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

Key Words

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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.

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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; Tavalga 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 [Piatt and Popper, 1981; Popper, 1983; Schellart and Popper, 1992; Popper and Piatt, 1993], physiology [Fay, 1981, 1988b, 1992b], vestibular senses [Piatt, 1983; Popper and Piatt, 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.

The Octavolateralis System

Acousticolateralis vs. Octavolateralis?

Historically, the ear, lateral line, and their central pathways in teleosts have been linked together as the acoustico-lateralis 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

1 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 sig-l nal 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/2 π , (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 within both the near- and farfields. It is practically impossible to predict nearfield particle motions from pressure measurements 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 swimbladder's fluctuating volume in a pressure field, within both the near- and farfields [e.g., Fay and Patricoski, 1980; Buwalda, 1981; Fay, 1984]. As will 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.

15

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 swim-bladders) [e.g., Chapman and Sand, 1974]; (b) the routine use of underwater motion sensors for sound field calibration (e.g., accelerometers, 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 (jawl⁶⁵⁵ 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 [Piatt 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

16

Popper/Fay

Sound Detection and Processing by

Fish

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

Species

Common Name

Family²

Order

Swimbladder

Sacculus

Connection

Pattern

Adioryx xantherythrus

squirrel fish

Holocentridae

Beryciformes

none

standard

■ Anguilla anguilla

European eel

Anguillidae

Anguilliformes

none

alternating

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
Cottus scorpius
sculpin
Cottidae
Scorpaeni formes
none
unknown
Cyprinus carpio
crucian carp
Cyprinidae
Cypriniformes
Weberian ossicles
vertical
Gadus morhua
cod
Gadidae
Gadiformes
none
dual
Gnathonemus petisii
Ubangi mormyrid
Mormyridae
Os teoglossiformes
air bubble by saccule
vertical
Ictalurus punctatus
channel catfish
Ictaluridae
Siluriformes
Weberian ossicles
vertical
Limanda limanda
lemon sole
Pleuronectidae
Pleuronecti formes
no swimbladder
standard
Lota lota
burbot
Gadidae
Gadiformes
none
dual
Melanogrammus aeglefinus
haddock
Gadidae
Gadiformes
none
dual
Merluccius merluccius
European hake
Merluccidae
Gadiformes
none
dual

Myripristis kuntee
 soldicrfish
 Holocentridae
 Beryciformes
 extends to ear
 opposing
 Opsanus tau
 oyster toadfish
 Batrachoididae
 Batrachoidi formes
 none
 standard
 Pomacentrus sp.
 damselfish
 Pomacentridae
 Perciformes
 none
 standard
 Raja clavata
 thornback skate
 Rajidae
 Raj i formes
 no swimbladder
 vertical (curved)
 Salmo gairdneri
 rainbow trout
 Salmonidae
 Sal m on i formes
 none
 standard
 Scomber scomber
 Atlantic mackerel
 Scombridae
 Perciformes
 none
 standard

¹ Common names from Migdalski and Fichter (1976). Taxonomic positions from Nelson (1984). Chondrichthyes (cartilaginous fishes).

Not studied with SEM but this is the presumed orientation pattern based upon data from closely related species. 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-otophysans*'. The superorder Ostariophysi also includes the series Anotophysyi (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 Piatt, 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].

17
Selected Major Fish Taxa and Their Relationships

- Pleuronectiformes Perciformes
- Beryciformes Cyprinodontiformes Tetraodontiformes Scorpaeniformes
- Gadiformes Batrachoidiformes
- Myctophiformes
- Salmoniformes
- Gonorynchiformes
- Cypriniformes
- Siluriformes
- Gymnotiformes
- Characiformes
- Clupeiformes Anguilliformes
- Osteoglossiformes
- Amiiformes
- Leptostostiformes
- Acipenseriformes
- Lepidosireniformes
- Coelacanthiformes

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.

Astronotus
60
Myripristis
50

Fig. 2. Behavioral audiograms for two hearing specialists, *Carassius auratus* [goldfish; Fay, 1969], and *Myripristis kuntzei* [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 1 uPa to follow current conventions (1 uPa=100 dB re: 1 uPa or 1 dyne cm⁻²).

m 140

o.
5. 130

o 120

m

H, no

100

90

80

70

C 3 0 ∞

"5

>

0)

re:

10

*Limanda**Carassius**100 **Frequency (Hz)**

1,000

Popper/Fay

Sound Detection and Processing by Fish

Some of the better-known hearing specialists are found among the taxonomic groups Osteoglossomorpha, Perci-formes (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 Piatt, 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 swim-bladder 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 Tavalga, 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; Sai-del 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 carried 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 Tavalga, 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 uPa, or alternatively, -45 dB re 1 dyne cm⁻¹) 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 (*Adioryxantherythrus*, 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 • cm²).

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 Tavalga, 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 Tavalga, 1967; Fay, 1980, 1985, 1989b, 1992a], and in *Gadus* and the haddock *Melano-grammus 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—utricle epithelium; o=otolith; pi = lagena epithelium; raa, rap, rl,m,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; Dijk-graaf, 1949; reviewed in Piatt, 1983; Popper and Piatt, 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 [Carlstrom, 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., Wersall, 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., Piatt 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 cell 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; Piatt 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; Piatt and Popper, 1981; Popper and Coombs, 1982; Popper, 1983; Schellart and Popper, 1992; Popper and Piatt, 1993]. Otolith shape and size vary considerably among species [e.g., Piatt 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 [Piatt 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-otophy-sans, 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 swim-bladder 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

Orientation Patterns

Chondrostel

DipneuBtl

Cfofleopieryall

Standard

Standard, Opposing Standard, Opposing Standard , Standard .Standard

Dual Standard

_____ Opposing

Anotophysl Standard

« Standard

----- Vertical

— Vertical

----- **Vertical**

----- **Vertical**

Standard, specialized utricle

Alternating

Standard, vertical

Curved vertical •Curved vertical Curved vertical Curved vertical Predict: Curved vertical

!

Dual

Opposing

Alternating

vertical

Curved Vertical

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. Piatt, 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 [Piatt, 1983; Popper and Piatt, 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?

25

Regional Responses of Otic End Organs Early investigators of fish ears suggested that each of the otic end organs subserves a single sensory modality and that there is a generally uniform response within each end organ [reviewed in Piatt and Popper, 1981]. Von Frisch [1938] and Dijkgraaf [1949] suggested that the saccule is the primary auditory organ, that the utricle is the primary vestibular otolith end organ, and that the lagena's function is unclear but probably auditory. More recently, hypotheses have arisen that each otic end organ may have both vestibular and auditory functions and that there may even be regionalization of intra-modal function within an end organ. For example, the saccule may respond to both auditory and vestibular stimuli, with different regions responding best to different frequencies [e.g., Enger, 1981] and different directions of particle motion [e.g., Piatt and Popper, 1981]. Although it is not yet possible to relate specific functions to specific ear regions, several investigations provide evidence for variation in response within individual epithelia: (a) hair cell orientation patterns [e.g., Piatt, 1977; Popper, 1977, 1981]; (b) lengths of cilia on hair cells and related tuning properties from epithelial regions with hair cells having different length ciliary bundles [e.g., Piatt and Popper, 1984]; (c) the presence of at least two physiologically distinct hair cell 'types' within individual end organs [e.g., Sugihara and Furukawa, 1989; Steinacker and Romero, 1992]; and (d) the presence of two ultrastructurally distinct hair cell 'types' within a single end organ [e.g., Chang et al., 1992]. Indirect evidence supporting this hypothesis also comes from studies showing that there are clear regional differences in innervation in the various otic end organs [e.g., Bell, 1981; Wegner, 1982; Saidel and Popper, 1983; Mathiesen and Popper, 1987; Popper and Saidel, 1990; Presson et al., 1992], suggesting differences in peripheral processing or central projections (see section on Innervation below). The bulk of the experimental data supporting this argument comes from just a few species (primarily the otophysan *Carassius* and three non-otophysans, *Astronotus*, *Gnathonemus petersii* and *Opsanus*). More extensive corroborative studies are needed.

Hair cell orientation patterns probably result in each epithelial region being responsive to motions along different axes [e.g., Schuijf and Buwalda, 1980; Fay, 1984; Schellart and Popper, 1992], thereby providing a fish with information about sound source direction [e.g., Schellart and Popper, 1992]. Variations in ciliary bundle length are related, at least in tetrapods, to differences in frequency response properties of the hair cells [e.g., Frishkopf and DeRosier, 1983]. Thus, fish end organs having variation in ciliary bundle length may have some crude frequency mapping along a particular end organ. However, with the exception of a single study using intense tonal stimulation to damage sensory hair cells [Enger, 1981], this has not

been explored directly. Less direct studies, investigating the response properties of eighth nerve fibers from rostral and caudal regions of the saccular macula in the otophysans *Carassius* and *Ictalurus punctatus* (channel catfish) support such a notion [Furukawa and Ishii, 1967; Moeng and Popper, 1984]. In these studies, primary afferents from the rostral saccule had higher best frequencies than those from the caudal end. The ciliary bundles on the rostral end of the epithelium in both species are short, a characteristic associated with high frequency response in other vertebrates, while those at the caudal end are long, a characteristic associated with response to low frequencies [Piatt and Popper, 1984].

Investigations on *Astronotus* suggest the presence of two distinct 'types' of hair cells in the utricle and, possibly, the saccule. Hair cells located in a region of the utricle known as the striola are immunoreactive to an antibody of S-100, a calcium-binding protein [Saidel et al., 1990a]; they are damaged by the ototoxic drug gentamicin sulphate [Yan et al., 1991; Lombarte et al., 1993]; and they are innervated by large diameter primary afferents having spike-initiating membrane near the hair cells [Saidel et al., 1990b]. Outside the striola (in the extrastriolar region), hair cells do not react to the S-100 antibody and are not sensitive to gentamicin, and the spike-initiating zones of the smaller diameter afferent fibers are below the epithelium. Transmission electron microscopy demonstrated that striolar cells have a number of organelles that are absent or substantially different in extrastriolar hair cells [Chang et al., 1992].

The conclusion from these studies has been that *Astronotus*, as amniotes, has two ultrastructurally distinct types of sensory hair cells rather than the single type II hair cell proposed by earlier investigators [e.g., Wersall, 1960]. Moreover, it is evident that the extrastriolar hair cells in the utricle of *Astronotus* closely resemble amniote type II cells and that the striolar hair cells are much like amniote type I hair cells [Chang et al., 1992]. They have been given the name 'type I-like'. While data are less extensive, it appears that both the saccule and lagena of *Astronotus* have both types of hair cells [Saidel et al., 1990a; Popper et al., 1992]. Considering that type I and type II hair cells in amniotes may be functionally distinct [e.g., Correia and Long, 1990], it is reasonable to speculate that the two types of hair cells in *Astronotus* also have different physiological response properties [Chang et al., 1992]. These data support the hypothesis that there is multi-functionality within the otic

26

Popper/Fay

Sound Detection and Processing by Fish

end organs of at least one species of fish. The specific functional significance of this finding is not yet apparent.

Physiological response properties have been studied in hair cells isolated from the saccules of two fishes: a hearing specialist, *Carassius* [Sugihara and Furukawa, 1989], and a nonspecialist, *Opsanus* [Steinacker and Romero, 1992]. Both studies have focused on the voltage- and calcium-dependent ionic conductances of the basolateral hair cell membrane and have identified calcium currents and several potassium currents. Some cells of *Carassius* have a voltage-dependent sodium conductance as well. In current clamp experiments, current steps evoke oscillating (resonant) voltage responses in some hair cells, and single initial spikes in others. These different voltage responses can be attributed to different ionic conductances.

In turtles [Crawford and Fetipace, 1981], the tuning of cochlear nerve fibers depends strongly on the electrical tuning of the hair cell membrane. At present, however, it seems unlikely that the resonant behavior of saccular hair cells in fishes determines the tuning characteristics of primary afferents. For example, there is no clear correspondence in the saccule of *Carassius* between the low resonant frequencies of isolated hair cells [Sugihara and Furukawa, 1989] and the characteristic frequencies of tuned saccular fibers [Fay and Ream, 1986]. Thus, electrical resonance of the hair cell membrane in *Carassius* may not be important in determining acoustic tuning.

In *Carassius*, spiking saccular hair cells come primarily from the rostral portion of the saccule, which is the region that responds to higher frequencies [Furukawa and Ishii, 1967] and has shorter ciliary bundles than the caudal region [Piatt, 1977; Piatt and Popper, 1984]. In *Opsanus*, no clear regionalization of response types was found [Steinacker and Romero, 1992].

The physiological data support the argument that there are multiple hair cell types within single end organs. However, it will be critical to obtain both ultrastructural and physiological data from a single species in order to determine if the physiological responses as determined in *Opsanus* and *Carassius* can be correlated with the immunocyto-chemical and ultrastructural data obtained from *Astronotus*. The significance for hearing of multiple hair cell types within a single end organ is not known, but these results suggest that the response properties of the ears of fishes are more complex than previously suspected.

Getting Sound to the Ear

Although it is clear that sound is transduced by the otolith organs of the inner ear, we have little more than speculation on the pathways of acoustic input to the ear. We

believe, for example, that in the hearing specialists, one or more of the otolith organs may respond to sound pressure as well as to acoustic particle motion. The response to sound pressure is thought to be mediated by mechanical coupling between the swimbladder or other bubble of air, and the inner ear. With this coupling, the motion of the swimbladder, as it expands and contracts in a pressure field, is brought to bear on the ear. In nonspecialists, however, the lack of a swimbladder, or its lack of coupling to the ear, probably results in substantial attenuation of the signal and little stimulation of the inner ear via the pressure pathway.

The function of the coupling mechanisms has not been explored since the 1950's when Poggendorf [1952] and Kleerekoper and Roggenkamp [1959] did extirpation experiments to test the function of the Weberian ossicles in catfish. While these experiments demonstrated that loss of the Weberian ossicles results in decrease in sensitivity and bandwidth, the specific contribution of the ossicles to hearing was not examined. Significant remaining questions include the gain of the Weberian ossicles and their response characteristics.

Similar questions arise with regard to the swimbladder. A few experimental studies [e.g., Sand and Enger, 1973; Popper, 1974] showed that the resonance frequency of the swimbladder is considerably above the frequency of best hearing and thus probably does not determine the shape of the audiogram. At the same time, we do not know the extent to which the dimensions of the swimbladder determine the audiogram for species in which the swimbladder projects directly to the ear (e.g., some squirrelfish, clupeids), or in species having complexly shaped swimbladders.

The presence of both direct and indirect stimuli to the ear may provide rich information to the animal for identifying the characteristics of sound sources [Fay, 1984; Popper et al., 1988; Rogers et al., 1988; Buwalda, 1981; Schellart, 1989a; Schellart and Popper, 1992]. In nonspecialists having relatively little input to the ears from the indirect pressure pathway, the information encoded at the ears is probably different than in hearing specialists. Questions arise, therefore, concerning the specific hearing capabilities of specialists and nonspecialists and whether there are fundamental differences in how they perform sound detection and processing.

Peripheral Neurophysiology

Primary afferents from one or more otolith organs carry coded information about the sound waveform to the brain. The saccule has been considered the primary sound recep-

27

Combined

Response Area

CF = 100 to 200 Hz

CF = 350 to 450 Hz

U220

/*•

* *

Fig. 6. Response areas (top) and frequency-threshold (tuning) curves for three representative fibers of the auditory (saccular) nerve of *Carassius* (U122, U220-dotted, and U41). In the top frame, each line connects spike rates obtained at the same sound pressure level, in 5-dB steps. Response areas have been normalized with respect to the maximum spike rate for each fiber. Curves in the bottom frame were obtained using a statistical criterion for threshold. These represent the three groups of tuned fibers with CFs in the range of 200, 500, and 1000 Hz [Fay and Ream, 1986]. Note that while each fiber can be unambiguously classified in terms of characteristic frequency (CF), the frequency selectivity of the tuning curves is poor, and all moderate-level tones between 200 and 800 Hz (the entire range of best hearing of this species) will stimulate fibers of all three types. [Unpubl. data from experiments reported in Fay, 1990, 1991.]

tor organ in many fish species [Fay, 1981], particularly the otophysans such as *Carassius*. We understand the hearing functions of the saccule in *Carassius* and the response properties of the saccular nerve relatively well, because it responds primarily to sound pressure, a quantity easily manipulated and measured in the lab. The responses of primary otolith organ afferents in response to sound have been studied in *Ictalurus* [Moeng and Popper, 1984], *Gadus* [Horner et al., 1981], *Cottus scorpius* (sculpin) [Enger, 1963], *Opsanus* [Fine, 1981] and *Carassius*. Most of what we know about saccular nerve physiology comes from studies of *Carassius*.

Neurophysiological studies on the saccular nerve of *Carassius* were begun by Furukawa and Ishii [1967] and have been continued by these investigators for over 25 years with a focus on the mechanisms of the synapses between saccular hair cells and primary afferents [e.g., Furukawa, 1978; Furukawa et al., 1978; Kyogoku et al., 1986]. A series of studies using more natural underwater sound stimulation [e.g., Fay, 1978a, 1980, 1984, 1985, 1990, 1991; Fay and Ream, 1986, 1992] has focused on the encoding of acoustic information using complex as well as simple stimuli.

Primary afferents from otolith endorgans in all species studied show at least four patterns of spontaneous activity (silent, regular, irregular, and bursting), and robust phase-locking. In the hearing nonspecialists studied (*Gadus*, *Cottus*, and *Opsanus*), fibers are relatively homogeneous in having lowest thresholds at 200 Hz or below. The two oto-physi studied (*Carassius* and *Ictalurus*) show more complexity with at least three populations of fibers with characteristic frequencies (CF) in the 200, 500, and 1,000 Hz range. The majority of fibers have Q_{10} dB values below 1.0 (indicating poor quality tuning), independent of center frequency. Figure 6 shows representative tuning curves for several saccular fibers from *Carassius*. The mechanisms underlying this frequency selectivity are not known, although it is probably not due to hair cell resonance [Sugi-hara and Furukawa, 1989].

In spite of some degree of peripheral frequency analysis revealed in iso-response tuning curves, tones at levels 20 to 30 dB above best threshold tend to stimulate fibers of all CF classifications. Although some peripheral selectivity is rescued by suppression mechanisms [Fay, 1990], peripheral frequency analysis is rather poor and probably cannot account for the acuity of frequency analysis observed

behaviorally (see above) without additional central processing (see below).

All fibers of the auditory nerve of *Carassius* show robust phase-locking to tones [e.g., Fay, 1978b], to statistical periodicities in noise [Fay et al., 1983], and to envelope structure [e.g., Fay, 1980]. The effect of frequency on the 'jitter' with which saccular afferents phase-lock to sound waveform and envelope accounts for behavioral frequency discrimination thresholds [Fay, 1978b], for the processing of envelope periodicity [Fay, 1982; Fay and Passow, 1982], and for the ability to discriminate differences in repetition noise 'pitch*' [Fay et al., 1983]. Most features of the sound waveform fine structure and envelope are precisely encoded by inter-spike times within individual fibers, and it has been hypothesized that this information can be used by the brain to analyze both the sound spectrum and the envelope structure in the time domain [e.g., Fay et al., 1983].

We understand much less well putative auditory functions of the other otolith organs (lagena and utricle), because the extent to which hearing in the usual environment is mediated by the sound pressure or particle motion waveforms, or whether one or multiple otolith organs function normally in hearing, is not yet clear. Although *Carassius* is specialized to encode sound pressure via the saccule, the saccule, lagena, and utricle are equally sensitive to whole-body acceleration, at least at frequencies up to 140 Hz [Fay, 1984]. The characteristics of underwater sound sources such as their spectra, waveforms, ratios of pressure to acceleration level, and their phase relations, vary with distance from the source within the nearfield [Kalmijn, 1989]. Thus, fish may use different end organs and strategies to detect and identify sound sources located at different distances, as well as to determine source direction and distance [Schuijff and Hawkins, 1983; Schellart and de Munck, 1987; Rogers et al., 1988].

Fay [1984] studied the response of saccular, lagenar, and utricular afferents in *Carassius* in response to linear, sinusoidal acceleration of the animal. Each afferent investigated showed a directional sensitivity pattern resembling a three-dimensional dipole with a single axis of best sensitivity. Afferents from the three organs showed a similar sensitivity at 140 Hz, with the most sensitive fibers responding to sinusoidal displacements of less than 1 nm (RMS). However, each organ has a characteristic distribution or pattern of directional sensitivities: primarily in the horizontal plane for the utricle; in the vertical plane for the lagena, and in one location for the saccule (about 15° azimuth and 40° elevation). Thus, information is relayed to the brain from the three otolith organs in a way consistent with the notion that

the resulting spatial patterns of neural activity can adequately represent the axis of particle motion. However, such a system of particle motion receivers is subject to an essential ambiguity about the direction of sound propagation. In other words, the axis of motion may be resolved, but which end of the axis points to the source?

Schuijf [1975, 1981] has shown that this (180°) ambiguity can be resolved through the simultaneous encoding of the particle motion and sound pressure waveforms and the processing of their phase relations. Hearing specialists encode the sound pressure waveform via at least one otolith organ that receives input from the swimbladder, and may encode the particle motion waveform via otolith organs that are more shielded from the gasbladder's influence. Thus, fish with some sensitivity to the pressure signal at least have access to the information required for sound localization. Whether, and to what extent, the localization problem is solved in this way is, however, unknown. The work on directional hearing in fishes leave us with many speculations about possible mechanisms [e.g., Schellart and de Munck, 1987; Popper et al., 1988; Rogers et al., 1988] but little data. To obtain these data requires experimental methods to independently measure and control both particle motion and sound pressure.

In general, neurophysiological studies have demonstrated many similarities in auditory function between *Carassius* and other vertebrates, including mammals [e.g., Coombs and Fay, 1989]. However, there has also been demonstration that response patterns of auditory (sacculus) nerve fibers of *Carassius* are unlike those of mammals in several respects. Chief among these are multimodal rather than continuous distributions of best frequency [Fay and Ream, 1986], continuous rather than multimodal distributions of best threshold [Fay and Ream, 1986], frequency-dependent shapes or profiles of peri-stimulus-time histograms (PSTH) [Fay, 1986], and the suppression of background spike activity by single tones [Fay, 1990, 1991]. The consequences of these patterns for hearing are generally unknown.

Innervation

Several models have been proposed for hearing in fishes that assume information from discrete regions of the sensory epithelium project separately into the CNS [e.g., Buwalda, 1981; Schellart and de Munck, 1987; Popper et al., 1988; Rogers et al., 1988]. However, little is actually known about the regional innervation of the otolith organs, or of topographic projections to brainstem nuclei.

The only systematic data on innervation of the saccular epithelium are for *Astronotus* [Saidel and Popper, 1983;

29

Popper and Saidel, 1990; Presson et al., 1992] and *Carassius* [Furukawa, 1981; Sento and Furukawa, 1987]. In both species, many afferent neurons divide rather widely to innervate large regions of the epithelium [Sento and Furukawa, 1987; Presson et al., 1992]. However, there is some evidence in both species that most neurons are restricted enough in their field of innervation to stay within one hair cell orientation group or region [Furukawa and Ishii, 1967; Furukawa, 1981; Saidel and Popper, 1983], and there appear to be separate neurons innervating the marginal and central regions of the epithelium in *Astronotus* [Presson et al., 1992]. Furukawa and Ishii [1967] reported a few neurons that innervate hair cells from opposing orientation, but it is not known if similar types of neurons are found in other species.

The size of the arbor of each neuron varies [Presson et al., 1992], and we do not know how many hair cells are innervated by any individual neuron. It is likely that each neuron must innervate large numbers of hair cells, since there are far more hair cells than afferent fibers [Popper and Hoxter, 1984; Mathiesen and Popper, 1987]. It is also likely that each neuron makes more than one synapse per hair cell [Popper and Saidel, 1990].

Little is known about efferent innervation of the ear, and the relations between efferent and afferent innervation. It is clear, however, that there are far fewer efferent neurons than hair cells [e.g., Sans and Highstein, 1984; Highstein, 1991; Roberts and Meredith, 1992], and the majority of hair cells, at least in the sacculus of *Astronotus*, receive efferent innervation [Popper and Saidel, 1990].

Analysis of the synaptology of individual hair cells of *Astronotus* [Popper and Saidel, 1990] reveals that there are from 2 to 15 afferent synapses per hair cell and a similar number of efferent synapses. While the number of afferent synapses on each hair cell does not vary systematically with position across the epithelium, there are more efferent synapses on hair cells located at the center of the epithelium than on hair cells at the margins. The functional significance of the variation in number of afferent synapses per cell is not known, but some of the variation may reflect the age of the hair cell - new hair cells might be innervated by fewer afferent neurons than 'older' hair cells (see 'Growth of the Ear', below). There are fewer data on hair cell innervation in other species. However, investigation of the

lagna of the gourami *Colisa labiosa* indicates considerable variation in the numbers of afferent and efferent synapses per cell [Wegner, 1982].

Several interesting questions need to be asked with regard to innervation of the ear: (1) Is the inter-specific variation found in numbers of neurons and synapses on

individual hair cells meaningful or only a consequence of the small sample size (both inter- and intra-specific)? (2)

What is the functional significance of a variable number of afferent or efferent synapses per cell, and in having efferent synapses on some populations of hair cells? (3) What is the area of the epithelium innervated by a single efferent neuron? This could have important consequences for the function of the efferent system, since an efferent neuron that innervates a broad expanse of sensory epithelium would have much coarser effects than a neuron that innervates only a small epithelial region. (4) Is the innervation found in *Astronotus* typical of all fishes, or are there differences in innervation among different species, and particularly between hearing specialists and nonspecialists? (5) Most importantly, what are the effects of efferent activation on the encoding of sound (and vestibular information) by the ear in fishes?

Growth of the Ear

There are large numbers of sensory hair cells in each of the otolith end organs in fishes. In contrast to most amniotes, the number of hair cells in fishes continues to increase substantially for many years post-embryonically [e.g., Corwin, 1983; Popper and Hoxter, 1984]. Studies of *Astronotus* show that a 2.0-cm long fish will have perhaps 5,000 hair cells in a single saccular epithelium, whereas a 19-cm fish may have over 250,000 hair cells [Popper and Hoxter, 1984]. This increase occurs during only two years of growth, suggesting the addition of well over 100 hair cells per day in each sacculus of a growing *Astronotus*. Similarly, increasing numbers of hair cells have been shown in the sacculus of *Carassius* [Piatt, 1977]. While earlier studies concentrated on the sacculus, it has recently been shown that the number of hair cells increase in each of the otolith end organs of a Gadiform, *Merluccius merluccius*, the European hake [A. Lombarte and A.N. Popper, unpubl. observ.]. It is likely that similar increases occur in most fishes.

It has also been demonstrated that there is a small increase in the number of afferent neurons innervating the sacculus in *Astronotus* [Popper and Hoxter, 1984]. Since the number of hair cells increases much more rapidly than the number of afferent neurons, it becomes clear that the ratio of hair cells to afferent neurons increases as fishes grow. This observation is further supported by neuroanatomical labeling studies of individual neurons in *Astronotus*; a work in preparation [J.C. Presson and A.N. Popper] reports that as the epithelium grows and adds hair cells, eighth nerve arbors also grow, thereby increasing the number of hair cells innervated by each afferent neuron. No data are avail-

30

Popper/Fay

Sound Detection and Processing by Fish

Forebrain

5 Area Dorsalis, Medial N. area 2 -*- Area Dorsalis, Medial N. area 4

i—*- Ventral Telencephalon

9

Thalamus

*■ Central Posterior N. of Thalamus

A A

■

Anterior Tuberal N. of Hypothalamus 1

Midbrain
t T
Central Toral Nucleus —j£ Medial Pretoral Nucleus
AAA

Fig. 7. Schematic diagram of the auditory portions of the brain of the channel catfish (*Ictalurus punctatus*) adapted from Striedter [1991]. At present, we assume that this is representative of the Otophysi and, perhaps, of most fish species as well.

Medulla

Eighth Nerve
Anterior Nucleus —'Dorsal Descending —Descending
Medial Auditory Nucleus

able about changes in efferent innervation with hair cell addition.

The functional significance of the addition of hair cells over the life of a fish is not known, nor do we have an understanding of the significance of the apparently substantial increase in the number of hair cells innervated by each afferent neuron. The only behavioral data even approaching this question come from a study on hearing sensitivity in different sized carp, *Cyprinus carpio* [Popper, 1974], where hearing capabilities did not change with the size of the animal (and, presumably, the number of hair cells). However, the question asked in that study did not directly address the effects of hair cell addition, and other factors, such as associated changes in swimbladder size and resonance, may have compensated for hair cell addition. In effect, the increase in the number of hair cells may compensate for physical changes in the size of the pressure detector, or vice versa, resulting in a stable hearing system over the life of the fish. If both did not grow concurrently, hearing capabilities might change over time. This hypothesis arises from one model of fish hearing [Popper et al., 1988; Rogers et al., 1988] but has not yet been tested.

The only physiological data germane to the question of the effects of an increase in number of hair cells innervated were obtained from recordings from the eighth nerve of *Raja clavata* (thornback ray) [Corwin, 1983] and *Carassius* [Sento and Furukawa, 1987] where sensitivity of a fiber was correlated with the number of hair cells innervated. If the number of hair cells increases with age, then in these species one might expect increased behavioral sensitivity with age. These data do not contradict the aforementioned behavioral results, but only indicate that physiological data from the eighth nerve may not tell the whole story concerning the effects of increases in number of hair cells innervated.

Central Nervous System

Afferent System

Recent neuroanatomical studies of the central auditory system of fish have shown a pattern of organization that is similar overall to that in other vertebrates [e.g., Bell, 1981; Echter, 1984, 1985a; Fritzsche et al., 1990; Bleckmann et al., 1991; Striedter, 1991; McCormick, 1992] (see fig. 7). Auditory nuclei and their afferent and efferent connections have been described in the medulla (anterior, tangential, magnocellular, medial, and descending octaval nuclei), in the midbrain (torus semicircularis, central toral nucleus, medial pretoral nucleus) and in the forebrain (at least six nuclei of the thalamus, hypothalamus, and telencephalic structures). Afferents from the saccule, lagena, and utricle

project with partially overlapping patterns to specific regions of the medullary nuclei [e.g., Bell, 1981; Meredith and Butler, 1983; Bleckmann et al., 1991; Highstein et al., 1992]. Afferents from the anterior, descending, and medial auditory nuclei of the medulla project to auditory areas of the midbrain [e.g., Striedter, 1991]. Moreover, there is clearly some interaction between the auditory and visual systems, since there are connections between the torus and the deep layers of the optic tectum [Page, 1970; Schellart, 1990]. It is presently unclear what signal transformations occur within the central nervous system (but see below).

Despite the recent increase in neuroanatomical data on central projections of the otic end organs in several species, there are still important and fundamental questions that need to be asked about afferent organization. In particular, while we know a bit about afferent projections from specific end organs, we know almost nothing about projections from regions within end organs. For example: (1) Do hair cells from different orientation groups within a single epithelium (see fig. 5) project to separate brainstem nuclei or regions of these nuclei? It is likely to be important to segregate such information, at least until it reaches a 'comparator' stage of the CNS in order to maintain the integrity of data on directional motion of the otolith and thus on sound source direction [Rogers et al., 1988]; (2) Similarly, are there distinct afferent projections from epithelial regions having hair cells with different length ciliary bundles (perhaps reflecting responses to different modalities or frequencies)? (3) Are there separate projections from regions having type II and type I-like hair cells [e.g., from the extrastricular and stricular regions of the utricle], as might be expected if these two morphologically distinct hair cell types are functionally distinct? These and other questions on the fine structure of afferent projections should be studied in both hearing specialists and nonspecialists.

Although there have been several neurophysiological studies of unit responses and unit clusters in the auditory CNS of fish [e.g., Enger, 1967; Page, 1970; Sawa, 1976; Horner et al., 1980; Schellart, 1983, 1989b; Plassmann, 1985; Echteler, 1985b; Nederstigt and Schellart, 1986; Schellart et al., 1987], there are few systematic data on tuning, phase-locking, selectivity for sound source direction, or for the representation of complex sounds in any area of the brain. A few generalizations can be made so far: (a) Units can be classified as tonic or phasic and as phase-locked or not phase-locked; (b) Frequency selectivity may be more acute in the midbrain than in primary afferents; (c) A crude, rostrocaudal tonotopic organization exists in the torus; (d) There is great diversity of response types based on PSTH shape; (e) Binaural cells exist in the torus and may subtract the input from one ear from that of the other [Horner et al., 1980]; and (f) Some midbrain-level units may be multimodal (e.g., auditory and visual).

Crawford and Fay [1990] have surveyed the response of toral units in mormyrids to tones and clicks and found some units with sharp tuning, evidence for inhibitory interactions, and selectivity for certain inter-click intervals. Fay and Lu [1992; Lu and Fay, 1992] have begun a systematic study of tuning, sensitivity, and phase-locking in the torus of *Carassius* which has so far indicated that some units phase-lock with an accuracy exceeding that of the periphery, that unit clusters often contain two units with different characteristic frequencies but which discharge approximately 180° out-of-phase with one another, and that the sharper tuning in some midbrain units is the result of inhibition from cells tuned at adjacent frequencies. This last observation is important and suggests central transformations that tend to 'rescue' a rate/place code for frequency that is smeared at the periphery. Important questions remain concerning the anatomical substrate for this central sharpening and the consequences that these interactions have for perception and spectrum analysis.

While we have only fragmentary data to date on the auditory CNS of fish, it is becoming clear that these structures and responses share much in common with those of other vertebrates, including mammals. For example, Lu and Fay [1992; Fay and Lu, 1992] report that in *Carassius*, midbrain units that do not phase-lock fall into several categories based on the shapes of peri-stimulus time histograms [also see Page, 1970], similar to some cochlear nucleus units described for mammals: onset, buildup, pauser, primary-like, and choppers [Rhode and Greenberg, 1992]. Choppers have regular interspike intervals that are not phase-locked to the stimulus, as is the case for mammals. Nederstigt and Schellart [1986] report similar, complex response patterns in the torus semicircularis of the rainbow trout, *Salmo gairdneri*. Thus, several species of fish show the general vertebrate plan for central auditory structures and processing, as well as for behaviorally defined aspects of hearing.

Of the many questions remaining to be investigated in the central auditory systems of fishes, five are of the highest priority: (1) How are phase-locked responses used in information processing and perception? (2) How are the frequency response areas of single cells sharpened, and what are the consequences for hearing of this sharpening? (3) What is the fate of directionally coded information from the periphery, and how is this used in sound source determination? (4) How do inputs from the various otolith

Sound Detection and Processing by Fish

organs and the two ears interact in the brain? (5) To what extent does the brain segregate and integrate information on sound pressure and particle motion, from the ears and from the lateral line system? It will also be of considerable interest to determine whether the auditory system in fishes has parallels in the very elegantly described electrosensory system of the electric fish *Eigenmannia* [Heiligenberg, 1991].

Efferent System

In anamniotes the efferent neurons arise from the octa-volateralis efferent nucleus (OEN) [Roberts and Meredith, 1991; see also Highstein, 1991]. The OEN also contains intermingled efferent neurons to the lateral line [Meredith and Roberts, 1987; Roberts and Meredith, 1989]. In fact, the same efferent units appear to innervate multiple end organs of the ear and lateral line [Claas et al., 1981; Bleckmann et al., 1991].

The number of efferent neurons has been determined in only a few species of fish, primarily in the saccule. The numbers vary from 131 in *Opsanus* [Highstein and Baker, 1986] to 31 in *Gnathonemus petersii* (Ubangi mormyrid) [Bell, 1981] and 40 in *Anguilla anguilla* (European eel) [Meredith and Roberts, 1987]. In each case, a portion of the neurons project contralaterally [reviewed in Roberts and Meredith, 1992].

The functional significance of the efferent system in all vertebrates, including fish, is an area of considerable question and debate. However, in at least some cases the efferent system serves to modulate the response of the afferent hair cells or afferent neurons in various end organs [see reviews by Highstein, 1991; Roberts and Meredith, 1989]. Efferent stimulation affects the responses recorded from afferent neurons in *Carassius* [Furukawa, 1981] and *Opsanus* [Highstein and Baker, 1986], and there is a decrease in the microphonic responses from the saccule of *Carassius* when the efferent system is stimulated centrally [Piddington, 1971a, b].

Many questions remain with regard to the role of the efferent system in fish. Based upon the extensive efferent innervation of hair cells in the saccule [Nakajima and Wang, 1974; Popper and Saidel, 1990], Iagena [Wegner, 1982], striola region of the utricle [Saidel et al., 1990a; Chang et al., 1992] and the crista of the semi-circular canals [Sans and Highstein, 1984], it is clear that the efferent system must play a role in some aspect(s) of inner ear function. Without understanding the function of the efferent system, it is not possible to fully understand the function of the ear in teleosts, and to develop appropriate models to understand signal processing in fish. There are some significant questions to be asked: (1) How and under what circumstances does the efferent system modulate afferent activity? (2) Is there any topographic relationship between central locations of efferent neurons and projection sites on the end organs? (3) Do different central sites subserve different modalities [e.g., auditory vs. vestibular]? (4) Are there differences in the OEN between hearing specialists vs. non-specialists that could be involved with the way that these animals process acoustic information? Just as hearing specialists appear to have a special primary eighth nerve area in the medulla that is not present in nonspecialists [McCor-mick, 1992], it is possible that we will find differences in the OEN that are related to how hearing specialists process sound?

Summary

Although we know considerably more about fish auditory systems than we did in 1973 [Popper and Fay, 1973], we are still seeking answers to the fundamental question, 'how do fish hear?'. Because of the relative wealth of data available on hearing in the goldfish, we can appreciate that this and other species hear and process sound with remarkable acuity, even when compared to many tetrapod species. Yet, even for the goldfish we do not know whether this species can localize sound sources, or how pressure and particle motion are used in sound perception. We now have a sense of how the inner ear receives signals, but we still know little about the role of the swimbladder and acoustic coupling mechanisms in most species. We have a reasonably good understanding of the structure of the ear, and some sense of how hair cells are stimulated, but we still must only speculate about how the otolith and sensory epithelia interact during acoustic stimulation, or how frequency selectivity arises in the saccule. We have little understanding of the functional significance of intra-epithelial variation in the structure of hair cells and their morphological and physiological orientations. Moreover, we do not know very much about the coding of the signals detected by ears of different structure, nor do we know whether or to what extent signals from different ear regions, are segregated or interact in the CNS.

We are starting to develop some appreciation of the connection of the ear to the medulla, and how the medullary nuclei are connected to higher brain centers. Still, we know little about the type(s) of processing conducted at any

level of the auditory CNS in fishes, and we have little understanding of the role of the efferent system in modulating afferent processing. Systematic studies on binaural

33

interactions and contralateral -connections have yet to be carried out.

Data for a few species suggest that there is substantial inter-specific variation in the structures of the peripheral and central auditory system among over 25,000 extant fish species. Perhaps the most interesting questions concern the consequences of structural and physiological variation for hearing behavior. The extensive data we now have on the sense of hearing in the goldfish [Fay, 1988a] indicates a remarkable general similarity to the sense of hearing of most other vertebrates investigated behaviorally. Is it the case that all vertebrates have essentially solved the same problems in hearing using a variety of mechanisms, or are the diverse morphologies we see among the fishes adaptations to particular processing tasks? In order to answer these sorts of questions, future studies will have to systematically explore auditory mechanisms in a few select and diverse species of hearing specialists and nonspecialists.

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34

Popper/Fay

Sound Detection and Processing by Fish

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35

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36

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37

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