Original Paper

Arthur N. Popper[a]
Richard R. Fay[b]

[a] Department of Zoology, University of Maryland, College Park, Md.;
[b] Department of Psychology and Parmly Hearing Institute, Loyola University of Chicago, Chicago, Ill., USA

Sound Detection and Processing by Fish: Critical Review and Major Research Questions

Abstract
The literature on fish hearing has increased significantly since our last critical review in 1973. The purpose of the current paper is to review the more recent literature and to identify those questions that need to be asked to develop a fuller understanding of the auditory capabilities and processing mechanisms of fishes. We conclude that while our understanding of fish hearing has increased substantially in the past years, there are still major gaps in what we know. In particular, the comparative functional literature is extremely limited, and we do not yet know whether different species, and particularly hearing specialists as compared to hearing nonspecialists, have fundamentally different auditory capabilities and mechanisms.

Introduction

In the 20 years since our first review of the literature on fish hearing [Popper and Fay, 1973], many new data have appeared, and new conceptions have been advanced regarding auditory mechanisms of fishes. The current paper, which is an outgrowth of a workshop on fish hearing that took place at the Airlie Conference Center (Warrenton, VA) in late October 1991, has two major purposes. First, we will provide a review of fish hearing as we now know it. The review is not intended to be exhaustive. Much of the older literature has already been reviewed in two volumes devoted to fish hearing [Schuijf and Hawkins, 1976; Tavolga et al., 1981] and in sections of two other volumes [Atema et al., 1988; Webster et al., 1992]. Specific reviews cover hearing capabilities of fishes [Popper, 1983; Fay,

1988a], peripheral structures and processing [Platt and Popper, 1981; Popper, 1983; Schellart and Popper, 1992; Popper and Platt, 1993], physiology [Fay, 1981, 1988b, 1992b], vestibular senses [Platt, 1983; Popper and Platt, 1993] and anatomy of the central nervous system [Northcutt, 1980, 1981; McCormick, 1981, 1992; McCormick and Braford, 1988]. The lateral line has been comprehensively reviewed in the papers in Coombs et al. [1989a].

The time now appears right to use the new data and theories to redefine the important questions that have yet to be answered in order to help bring our understanding of fish hearing to a level comparable to that existing for other vertebrate groups. Thus, the second purpose of this paper is to present our suggestions for areas that need to be emphasized in future studies of fish hearing.

Dr. Arthur N. Popper
Department of Zoology
University of Maryland
College Park, MD 20742 (USA)

The Octavolateralis System

Acousticolateralis vs. Octavolateralis?

Historically, the ear, lateral line, and their central pathways in teleosts have been linked together as the acousticolateralis system [reviewed by Popper et al., 1992]. The basis for this linkage has been a presumed phylogenetic relationship between the systems, including the sharing of embryonic origin, innervation, and function in hearing. However, some recent neuroanatomical evidence has argued against homology [e.g., Wever, 1974; Northcutt, 1981]. Still, there are probably functional interactions between the systems both in terms of signals detected [chapters in Coombs et al., 1989a], peripheral mechanics [e.g., Blaxter et al., 1981], and there may be overlap in central processing areas of the brain [e.g., Schellart, 1983; Schellart and Kroese, 1989; Striedter, 1991]. Since both the ear and lateral line are hair cell-based systems, and since there may be functional overlap between the systems, the term *octavolateralis* has become the preferred term to describe the combined systems and their relationship [Nieuwenhuys, 1967; Northcutt, 1981; McCormick, 1982; Popper et al., 1992].

Interactions between the Ear and Lateral Line

The functional relationship between the ear and the mechanosensory lateral line has not been fully defined. Both systems detect water motions; the lateral line is responsive to relative movement between the animal and surrounding water; the ear is responsive to the relative motion between the otolith and the fish's body, and to sound pressure. The two systems overlap in frequency range, with the lateral line responding over a frequency range of several Hz to about 200 Hz, and the ear from several Hz to several thousand Hz in some species. The source distance over which the two systems respond differs, from a body length or two for the lateral line, to considerably greater distances for the ears.

While we will not specifically discuss this in the sections that follow, there are still important questions to be asked with regard to the functional relationships between the ear and the mechanosensory lateral line. Morphologically, a number of species have intimate ties between the ear, swimbladder, and lateral line. In clupeids (herring-like fishes) for example, an extension of the ear actually terminates at a membrane entering into the lateral line canals [Blaxter et al., 1981]. The functional significance of this type of inter-connection is not known, but this could be a mechanism to stimulate the lateral line with a pressure signal mediated by the swimbladder (see section on 'Getting Sound to the Ear'). Clearly, this is an area that needs further experimental investigation, since connections of this type are not uncommon [e.g., Webb and Blum, 1990; Bleckmann et al., 1991].

Because of the functional overlap between the two systems, it is likely that there is some interaction between them in the CNS. However, while there is evidence for anatomical overlap [e.g., Schellart, 1983; Schellart et al., 1987; Striedter, 1991; Wubbels et al., 1991], the functional implications of such overlap are not known at any level of the CNS.

Acoustics

Propagated sound in any medium consists of both pressure fluctuations and particle motions. Particle motions have been classified as those occurring in the 'nearfield' and those occurring in the 'farfield'. Farfield particle motions always accompany propagated sound in a free field, and can be predicted from pressure measurements. Nearfield particle motions are hydrodynamic flows that occur near vibrating sources and attenuate rapidly (usually within one wavelength from the source), depending on whether the source is a monopole, a dipole, or a more complex type [van Bergeijk, 1967].

The distance over which nearfield particle motion exceeds farfield motion is limited to a frequency-dependent distance of wavelength/2π (approximately 1/6 of a wavelength) from a monopole source [reviewed in Kalmijn, 1988, 1989; Rogers and Cox, 1988]. The region from the source to this point has been classically called the acoustic nearfield, while the region beyond this point has been called the acoustic farfield [van Bergeijk, 1967]. It is important to understand, however, that pressure fluctuations and particle motions occur withing both the near- and farfields. It is practically impossible to predict nearfield particle motions from pressure measuremens within the nearfield.

The otolith organs of fish are capable of detecting particle motion 'directly' via the inertial response of the otoliths to motion, and 'indirectly' via the swimbaldder's fluctuating volume in a pressure field, within both the near- and farfields [e.g., Fay and Patricoski, 1980; Buwalda, 1981; Fay, 1984]. As well be discussed below, this dual sensitivity may provide the animal with valuable information about sound source characteristics, including distance and location [Buwalda, 1981; Schuijf and Hawkins, 1983; Fay, 1984; Popper et al., 1988; Rogers et al., 1988; Schellart, 1989a]. Sensitivity to both sound pressure and particle motion has made the experimental analysis of hearing in fish rather difficult, and the literature, at times, confusing.

For example, specifying a sound detection threshold in a behavioral or physiological experiment requires a determination of whether pressure or particle motion is the effective stimulus. The answer may depend upon species, frequency, distance from the source, and the characteristics of the acoustic test environment.

The results of behavioral and neurophysiological laboratory investigations of hearing by fish generally have been compromised by the very complex problems of underwater acoustics in small laboratory tanks [Parvulescu, 1964, 1967; Kalmijn, 1988; Rogers and Cox, 1988]. In small tanks, the nearby surfaces result in extensive, reflected, acoustic energy that becomes a large proportion of the total acoustic energy in the tank. These complex standing wave patterns create unpredictable, frequency-dependent nodes of pressure and particle motion. In addition, studies of sound source localization and distance perception cannot be carried out in such an acoustic environment, because the complex acoustics destroy the cues normally present in more natural environments. While such tanks can be used for experiments on thresholds and sound discrimination in a few species that are particularly sensitive to sound pressure, such as otophysans (= ostariophysans in the older literature) and mormyrids (see below), they become problematic for studies on species that are not specialized to detect sound pressure.

Since particle motion cannot be simply predicted from pressure measurements within the nearfield, both motion and pressure must be measured and independently manipulated. This has rarely been achieved in any study of fish hearing [but see van den Berg and Schuijf, 1985]. The literature contains many data and conclusions about hearing sensitivity and bandwidth that were obtained under the untested assumption that the system under investigation was pressure-sensitive [see Fay, 1988a, for a review]. We now know that some of these data and conclusions are probably wrong, and that our general understanding of hearing in fish has been limited and even confused as a result.

Methods to solve these problems could include some of the following: (a) the selection of species for study that are known to be primarily pressure-sensitive (e.g., hearing specialists) [e.g., Fay, 1969] or primarily displacement-sensitive (e.g., sculpin, flatfish, and other species lacking swimbladders) [e.g., Chapman and Sand, 1974]; (b) the routine use of underwater motion sensors for sound field calibration (e.g., acelerometers, optical motion sensors, hot-wire anemometers) [e.g., Buwalda, 1981; Coombs et al., 1989b]. These are available at present, but their proper use is not widespread; (c) the performance of behavioral and physiological hearing experiments in a natural body of water where sound source distance can be manipulated up to several meters, and sound reflections can be minimized [e.g., Chapman and Hawkins, 1973; Schuijf and Buwalda, 1975; Hawkins and Sand, 1977; Schellart and Buwalda, 1990]; and (d) the synthesizing of sound fields in the laboratory and the independent manipulation and measurement of sound pressure and particle motion [e.g., Myrberg and Spires, 1980; Buwalda, 1981].

None of these solutions is easy, and most tend to limit the questions we can reasonably ask of any given species. However, a general recognition of these problems and possible solutions are required for significant advancements in our understanding of hearing in fish.

The Diversity of Fish

The term 'fish' generally refers to all extant aquatic anamniotic vertebrates found in the taxonomic superclass Agnatha (jawless fishes), and classes Chondrichthyes (cartilaginous fishes including sharks and rays) and Osteichthyes (bony fishes). Virtually nothing is known of hearing in agnathans, and the literature on cartilaginous fishes has been reviewed recently [Corwin, 1981, 1989]. By far the greatest body of data are from the bony fishes, the primary subject of this paper.

The Osteichthyes comprise the largest of all vertebrate groups, with over 25,000 extant species [Nelson, 1984]. The taxonomic, anatomical, behavioral and physiological variation among fishes is immense and includes both the ear and the peripheral structures associated with the ear [e.g., Retzius, 1881], leading to the suggestion that various species may detect and process sound in different ways, depending upon their peripheral auditory structures, the acoustic characteristics of their usual environment, or even upon their taxonomic positions [Popper and Coombs, 1982; Popper, 1983; Schellart and Popper, 1992]. This diversity has lead several investigators to caution against referring to 'the' fish with regard to hearing or the auditory system [Platt and Popper, 1981; Schellart and Popper, 1992], since the taxa are too broad and the variations too great to permit such generalizations without our having a more comprehensive understanding of audition among fishes.

The bony fishes are divided into four subclasses, as illustrated in figure 1 [see Lauder and Liem, 1983, and Nelson, 1984, for general taxonomy]. Most of the species that have been studied with regard to hearing fall within the largest of these subclasses, the Actinopterygii. We will primarily deal

Table 1. Species referred to in text with common names and taxonomic position (see figure 1)

Species	Common Name[1]	Family[2]	Order	Swimbladder Connection	Saccular Pattern
Adioryx xantherythrus	squirrelfish	Holocentridae	Beryciformes	none	standard
Anguilla anguilla	European eel	Anguillidae	Anguilliformes	none	alternating[4]
Arius felis	marine catfish	Ariidae	Siluriformes	Weberian ossicles	vertical
Astronotus ocellatus	oscar	Cichlidae	Perciformes	none	standard
Carassius auratus	goldfish	Cyprinidae	Cypriniformes	Weberian ossicles	vertical
Colisa labiosa	thicklip gourami	Anabantidae	Perciformes	none	standard[4]
Cottus scorpius	sculpin	Cottidae	Scorpaeniformes	none	unknown[5]
Cyprinus carpio	crucian carp	Cyprinidae	Cypriniformes	Weberian ossicles	vertical
Gadus morhua	cod	Gadidae	Gadiformes	none	dual
Gnathonemus petersii	Ubangi mormyrid	Mormyridae	Osteoglossiformes	air bubble by saccule	vertical
Ictalurus punctatus	channel catfish	Ictaluridae	Siluriformes	Weberian ossicles	vertical
Limanda limanda	lemon sole	Pleuronectidae	Pleuronectiformes	no swimbladder	standard
Lota lota	burbot	Gadidae	Gadiformes	none	dual
Melanogrammus aeglefinus	haddock	Gadidae	Gadiformes	none	dual
Merluccius merluccius	European hake	Merlucciidae	Gadiformes	none	dual
Myripristis kuntee	soldierfish	Holocentridae	Beryciformes	extends to ear	opposing
Opsanus tau	oyster toadfish	Batrachoididae	Batrachoidiformes	none	standard
Pomacentrus sp.	damselfish	Pomacentridae	Perciformes	none	standard
Raja clavata[3]	thornback skate	Rajidae	Rajiformes	no swimbladder	vertical (curved)
Salmo gairdneri	rainbow trout	Salmonidae	Salmoniformes	none	standard
Scomber scomber	Atlantic mackerel	Scombridae	Perciformes	none	standard[4]

[1] Common names from Migdalski and Fichter (1976).
[2] Taxonomic positions from Nelson (1984).
[3] Chondrichthyes (cartilaginous fishes).
[4] Not studied with SEM but this is the presumed orientation pattern based upon data from closely related species.
[5] Data on hair cell orientation patterns not available for any member of this taxonomic order.

with the subdivision Teleostei, which contains over 20,000 marine and freshwater species [Nelson, 1984]. (See table 1 for the scientific and common names of all of the species discussed in this paper, along with their taxonomic positions.)

Among teleosts, the most often discussed species (with regard to hearing) are members of the series Otophysi which is part of the superorder Ostariophysi (fig. 1). The Otophysi (= otophysans) represent a group of about 6,000, mostly freshwater, species that includes the order Cypriniformes (e.g., goldfish, carp, minnows), Siluriformes (catfish), Characiformes (characins) and Gymnotiformes (knifefish). (In the older literature the otophysans are referred to as ostariophysans.) In the otophysans, the swimbladder is coupled to the inner ears via a series of bones, the Weberian ossicles. This connection is thought to enhance hearing sensitivity and bandwidth [von Frisch, 1938; Dijkgraaf, 1949; Poggendorf, 1952; Kleereloper and Roggenkamp, 1959]. All species without Weberian ossicles have been referred to by the *non-taxonomic* term 'non-oto-physans'. The superorder Ostariophysi also includes the series Anotophysi (order Gonorynchiformes) (see fig. 1), a group of fishes that have primitive Weberian ossicles [Rosen and Greenwood, 1970] but an ear that has many characteristics in common with non-otophysans [Popper and Platt, 1983].

While the otophysans have the best known adaptation for hearing, a number of other species in widely diverse taxa also have specializations that probably enhance hearing (see fig. 2 for representative audiograms). Fishes (including otophysans) having specializations that enhance hearing have been referred to as hearing 'specialists', whereas fishes that do not have such specializations are 'nonspecialists' or 'generalists'. Hearing specialists tend to have a wider hearing bandwidth and greater sensitivity than nonspecialists. The limited behavioral data suggest that frequency and intensity discrimination performance may not be as acute in nonspecialists as in specialists [Fay, 1988a; see section on 'Behavior' below].

Selected Major Fish Taxa and Their Relationships
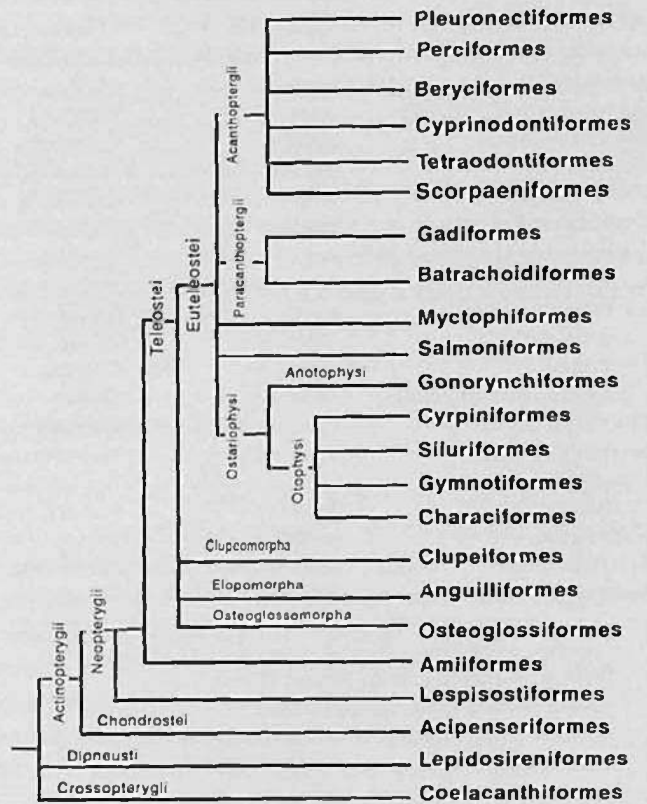
Fig. 1. Taxonomic relationships of the major orders of bony fishes cited in the paper or for which we have data on auditory system structure and/or function [see Fay, 1988a; Schellart and Popper, 1992]. Information modified from Nelson [1984]. See table 1 for species mentioned in text.

Fig. 2. Behavioral audiograms for two hearing specialists, *Carassius auratus* [goldfish; Fay, 1969], and *Myripristis kuntee* [a squirrelfish; Coombs and Popper, 1979], two nonspecialists having a swimbladder, *Adioryx xantherythrus* [another squirrelfish; Coombs and Popper, 1979], and *Astronotus ocellatus* [the oscar; Yan and Popper, 1992], and a nonspecialist without a swimbladder, *Limanda limanda* [a flatfish; Chapman and Sand, 1974]. Note that thresholds are expressed as sound pressure levels, and that this may be inappropriate for the nonspecialists if their behavioral thresholds depend on the detection of particle motion. Data are presented as threshold re: 1 μPa to follow current conventions (1 μPa = 100 dB re: 1 μbar or 1 dyne cm⁻²).
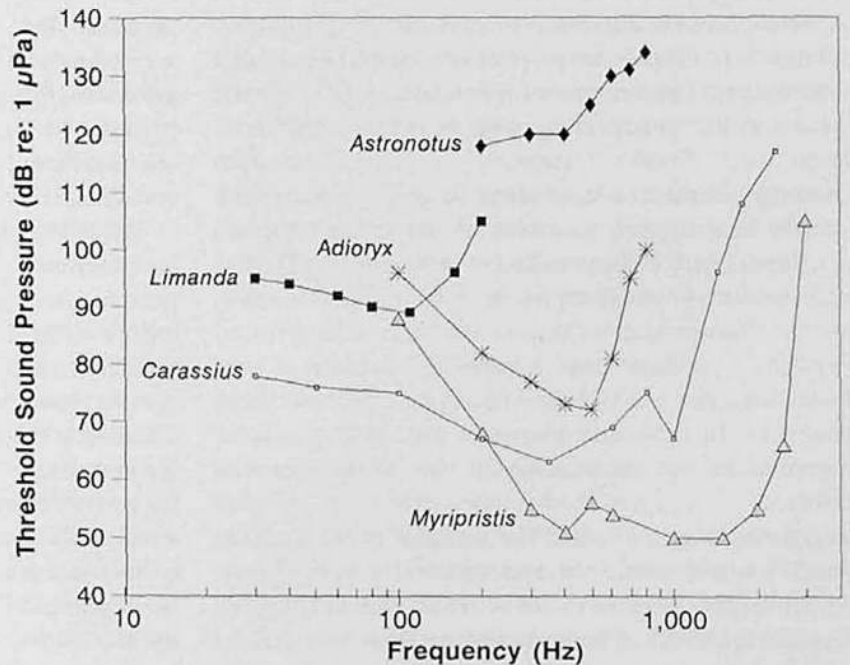
Some of the better-known hearing specialists are found among the taxonomic groups Osteoglossomorpha, Perciformes (especially the Anabantidae), Beryciformes (especially the Holocentridae), and Clupeiformes (fig. 1). Despite the taxonomic diversity among these (and other) specialists, it is often the case that these groups share similar specializations for hearing [Popper and Coombs, 1982]. For example, otophysans and mormyrids (Osteoglossiformes) have similar specialized hair cell orientation patterns in the saccule (see below), gas bladders in close mechanical contact with the ears [Popper, 1981], and similar hearing capabilities [McCormick and Popper, 1984]. Yet the species are not closely related [Lauder and Liem, 1983]. Thus, these specializations have probably arisen independently [Popper and Platt, 1983].

Even though there are hearing specialists among each of these taxonomic groups, most of these groups also contain numerous species that are nonspecialists. Thus, among the family Holocentridae (Beryciformes in fig. 1) there is a genus of hearing specialists, *Myripristis*, all of which have anterior extensions of the swimbladder that abut the ear, and a genus of nonspecialists, *Adioryx*, in which the swimbladder terminates far from the ear [Coombs and Popper, 1979] (see fig. 2). Among the Siluriformes, at least one marine species, *Arius felis*, has a greatly enlarged utricle that appears to be used for detection of low frequency sounds (100–200 Hz), while other silurids (and other otophysans) do not have the hypertrophied utricle or the excellent low frequency hearing [Poggendorf, 1952; Popper and Tavolga, 1981]. Similar differences can be found within the anabantids (Perciformes) and osteoglossids (Osteoglossiformes) where some species are hearing specialists and others are not [Coombs and Popper, 1982; Saidel and Popper, 1987]. We predict that such diversity would be found among other taxa if studied sufficiently. At the same time, it should be noted that within genera of closely related species, such as the genus *Pomacentrus* (damselfish, Perciformes), all species studied have very similar audiograms [Myrberg and Spires, 1980].

Behavior

To What do Fish Listen?

It is now well accepted that fish can hear in the general sense of the word as applied to other vertebrates [see papers in Webster et al., 1992]. Like many other vertebrates, some fishes vocalize in a variety of behavioral contexts, including courtship, mating, and agonistic interactions [e.g., Demski et al., 1973; Myrberg, 1981; Hawkins

and Myrberg, 1983; Crawford, 1991]. Clearly, vocalization mechanisms must be matched to hearing capacities for vocalization to have adaptive value. Many other species are not known to vocalize, including some that hear well (e.g., goldfish, *Carassius auratus*). Myrberg [1981] has suggested that an important function of hearing is the 'interception' of the communication sounds of other species. Although interception undoubtedly occurs, it still seems unlikely that auditory function can be fully understood only with regard to the processing of communication sounds. There must be more general functions of hearing. What are these functions?

This question is seldom asked of visual systems. Complex, biologically significant signals in the visual world are not restricted to intraspecific communication signals, but include just about every pattern of light produced or reflected from most objects in the environment. The most general function of visual systems is to image the immediate scene and resolve the individual objects within it. We believe the most general function of auditory systems is something similar. Most objects in the underwater environment scatter sound (e.g., the water surface, the bottom, the general landscape, other animals and plants), and anything that moves generates sound. An awareness of the presence and location of objects – the general structure of the environment – certainly is necessary for moment-to-moment and longer-term behavior that is appropriate for feeding, social interaction, avoiding predation, reproduction, and all the behaviors that tend to propagate the animal's genes. In our view, the most general function of hearing is not so much to decode acoustic messages as it is to identify and locate the objects (sound sources and scatterers) comprising the environment, and perhaps to form an image of the auditory scene [Bregman, 1990; also see Myrberg, 1981].

Some sound sources are relatively continuous and chaotic (e.g., water surface sounds from the wind, rain, and flowing water), while others may be brief, spectrally and temporally patterned, and may have communicative value [Schellart and Popper, 1992]. Many of these sounds may occur simultaneously and reach the ears as complex mixtures. The problem facing the ears and brain is to segregate acoustic components from the several sources into groups that belong to the appropriate source. Viewing the problem in this way, we could say that all objects that may produce or scatter sound simultaneously are equally 'biologically significant', in the sense that no source can be identified or localized without significant processing of the simultaneous sounds from the other sources.

In an analogy with vision, the 'ground' must be as well processed as the 'figure' in order for the figure to be per-

ceived as an object, and in many cases, the structure of the 'ground' helps define the 'figure' [Hebb, 1949]. In other words, both 'signals' and 'noise' require analysis, because the sources of both must be understood to some degree before the source of either one can be identified and located. The answer to the question, 'What do fish listen to?' is 'all sounds', including what is termed 'ambient noise' [Rogers, 1986; Rogers et al., 1989; Lewis and Rogers, 1992].

Behavioral Studies of Hearing

Behavioral studies of hearing in fish have been extensively reviewed recently [Fay, 1988a]. Studies have been caried out in small laboratory tanks [e.g., Fay and Coombs, 1983; Yan and Popper, 1992], in natural environments [e.g., Chapman and Hawkins, 1973; Chapman and Johnstone, 1974; Hawkins and Sand, 1977], and in controlled sound fields synthesized in the laboratory [Schuijf, 1975; Schuijf and Buwalda, 1975; Buwalda et al., 1983; Schellart and Buwalda, 1990]. Behavioral methods include classical respiratory [e.g., Fay, 1992a] and cardiac conditioning [e.g., Chapman and Hawkins, 1973], instrumental avoidance conditioning [e.g., Jacobs and Tavolga, 1967, 1968], and operant conditioning [e.g., Yan and Popper, 1992], in combination with a variety of psychophysical methods such as adaptive tracking and the method of constant stimuli. Apart from the results of experiments on hearing sensitivity, most of what we know about discrimination acuity and auditory perception in fish comes from experiments on a single species, *Carassius*.

Hearing Sensitivity and Bandwidth

Hearing sensitivity in quiet (the audiogram) has been determined for over 50 teleost and three shark species [reviewed in Fay, 1988a]. Some of these data are difficult to interpret, because we are not certain whether sound pressure or particle motion is the adequate stimulus (see section on 'Acoustics'), and in other cases we cannot be certain whether background noise may have determined thresholds. The general pattern emerging, however, is that hearing specialists detect sound pressure with greater sensitivity (as low as 55 dB re: 1 μPa, or alternatively, −45 dB re 1 dyne cm^{-2}) and in a wider bandwidth (to 3 kHz) than nonspecialists. Figure 2 includes behavioral audiograms for two hearing specialists (*Carassius* and *Myripristis kuntee*, a soldierfish), two nonspecialists that have a swimbladder (*Adioryx xantherythrus*, a squirrelfish, and *Astronotus ocellatus*, the oscar), and one nonspecialist without a swimbladder (*Limanda limanda*, the lemon sole). Note that thresholds are expressed as sound pressure levels. Use of sound

pressure is strictly correct only for the hearing specialists that have been shown to respond in proportion to sound pressure. It is not yet clear whether the thresholds for the three other species should be expressed in terms of sound pressure or particle motion amplitudes. In best absolute sensitivity, hearing specialists are similar to most other vertebrates when thresholds determined in water and air are expressed in units of acoustic intensity (in Watts · cm^{-2}).

Hearing in Noise

It is likely that most listening in the natural world takes place in the presence of multiple sound sources and against a background of detectable ambient noise [e.g., Hawkins and Chapman, 1975]. Thus, the questions of what fish hear in natural environments will be determined by the interfering effects of background sounds ('maskers') on the detection of another sound ('signal'). Masking effects on sound detection have been studied in 11 species by a variety of experimental designs [Fay, 1988a]. In general, signal detection has been shown to depend on masker level, frequency, and other characteristics. For several species, ambient noise measurements alone allow predictions of the detectability of given tone signals. All fish species investigated show the operation of psychophysically-defined 'auditory filters' [Fay, 1992a], which restrict the bandwidth of sounds interfering with the detection of designated signals. Filters with similar characteristics have been found among all vertebrates investigated [Fay, 1988b, 1992b] and are thus probably primitive features of all auditory systems. Since the detection of a given signal is likely to be determined by the presence of simultaneous, interfering sources, adaptations for sound detection sensitivity probably include strategies for grouping the sound components from individual sources, and segregating those that belong to different sources. Auditory filters are used for this sort of signal processing.

Frequency Analysis

Sound sources can often be identified on the basis of the frequency components present. The ability to determine these components, or to discriminate between sounds on the basis of frequency (frequency analysis), is present in all vertebrates investigated, including fish. As discussed above, *Carassius, Gadus morhua* (cod) and several other species appear to analyze a sound's spectrum using auditory filters. Such species have been shown to discriminate between pure tones of different frequency with an acuity in the range demonstrated by other vertebrates: 3 to 5% [Jacobs and Tavolga, 1968; Fay, 1970a, 1988a, 1989a]. We know from stimulus generalization experiments [Fay,

1970b, 1992] that *Carassius* not only can discriminate between pure tone frequencies, but also appears to order them on a perceptual continuum similar to the human perception of pitch.

Frequency discrimination abilities could arise either by processing the outputs of the peripheral filter array (i.e., in the frequency domain), or by processing inter-spike times within or between peripheral channels (i.e., in the time domain). A controversy regarding which of these processing strategies is actually used by nervous systems has been the basis of auditory theory applied to human hearing for over a century [Wever, 1949]. Studies of frequency analysis in fish have played a part in this issue, because fish lack a basilar membrane-like structure and thus were not expected to show peripheral mechanical filtering of the type observed in most terrestrial vertebrates [von Frisch, 1938; van Bergeijk, 1967]. A demonstration of frequency discrimination in fish was thought to favor an explanation for frequency analysis based on time-domain processing [e.g., Fay, 1970a]. Neurophysiological studies (see below) have clearly demonstrated crude frequency selectivity in primary afferent fibers of the saccule of *Carassius* [Furukawa and Ishii, 1967; Fay and Ream, 1986], and an apparent sharpening or enhancement of this selectivity at the level of the midbrain [e.g., Lu and Fay, 1992]. There is, at present, no direct evidence that sound qualities such as pitch are processed in the time domain, and, thus, the fundamental controversy on the neural mechanisms underlying behaviorally defined frequency analysis remains for all vertebrates, including fish.

Sound Level Processing

The ability to detect a change in the overall level of a sound is a simple yet important hearing function for all animals. Not only does this ability seem to have obvious survival value (e.g., its role in the perception of source distance and changes in distance), but is also a most important component in the identification of sources through their characteristic spectral shapes (e.g., perceiving the relative amplitudes of multiple frequency components). Level discrimination also plays an important role in the detection of sound in noisy backgrounds, since detection may be a decision about an increment in level within one or several peripheral auditory filters.

Level discrimination has been extensively studied in *Carassius* [Jacobs and Tavolga, 1967; Fay, 1980, 1985, 1989b, 1992a], and in *Gadus* and the haddock *Melanogrammus aeglefinus* [Chapman and Johnstone, 1974]. Recent results on *Carassius* show that level discrimination thresholds are as low as 1.5 dB, are generally independent of frequency, and improve with overall level and signal duration. These patterns of level discrimination are similar to those for all other vertebrates investigated, including several mammals and birds. Thus, at present there are no indications of specially adapted mechanisms for level discrimination, and no reasons to believe that this hearing capacity has changed significantly during vertebrate evolution.

Temporal Pattern Processing

Most sounds have time-varying characteristics such as overall envelope, the envelopes of individual frequency components, patterns of level and frequency fluctuation, and waveform structure represented in the time-domain. The time patterns of envelope and waveform fluctuation are probably important for the detection, identification, and classification of sound sources, and for information-bearing features of fish vocalizations [Myrberg et al., 1978; Spanier, 1979; Crawford, 1991]; they are likely to be used in individual recognition as well [Myrberg and Riggio, 1985].

Temporal processing has been studied using psychophysical methods in *Carassius* in terms of the minimum detectable silent gap in continuous noise [Fay, 1985], the sensitivity with which rapid variations in the envelope of a continuous noise or tone can be detected [Fay, 1980], and the acuity with which small changes in temporal interval can be processed [Fay, 1982; Fay and Passow, 1982]. In addition, thresholds for detecting a brief sound, as studied in *Carassius* and *Gadus*, tend to decline as sound duration increases to several hundred milliseconds. Temporal integration such as this is a characteristic of all vertebrate species studied [Fay, 1988a]. In general, temporal processing in fishes is limited by their rather restricted low-frequency hearing range, but in some respects the temporal processing capabilities of fishes are well within the range expected for vertebrates [Fay, 1992a].

Sound Source Localization

The ability to locate sound sources is probably one of the most important functions served by auditory systems among all animals. While most vertebrates have solved many of the same problems in hearing, the mechanisms and structures comprising these solutions may differ across taxa. Among terrestrial animals, the differences between sounds reaching the two ears are cues for determining the direction to the source, at least in the horizontal plane. Among some amphibians, reptiles and birds, however, the ears may function as pressure-gradient receivers [reviewed in Fay and Feng, 1987], each with its own directional sensi-

tivity function. In most mammals, individual ears are also directional receivers by virtue of their directional filtering of complex spectra. These properties permit vertical localization and may aid in azimuthal localization.

Behavioral data on sound localization by fishes are extremely limited, in part due to the difficulties in developing arenas in which to set up an appropriate acoustic stimulus [see Schuijf, 1975; Buwalda, 1981]. The available data, however, do demonstrate that some species of fish are capable of localizing sources with an accuracy of 10 to 20 degrees in both azimuth and elevation [Chapman and Johnstone, 1974; Schuijf, 1975; Hawkins and Sand, 1977; Buwalda, 1981], that otophysans may be capable of localization [Schuijf et al., 1977], and that codfish are able to discriminate between sources differing only in distance [Schuijf and Hawkins, 1983].

Despite the substantial increase in our knowledge of sound localization capabilities over the past 20 years there is still a paucity of data on this very fundamental aspect of hearing. The stimulus conditions required for sound localization behavior, the cues used, and the neural mechanisms underlying directional hearing in fish are not known [but see Buwalda, 1981; Schuijf, 1981; Popper et al., 1988; Schellart, 1989a]. A few of the specific questions that need to be asked include: (1) How well do fishes localize noises and other biologically relevant sounds such as pulsed signals? Most of the data are for pure tones, while biologically relevant signals are broad-band signals that may be more difficult to localize [see Schellart and Popper, 1992]; (2) Can hearing nonspecialists localize as well as specialists? There may be differences in localization capabilities, since specialists have both pressure and particle displacement cues, while only the latter are available to nonspecialists [see Buwalda, 1981; Schuijf, 1981; Popper et al., 1988; Schellart, 1989a; Schellart and Popper, 1992]; (3) Do otophysans localize as well as other hearing specialists? Differences between these fishes may be present, since the otic end organs involved in hearing may differ; (4) What are the central mechanisms involved in localization, and are these the same in otophysans, non-otophysan specialists, and nonspecialists [see Buwalda, 1981; Popper et al., 1988; Rogers et al., 1988]? Finally, (5) how well do various species determine sound source distance?

*Determining the Nature of a Sound Source*
The sense of hearing informs listeners about the existence, spatial location, and identity of sound sources. Perceiving one sound source among many requires that the several frequency components of a single source be recognized as a group that belongs together. At the same time,

correctly identifying a sound source requires information about the individual frequency components belonging to the source. Thus, listening is simultaneously synthetic (grouping components belonging to a single source) and analytic (analyzing the individual components making up the group) [e.g., Hartman, 1988]. This is the essential problem for hearing in general, and it seems likely that all vertebrate auditory systems function, to some degree, both to group and to analyze simultaneously the frequency components of complex sounds so that their sources may be correctly determined. To what extent do fish listen analytically and synthetically to determine underwater sound sources?

All vertebrate animals investigated are able to discriminate between successive sounds of different frequency or spectral patterns (see above). Only for *Carassius*, however, is there behavioral evidence that a species may be able to identify, or 'hear out', the individual frequency components making up complex sounds: that is, to listen analytically [Fay, 1992a]. (Similar questions have not been asked of other fish species!) In these behavioral experiments, animals were classically conditioned to respond to a two-tone complex, and then tested for response to novel pure tones, including those making up the conditioning complex. Animals responded (generalized) to the pure tone frequencies making up the conditioning complex more than to other frequencies. Thus, *Carassius* can acquire independent information about the simultaneous frequency components of a complex sound mixture, and can listen analytically.

An earlier study using similar methods demonstrated that *Carassius* is also capable of a sort of synthetic listening [Fay, 1971]. In this experiment, animals were conditioned to respond to a 40 Hz pure tone and then tested with a 1 kHz tone that was amplitude modulated at various rates at and near 40 Hz. In this case, responses were greatest to a 40 Hz modulation, and declined for modulation rates above and below 40 Hz. This generalization gradient demonstrated the near equivalence of pure tone and envelope periodicity (i.e., 'periodicity pitch').

Perhaps the most significant generalization from the behavioral work reviewed in this section has been that in spite of wide differences in habitat, inner ear structure, and taxonomic grade, all vertebrates including fishes (at least hearing specialists!) appear to have solved many of the same general problems of auditory perception. However, as discussed below, the structures and possibly the mechanisms underlying these solutions may differ among species.
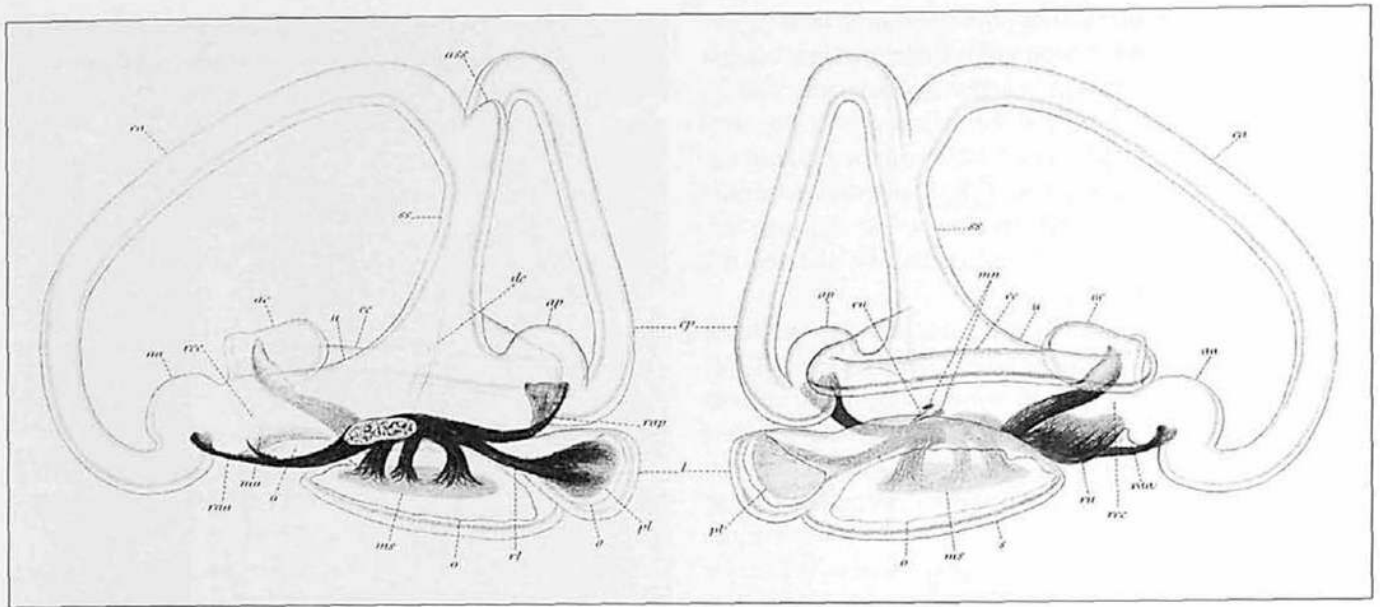
Fig. 3. Schematic illustration of the ear of a teleost fish. *Scomber scomber* (Atlantic mackerel), as illustrated by Retzius [1881]. Medial view on the left, lateral view on the right. aa, ac, ap = cristae of anterior, horizontal and posterior semicircular canals; ass = apex of crus commune; ca, ce, 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, rrc, rt, ru, rua = rami of eighth nerve to various end organs; s = saccule; ss = crus commune; u = utricle.

The Periphery

Ear Structure

The ears of bony fishes consist of three semicircular canals and three otolith organs, the saccule, utricle, and lagena (fig. 3). Some species have a seventh end organ, the macula neglecta (see lateral view of *Scomber scomber*, the Atlantic mackerel, in fig. 3), but the function of this generally diminutive structure is unknown in bony fishes [see discussion in Corwin, 1981, 1989, regarding cartilaginous fishes]. Historically, the semicircular canals and utricle were presumed to be involved in vestibular senses, and the saccule and lagena in audition [e.g., von Frisch, 1938; Dijkgraaf, 1949; reviewed in Platt, 1983; Popper and Platt, 1993]. Investigations over the past 15 years, however, have lead to the suggestion that there is substantial functional overlap, at least among the three otolith organs [Popper et al., 1982; Schellart and Popper, 1992].

Each of the otolith organs has a sensory epithelium (often referred to as the 'macula') which lies in close contact with a dense calcareous structure, the otolith. Unlike the otoliths in primitive bony fishes and in cartilaginous fishes, the otoliths in teleosts are a single structure rather than a gelatinous mass containing otoconial particles [Carlström, 1963].

The sensory epithelium contains numerous sensory hair cells (fig. 4) that are similar to those found in the lateral line of fishes as well as the ears of terrestrial vertebrates [e.g., Wersäll, 1960; Flock, 1971]. The hair cells have the typical apical ciliary bundle which projects into the lumen of the end organ. The otolith and sensory epithelium are coupled together by a thin, gelatinous, otolith membrane in which the cilia are embedded. Although little is known about the mechanical properties of the otolith membrane due to its fragile nature [but see Dunkelberger et al., 1980], it should serve to restrict the range of motion of the otolith relative to the epithelium.

Scanning electron microscopy of the sensory hair cells has revealed two critical findings, one regarding the length of the cilia in different epithelial regions and the second regarding how the cilia are oriented. First, the lengths of the ciliary bundles vary in different end organs, and even within different regions of the same end organ [e.g., Platt and Popper, 1981, 1984]. The longest ciliary bundles are often found at the edges of the epithelium, while shorter bundles tend to be more centrally located [e.g., Popper, 1977, 1981, 1983].

The second major finding is that hair cells occur in groups having similar morphological orientations, and that each epithelium may be divided into regions defined by the

hair cell orientation groups (fig. 5). Orientation of hair cells is defined in terms of the morphology of the ciliary bundle (fig. 4). Each ciliary bundle contains a single true cilium, the kinocilium, and a large number of microvillus-like stereocilia. The kinocilium is always located at one side of the ciliary bundle, and the lengths of the stereocilia generally decrease away from the kinocilium. A line through the kinocilium and bisecting the ciliary bundle defines the orientation axis of the hair cell.

Morphological polarization of hair cells is correlated with their physiological polarization [e.g., Flock, 1971; Hudspeth and Corey, 1977]. Recordings from hair cells or from primary afferents have shown that the greatest response occurs when the ciliary bundle is bent along the orientation axis toward the kinocilium. Displacement in other directions produces a response that is a cosine function of the direction of displacement relative to the major axis of the bundle [e.g., Flock, 1971; Hudspeth, 1985]. As a result of the physiological polarization, each individual hair cells is directionally sensitive to motion stimuli.

As a relative motion occurs between the otolith and underlying sensory epithelium, arrays of differently-oriented hair cells from the three otolith organs of both ears will provide the CNS with detailed information about the direction and pathway of motion [e.g., Schuijf, 1981; Buwalda, 1981; Platt and Popper, 1981; Popper et al., 1982; Fay, 1984; Schellart and Popper, 1992]. The functional significance of this input will be discussed below.

Diversity Among Fish Ears

Inter-specific diversity in the structure of fish ears is quite extensive [see reviews in Retzius, 1881; Platt and Popper, 1981; Popper and Coombs, 1982; Popper, 1983; Schellart and Popper, 1992; Popper and Platt, 1993]. Otolith shape and size vary considerably among species [e.g., Platt and Popper, 1981; Popper, 1983]. Thus, different acoustic signals may result in different motions of the otoliths relative to the sensory epithelium [Popper et al., 1982]. The precise pattern of motion (or orbital) is likely to be affected by characteristics of the otolith, including its mass and center of gravity. Thus, differently shaped otoliths should potentially have different orbitals [Popper et al., 1982; Schellart and de Munck, 1987]. However, with the exception of one study [Sand and Michelsen, 1978], otolith motion to sound stimuli has never been directly observed.

Diversity is particularly apparent in the hair cell orientation patterns of the ear, especially in those end organs associated with audition [Platt and Popper, 1981]. The saccular macula in most non-otophysan teleosts (with the known
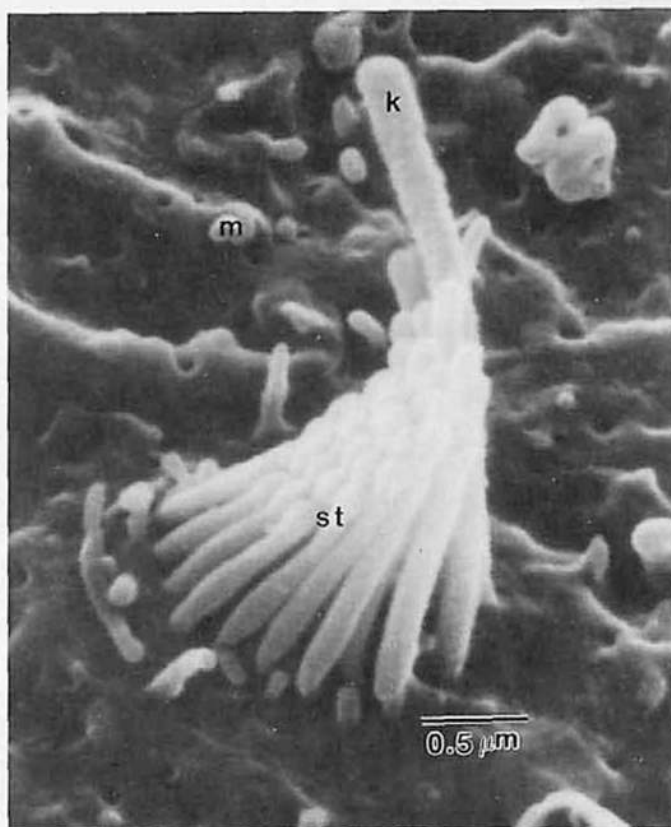

Fig. 4. Scanning electron micrograph of the saccular sensory epithelium of the burbot, *Lota lota*. The photo shows a ciliary bundle on a sensory hair cell. The cell is oriented so that the kinocilium (K) is towards the right. M = microvilli; St = stereocilia.

exception of the mormyrids) has hair cells organized into four discrete groups (or quadrants), with two groups oriented on the rostral-caudal axis and two on the dorsal-ventral axis (fig. 5). In contrast, the saccular epithelium in the otophysans (and the mormyrids) has only two groups, one oriented dorsally and the other ventrally (vertical pattern in fig. 5). Within the four-quadrant pattern of the non-otophysans, there is some variation, but in each case where variation from the most common ('standard') pattern occurs, the end organ always has an intimate connection to a swimbladder or to some other air bubble. This correlation suggests that these orientation patterns are associated with specializations for detecting sound pressure [Popper and Coombs, 1982; Schellart and Popper, 1992].

Some species of clupeids (herrings and relatives) and the marine catfish, *Arius*, have specializations of the utricle rather than, or in addition to, specializations of the saccule [Blaxter et al., 1981; Popper and Tavolga, 1981]. This is in
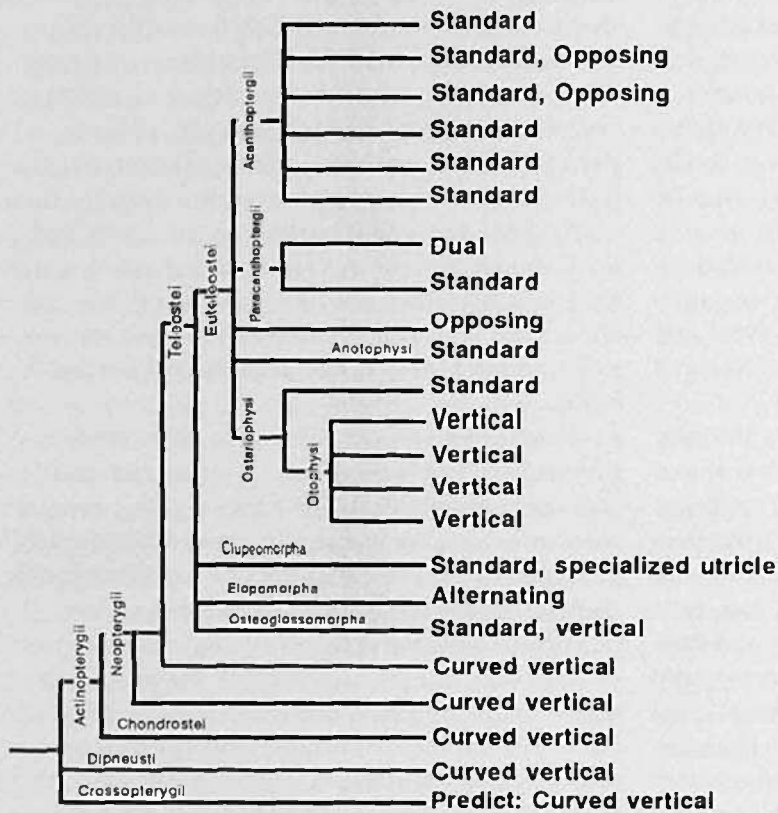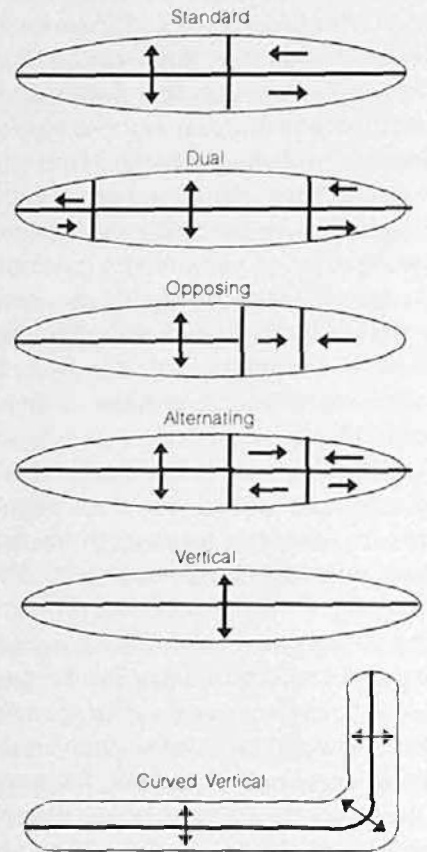
Fig. 5. Six different saccular hair cell orientation patterns found among bony fishes are shown on the right. The distribution of these patterns among the various taxa is shown in the outline on the left which is modified from figure 1. Each of the saccular hair cell orientation patterns are divided into regions, with all of the sensory hair cells in each region being oriented in the same direction (see fig. 4). The arrow in each region (regions are separated by solid lines) indicates the orientation of the kinocilium relative to the stereocilia on all of the hair cells in a particular region.

The curved vertical pattern is found in non-teleost actinopterygians [e.g. Popper, 1978] as well as in lungfish (Dipneusti) [A.N. Popper, unpubl. observ.]. While data are not available for the Crossopterygii, which includes the coelacanth (*Latimeria*), preliminary examination of tissue from that species suggests that it has the vertical (curved) pattern [A.N. Popper and C. Platt, unpubl. observ.]. Based upon a few species, it appears that cartilaginous fishes have the curved vertical pattern [e.g. Corwin, 1981, 1989].

contrast to the normally conservative structure of the utricle in other vertebrates [Platt, 1983; Popper and Platt, 1993]. Specializations of hair cell orientation patterns appear to be closely associated with enhanced hearing, regardless of which end organ is involved [Popper and Coombs, 1982; Schellart and Popper, 1992].

Given the diversity of ear structures, hair cell orientation patterns, and hearing capabilities observed among fishes, a most important question concerns the functional significance of morphological differences and the extent to which one can generalize among species regarding the mechanisms underlying hearing abilities. Does the diversity we encounter suggest that different species accomplish the same acoustic task in different ways, or does it suggest that different species do different things acoustically?