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Hair cell heterogeneity and ultrasonic hearing: recent advances in understanding fish hearing

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The past decade has seen a wealth of new data on the auditory capabilities and mechanisms of fishes. We now have a significantly better appreciation of the structure and function of the auditory system in fishes with regard to their peripheral and central anatomy, physiology, behaviour, sound source localization and hearing capabilities. This paper deals with two of the newest of these findings, hair cell heterogeneity and the detection of ultrasound. As a result of this recent work, we now know that fishes have several different types of sensory hair cells in both the ear and lateral line and there is a growing body of evidence to suggest that these hair cell types arose very early in the evolution of the octavolateralis system. There is also some evidence to suggest that the differences in the hair cell types have functional implications for the way the ear and lateral line of fishes detect and process stimuli. Behavioural studies have shown that, whereas most fishes can only detect sound to 1–3 kHz, several species of the genus *Alosa* (Clupeiformes, i.e. herrings and their relatives) can detect sounds up to 180 kHz (or even higher). It is suggested that this capability evolved so that these fishes can detect one of their major predators, echolocating dolphins. The mechanism for ultrasound detection remains obscure, though it is hypothesized that the highly derived utricle of the inner ear in these species is involved.

Keywords: hair cell; ultrasonic hearing; fishes; hearing; evolution

1. INTRODUCTION

In the 15 years since the first meeting on the sensory biology of aquatic animals (Atema *et al.* 1988), there have been significant advances in our understanding of the mechanisms by which fishes detect and process sound (reviewed in Popper & Fay 1999). From the perspective of this author, these advances have been made in several areas including (in no particular order) hair cell ultrastructure, psychoacoustics, mechanisms of sound-source localization, hearing range, central anatomy of the auditory system and the relationship between hearing and communication. Some of these areas are considered by other authors in this issue (e.g. infrasound detection by Sand & Karlson (this issue), sound-source localization by Fay & Edds-Walton (this issue) and the relationship between hearing and sound production by Ladich (this issue)), while other topics have been the subject of recent reviews (e.g. central auditory pathways (McCormick 1999), the evolution of the auditory system (Popper & Fay 1997) and auditory psychoacoustics (Fay & Megela Simmons 1999)).

This paper will discuss several issues which have arisen in the author's laboratory and which provide some additional insight not only into the structure and function of the auditory system in fishes, but also into the evolution of the vertebrate auditory system.

2. SENSORY CELLS OF THE EAR

The transducing elements of the auditory and vestibular systems of fishes are the sensory hair cells of the inner

ear. These cells are quite typical of those found in the ear and lateral line of other vertebrates (Chang *et al.* 1992). The sensory hair cells have a cell body which is innervated by afferent (and sometimes efferent) neurons and an apically positioned bundle of cilia which project into the lumen of the ear.

In the earliest analysis of sensory hair cells using transmission electron microscopy (e.g. Wersäll 1961) it was suggested that there are at least two distinct types of sensory hair cells (called type I and type II) in the vestibular portion of the amniote ear (reptiles, birds and mammals). These data supported the notion that anamniotes (amphibians, fishes and agnathans) had only type II hair cells in the ear and lateral line. The presumed basis for this dichotomy was that the function of the ear in amniotes is more complex than in anamniotes and so there arose the need for hair cells which presumably were best adapted for different roles. Moreover, since the original description of type I and II hair cells we now know that there are more than two hair cell types in amniotes. Thus, birds have tall and short hair cells on the basilar papilla and mammals have morphologically and functionally distinct inner and outer hair cells in the cochlea (e.g. Echteler *et al.* 1994).

Work on a number of fish species has supported the idea of there only being a single type of hair cell in anamniotes (reviewed in Chang *et al.* 1992). Indeed, although studies in the 1980s hinted at the possibility of there being several types of hair cell in fishes, this was never explored in any depth and the variation was never considered as having functional significance (see Popper & Fay 1999).

However, more recent investigations have led to another view of sensory hair cells in fishes. The results of these studies, which are discussed below (§2(a)–(d)), support four hypotheses.

- (i) Hair cell heterogeneity exists in fishes as well as in amniotes (few data are available for amphibians).
- (ii) Hair cells in fishes are likely to be homologous to amniote type II and type I hair cells.
- (iii) Hair cell heterogeneity arose very early in fishes and perhaps even as early as the origin of the octavo-lateralis system.
- (iv) There may be a discrete functional significance to having different types of hair cell in fishes and this would certainly have relevance to future studies of how fishes detect both vestibular and auditory signals.

(a) Hair cell heterogeneity

A number of studies have shown differences in the responses of sensory hair cells in discrete locations in the utricle of the cichlid *Astronotus ocellatus* (the oscar) to treatment with the ototoxic drug gentamicin sulphate (Yan *et al.* 1991) and to the calcium-binding antibody S-100 (Saidel *et al.* 1990). For example, the cells found in the region of the utricular epithelium called the striola were damaged by gentamicin, whereas cells in other, extra-striola regions were not damaged. Subsequently, a study using serial reconstruction of sensory hair cells and transmission electron microscopy revealed several distinct differences in the ultrastructure of the hair cells in the striola and extrastriola regions (Chang *et al.* 1992). These included the presence of very large subnuclear bodies of endoplasmic reticulum and large mitochondria in the striolar hair cells, but not in the extrastriolar hair cells. Moreover, the striolar hair cells had smaller synaptic bodies associated with synapses than found in the extrastriolar hair cells. Finally, whereas the striolar hair cells received both afferent and efferent innervation, the extrastriolar hair cells only had afferent innervation.

Based upon these studies and similar results in the saccule and lagena of *Astronotus* as well as in the goldfish (*Carassius auratus*), it became apparent that several distinctly different types of hair cell are present in the ears of at least some fish species (e.g. Chang *et al.* 1992; Saidel *et al.* 1995; Lanford & Popper 1996). Furthermore, examination of older work on elasmobranchs showed figures which contained some cells with large subnuclear structures and other dichotomies which bore a striking resemblance to the two types of hair cell seen in *Astronotus* and *Carassius* (reviewed in Chang *et al.* 1992).

(b) Sensory hair cells in fishes resemble those found in amniotes

In comparing the striolar and extrastriolar hair cells of fishes with the type I and type II hair cells of amniotes, it became apparent that the extrastriolar hair cell of fishes is very much like the amniote type II hair cell and that there are many features in common between the striolar hair cell and the amniote type I cell (Chang *et al.* 1992). Indeed, the only significant difference between the amniote type I cell and anamniote striolar cell is the presence of a large nerve calyx which surrounds the amniote cell

and which is not seen in fish cells. However, in subsequent studies, Lanford & Popper (1996) identified a calyx in some striolar-like hair cells of the crista of *Carassius*, showing that it is very possible for fishes to have such structures. While the calyx is not found in all (or perhaps even most) fish striolar-like hair cells, it is clear that the calyx is not unique to amniotes. As a result of these observations, the striolar hair cell in fishes has been given the name 'type I-like' (Chang *et al.* 1992).

(c) Hair cell heterogeneity arose early in vertebrate history

While the fossil record regarding fishes ears reveals nothing about the origin of the ear or the origin and evolution of soft tissues such as the sensory hair cells, there are some interesting observations which suggest very early evolution of hair cell heterogeneity. It must be borne in mind that, while the ear and lateral line share the same sensory hair cell as the mechanoreceptor, the old idea that the ear arose from the lateral line is highly suspect (see Popper *et al.* 1992). Indeed, the modern view is that of the octavo-lateralis hypothesis whereby the ear and lateral line arose independently, although they may share a common ancestor structure in which the hair cell arose (see Popper *et al.* (1992) for a review).

Two pieces of information are of interest here. First, work on the hair cells of the ear of agnathans has revealed striking hair cell heterogeneity (Hoshiro 1975) which, while not like that found in fishes, suggests that heterogeneity is ubiquitous among vertebrates. Second, gentamicin studies have suggested that the lateral line canal neuromasts are probably type I-like cells and the free neuromasts are more than likely type II hair cells (Song *et al.* 1995). This argument has been supported by several other observations (J. Song and A. N. Popper, unpublished results) using S-100 and ultrastructure.

The results of these studies suggest that hair cell heterogeneity arose very early in the evolution of vertebrates and that the genetic capabilities for such heterogeneity may have been found in the very earliest sensory hair cells. While it is not known whether the various types of hair cells found in the ear and lateral line of fishes are functionally the same, the significant observation is that their heterogeneity is fundamental to vertebrate hair cell systems.

(d) Functional significance of heterogeneity

While there have been few studies which have suggested different hair cell functions in fishes, it now appears that the various hair cell types may have evolved for functional differences in fishes as they have in amniotes (see Saidel *et al.* 1995; Lanford & Popper 1996; Popper & Fay 1999, Lanford *et al.* 2000). At the same time, far more work needs to be performed in order to fully correlate different fish hair cell types with function, just as we need a good deal more work in order to understand the overall function of the sensory receptors in fishes.

3. HEARING RANGE OF FISHES

Behavioural studies have been conducted in over 75 teleost species in order to determine the range of sounds

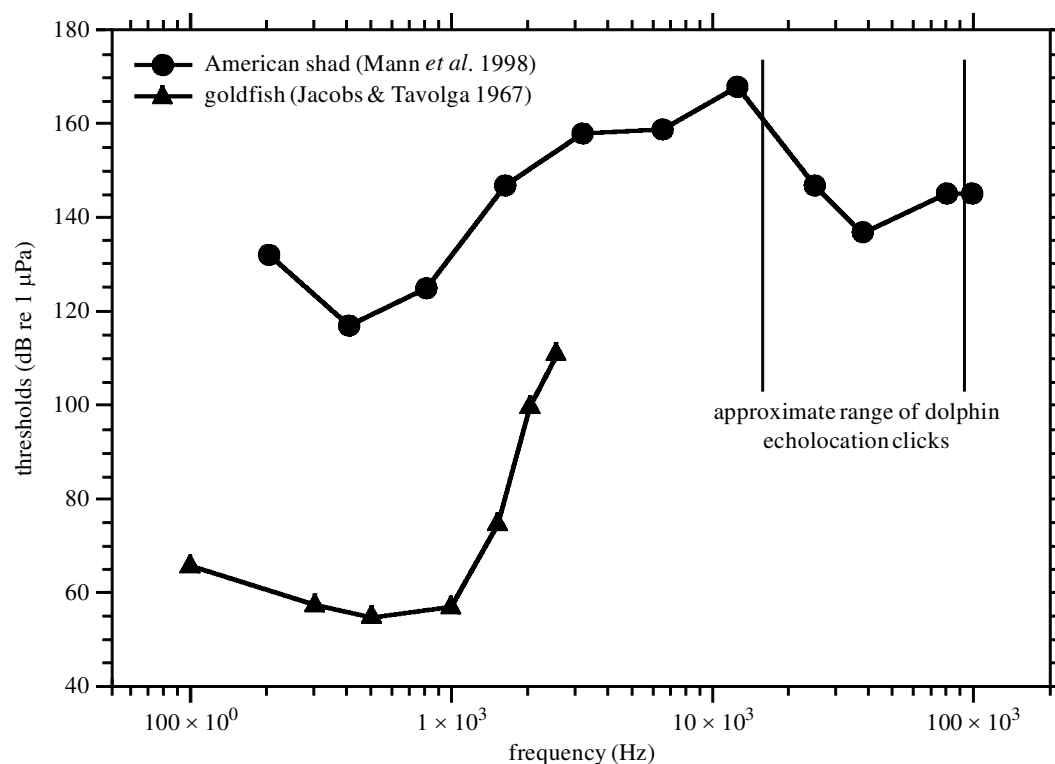


Figure 1. Hearing sensitivity measures of the American shad as compared with data for the goldfish. These audiograms show the lowest sound pressure level detectable by a species at each frequency tested using a behavioural paradigm. The area between the two vertical lines indicates the general frequency range which might be emitted by a dolphin predator of a fish which can detect ultrasound. (Data from Jacobs & Tavolga (1967) and Mann *et al.* (1998).)

that fishes can detect and the sensitivity of fishes at each frequency (reviewed in Popper & Fay 1999). These results have shown that, while there is wide diversity in the hearing range and sensitivity of fishes, only a few species hear sounds above 3000 Hz and most species can hear no higher than 1000 Hz. Similar data have suggested that most fishes can detect sounds to somewhat below 50 Hz (see Sand, this issue).

The variation in the hearing capabilities of fishes is clearly related to the presence or absence of specializations in the peripheral auditory system which might enhance hearing. Thus, species which hear a wider range of frequencies such as *Carassius* have specializations which improve the acoustic coupling between the swim bladder, a pressure receiving organ and the inner ear (e.g. Popper & Fay 1999). These fishes are generally referred to as hearing specialists and they are found in diverse teleost taxa and exhibit a wide range of structures for enhancing hearing. In contrast, most other fishes may be called hearing generalists or non-specialists. These fishes do not hear as well as specialists and they primarily detect sounds without the help of the swim bladder (Popper & Fay 1999).

In the early 1990s reports started to appear in the peer-reviewed and 'grey' literature which suggested that a number of fishes of the genus *Alosa* in the order Clupeiformes (herrings and relatives) might be detecting much higher frequencies than other species (e.g. Ross *et al.* 1995; reviewed in Mann *et al.* 1998). These reports showed that subjecting species of *Alosa* to ultrasonic pulses (ca. 126 kHz) resulted in the fishes swimming away from the

source. Indeed, the response was so powerful that these kinds of sounds were adopted as a suitable method of keeping responsive species from entering water intakes to power plants at a number of locations in the USA (e.g. Ross *et al.* 1995). However, the precise nature of the sounds used to repel fishes was never made clear in these papers. While the evidence strongly suggested that several species of *Alosa* might be detecting ultrasound, the studies did not use rigorous behavioural methods, nor did they examine the actual hearing capabilities of these species. Thus, we have almost no data on the ultrasound hearing of these species.

More recently, Mann *et al.* (1997, 1998) examined sound detection in the American shad (*Alosa sapidissima*). The animals were tested using rigorous psychophysical methods as well as carefully controlled pure tones in order to ensure that the signals did not contain spurious energy at unwanted frequencies. These studies demonstrated that the American shad could detect sounds to at least 180 kHz (figure 1). Detection in this species was best up to ca. 3 kHz, although it was far poorer than hearing in the goldfish. However, whereas goldfish could not detect sounds above 3 kHz, even when tested with the ultrasonic signals used for the American shad (Mann *et al.* 1997), the shad continued to show reasonably good detection to 180 kHz, the limit of the sounds which could be produced.

Additional studies have shown that the American shad responds vigorously to pulses which resemble the echolocation signals of dolphins, their major predator (Mann *et al.* 1998). This led Mann *et al.* (1998) to suggest that the

ultrasonic hearing in this species evolved as a predator avoidance mechanism. Indeed, the sensitivity of the American shad is sufficient for detecting dolphins which are up to 100 m from the fishes if the dolphins are emitting their highest intensity signals.

While these studies showed that American shad and, presumably, other members of the genus *Alosa* (Ross *et al.* 1995) are able to detect ultrasound, the mechanism by which these signals are detected is not yet clear. However, based upon an analysis of possible receptors, Mann *et al.* (1998) proposed that the highly derived utricular region of the Clupeiformes' inner ear is likely to be involved in ultrasound detection. However, this hypothesis remains to be tested.

4. SUMMARY

There have been significant advances in our understanding of fish hearing over the past decade. We now have a substantially better understanding of the anatomy of the peripheral and central structures involved in hearing. We also have important new data on the physiological mechanisms and, in particular, those involved with one of the major functions of hearing, i.e. sound-source localization. We have a better idea that the auditory periphery of fishes is likely to be involved in a good deal of signal processing, at least if we make the assumption that multiple types of hair cell are involved in different functions. Moreover, the importance of the periphery for processing is elegantly clear when we consider that it has probably evolved as a highly effective analyser for determining sound-source direction.

We also have a significantly better appreciation of the possible hearing range of fishes. While most fishes probably do not detect either ultrasound or infrasound, these findings further reinforce the notion that the auditory system of fishes is capable of adapting to a wide range of selective pressures in order to enhance the survival of a species. Finally and, while not discussed here specifically, other recent data on fish hearing (cf. Fay, this issue; Ladich, this issue; Sand, this issue) have provided additional and important insight into vertebrate hearing in general. In particular, they enable further speculation about one of the topics of most fascination to scholars interested in the auditory system—the evolution of vertebrate hearing (see Popper & Fay 1997).

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