-like than in type II hair cells.

While physiological data are absent about type I-like and type II hair cells in the oscar, some interesting data from hair cells isolated from the goldfish saccule is pertinent. Using patch clamp studies, Sugihara and Furukawa [52] found that two cell types could be differentiated by the physiological characteristics of frequency response and spontaneous activity and these physiological differences correlated with morphological shapes. These two cell types correlate in shape to cell types we have identified as being type II and type I-like in the goldfish saccule, further implying that the two cell types are indeed physiologically different [48, Saidel et al., submitted].

The second question of considerable interest is the evolutionary implications of two hair cell types in fish ears. While,

as indicated earlier, we cannot easily speculate about homology between the hair cells found between amniotes and fishes, it is safe to suggest that the hair cell heterogeneity is not a uniquely amniote characteristic. With the presence of inner and outer hair cells in mammals, tall and short hair cells in the avian basilar papilla, and type I and type II hair cells in vestibular epithelia, it is clear that heterogeneity has flourished among amniotes. The presence of multiple receptor cell types in fishes as in homeothermic vertebrates implies a fundamental vertebrate dichotomy in the processing of mechanoreception by different ear endorgans. This dichotomy, a type of "parallel processing," apparently has existed since early in the evolution of the vertebrate ear. Finding more than one hair cell type and "information channel" in the otolithic organs of fish — as in other vertebrates — also suggests that all vertebrate otolithic organs derive two (or more) classes of information from the periphery.

FUNCTIONAL IMPLICATIONS OF REGIONALIZATION IN HAIR CELL STRUCTURE

The combination of morphological and physiological data on hair cells in the goldfish saccule [52] suggest that

and caudal regions of the saccule have
perties. Other data on eighth nerve re-
ral and caudal saccule in goldfish and
catfish (*Ictalurus punctatus*), support
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6]). The report of variation in ciliary
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ndorgans, but not in others. Thus, dif-
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rs other than the sensory epithelia pro-
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ggest that the mode of stimulation of
lls could differ.

is leave us with tantalizing questions
of regionalization. Regionalization in
closely related to frequency response
regions of the ear. Some fish species
frequency and intensity (reviewed in
ism involved is not known. It is possi-
n is involved in providing differential
frequency axis) signals used for behav-
— although it may be that frequency
s not important for fishes. Indeed, it
at frequency discrimination in fish can
basis of central processing of signals

STIBULAR RESPONSES?

pect to regionalization of the sensory
f fishes may be involvement with re-
nodalities. It is possible that some re-
pithelia respond best to very low fre-
ut (change in body position) while
to higher frequency acoustic signals.
water are part of the same continuum,
le endorgan to both "types" of signals
too surprising.

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