

Original Paper

Brain, Behavior
and Evolution

Brain Behav Evol 1999;53:288-304

Did Auditory Sensitivity and Vocalization Evolve Independently in Otophysan Fishes?

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Key Words

Otophysan fishes · Hearing specialists · Weberian ossicles · Sound production · Auditory sensitivity · Correlated evolution · Acoustical communication · Predator avoidance

Abstract

Otophysine fishes have a series of bones, the Weberian ossicles, which acoustically couple the swimbladder to the inner ear. These fishes have evolved a diversity of sound-generating organs and acoustic signals, although some species, such as the goldfish, are not known to be vocal. Utilizing a recently developed auditory brainstem response (ABR)-recording technique, the auditory sensitivities of representatives of seven families from all four otophysine orders were investigated and compared to the spectral content of their vocalizations. All species examined detect tone bursts from 100 Hz to 5 kHz, but ABR-audiograms revealed major differences in auditory sensitivities, especially at higher frequencies (>1 kHz) where thresholds differed by up to 50 dB. These differences showed no apparent correspondence to the ability to produce sounds (vocal versus non-vocal species) or to the spectral content of species-specific sounds. All fishes have maximum sensitivity between 400 Hz and 1,500 Hz, whereas the major portion of the energy of acoustic signals was in the frequency range of 100–400 Hz (swimbladder drumming sounds) and of 1–3 kHz (stridulatory

sounds). Species producing stridulatory sounds exhibited better high-frequency hearing sensitivity (pimelodids, doradids), except for callichthyids, which had poorest hearing ability in this range. Furthermore, fishes emitting both low- and high-frequency sounds, such as pimelodid and doradid catfishes, did not possess two corresponding auditory sensitivity maxima. Based on these results it is concluded that selective pressures involved in the evolution of the Weberian apparatus and the design of vocal signals in otophysines were others (primarily predator or prey detection in quiet freshwater habitats) than those serving to optimize acoustical communication.

Introduction

Sound perception is a sensory modality which evolved early in vertebrate evolution [Popper et al., 1992]. All recent fish species are clearly able to detect low frequency sounds and several groups have developed accessory hearing structures for sound pressure detection at higher frequencies. These species – usually termed hearing specialists – are characterized by possessing a close connection between an air-filled cavity within the body and the inner ear. These air-filled spaces can either lie adjacent to the inner ear such as in labyrinth fishes [Bader, 1937] and mormyrids [Stipetić, 1939], or the swimbladder is connected via an elongated

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0006-8977/99/0536-0288\$17.50/0

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anterior extension [some holocentrids – Coombs and Popper, 1979] or small ossicles [otophysans – von Frisch and Stettner, 1932] to the auditory organ. However, the function and thus the constraints for the evolution of accessory hearing structures are not understood. Several investigators argue that hearing gives fishes general information about their acoustic environment, such as sound source location [Popper and Fay, 1997]. This however, does not explain which sound sources fishes had to listen to during their evolution, which information they needed to extract from their environment, and whether these tasks are managed differently by generalists and specialists.

Two major reasons for the evolution of hearing and particular hearing abilities are the necessity to perceive/detect the sounds of conspecifics or sounds of predators or prey. The detection of predators' sounds was obviously a driving force in the evolution of hearing organs in many insect families such as moths and preying mantis [Hoy, 1992]. Insects flying at night are well tuned to the frequencies of the echolocating clicks of bats [Yager and May, 1990]. Also, some clupeid fishes can detect echolocation sounds of dolphins [Mann et al., 1997].

The second major purpose of hearing in invertebrates (crustaceans, insects) as well as most vertebrates is the detection of intraspecific acoustic signals. Numerous fish species possess elaborate sound-producing mechanisms and vocalize in the course of various intraspecific interactions [Myrberg, 1981; Ladich, 1997a; Ladich and Bass, 1998]. In order to maximize the effectiveness of intraspecific communication by sound, natural selection would favor that the main energy content of sounds is generated within the best hearing range of a particular fish species. A few studies have addressed this question. Cohen and Winn [1967] observed a correlation between the fundamental frequency of sounds and the saccular microphonic response at approximately 150 Hz in the midshipman *Porichthys notatus*, whereas a slight mismatch was observed in the close relative, the oyster toadfish *Opsanus tau* [Fine, 1981]. In the damselfish *Eupomacentrus* the sound energy spectrum matches the audiogram in the region of greatest sensitivity between 500 and 600 Hz [Myrberg and Spires, 1980]. Stabentheiner [1988] found that the frequency spectrum of typical drumming sounds (barks) covers the range of the best hearing (100–600 Hz) in the piranha *Serrasalmus nattereri*. Schellart and Popper [1992] analyzed best frequencies of hearing and dominant frequencies of sounds in 15 species of mostly marine teleosts and found a correlation coefficient of 0.56. In a recent study Ladich and Yan [1998] demonstrated that such a correlation also exists in one species producing high-pitched sound (800–1500 Hz), the croaking gourami *Trichopsis vittata*.

These correlations suggest that sound-producing mechanisms did evolve in correlation with hearing abilities in fishes. However, several points contradict this assumption. Morphologically similar sonic organs are found in hearing specialists (catfishes) as well as hearing generalists (toadfishes). Swimbladder drumming muscles and subsequently low-frequency sounds evolved in both groups. Cohen and Winn [1967] argue that midshipman cannot hear most of the higher frequencies of sounds (250–1500 Hz). This is mainly because hearing generalists are limited to detecting the particle motion component of sound waves which is usually restricted to frequencies below 50–200 Hz [Cohen and Winn, 1967; Chapman and Hawkins, 1973; Myrberg and Spires, 1980]. Hearing specialists, on the other hand, can detect the sound pressure component at much higher frequencies and thus do not face these limitations. Therefore, fishes possessing different hearing abilities detect different ranges of the drumming sound spectra, which indicates that the overall sound spectrum does not perfectly match the hearing sensitivity.

In order to analyze the correlated evolution of sonic and hearing organs in more detail a comparative study was conducted including a large group of hearing specialists that possess a variety of different sound-generating mechanisms: otophysan fishes. They are characterized by having 2–4 Weberian ossicles (tripus, intercalarium, scaphium, claustrum), modifications of the anterior vertebrae, which is thought to enhance hearing abilities by facilitating sound transmission from the swimbladder to the inner ear [Chranilov, 1927; von Frisch and Stettner, 1932]. Contrary to this unique accessory hearing structure, otophysans emit either low-frequency sounds via swimbladder (drumming) muscles (e.g. characids and catfishes) or broad-band high-frequency sounds generated by various mechanisms (e.g. pectoral fins in catfishes) [Markl, 1971; Ladich, 1997b]. In cypriniforms that are known to be vocal, the sound-producing structures have not been described so far [see Valinski and Rigley, 1981; Ladich, 1988]. Representatives of some catfish families (doradids, pimelodids) even possess two sonic organs [Ladich and Fine, 1994; Ladich and Bass, 1998], and many otophysans are not known to be vocal (e.g. most cyprinids and knifefishes).

If the major constraints in the evolution of hearing and sonic organs in otophysans fishes are the facilitation of acoustical communication, then a match between spectral content of sounds and best hearing sensitivity would be expected. Therefore, the aim of the present study is two-fold. The first is to analyze hearing sensitivities in representatives of all otophysan orders (Cypriniformes, Characiformes, Siluriformes, Gymnotiformes) in order to determine

Table 1. Order, family, species, size range and number of individuals used in this study. Systematics after Nelson [1994]

Order	Family	Species	Size range (g)	N
Cypriniformes	Cyprinidae	<i>Carassius auratus</i>	6.1–18	8
	Cobitidae	<i>Botia modesta</i>	4.0–13.3	7
Characiformes	Characidae	<i>Serrasalmus nattereri</i>	21.0–29.5	6
Siluriformes	Doradidae	<i>Platydoras costatus</i>	6.4–24.5	13
		<i>Agamyxis pectinifrons</i>	2.1–7.9	12
	Pimelodidae	<i>Pimelodus blochii</i>	10.3–34.9	11
		<i>Pimelodus pictus</i>	5.4–10.0	11
	Callichthyidae	<i>Corydoras paleatus</i>	2.8–9.9	10
Gymnotiformes	Sternopygidae	<i>Eigenmannia virescens</i>	8.4–11.8	6

if the enhanced hearing abilities vary. Vocalizing and non-vocalizing species were chosen in order to determine whether the former possess lower hearing thresholds. The second goal is to investigate whether auditory sensitivity matches the differences in main energies of sounds produced in vocalizing species.

The auditory brainstem response (ABR)-recording technique, an electrophysiological non-invasive far-field recording method recently adapted to fishes by Yan [Kenyon et al., 1998], was used to analyze auditory thresholds of two representatives of cypriniforms (family Cyprinidae and Cobitidae), one characiform (family Characidae), five siluriforms (families Pimelodidae, Doradidae and Callichthyidae) and one gymnotiform (family Sternopygidae). The audiograms were then compared to spectra of specific sounds produced by tested species.

Materials and Methods

Otophysans were obtained from local pet suppliers and maintained in aquaria at $28 \pm 1^\circ\text{C}$. Aquaria were planted, equipped with half flower pots as hiding places and filtered by external filters. Fishes were fed live *Tubifex* worms every second day. Efforts were made to provide quiet environments for the animals (e.g. no submerged pumps or air stones). The average sound pressure level in holding tanks was between 100 and 110 dB re 1 μPa (RMS Slow). Nine species out of seven otophysan families were used during this study (table 1). Data for the ninth species, *Carassius auratus*, were taken from Kenyon et al. [1998] for comparative purposes. Except for *Corydoras paleatus*, fishes were immature and sexing was not possible without sacrificing the fish. In *Corydoras paleatus* no difference was found in auditory thresholds between sexes and therefore data were pooled for further analysis.

Experiments were performed under the permission of the Austrian Commission on Experiments in Animals (GZ 68.210/19.Pr/4/97).

Auditory Sensitivity Measurements

The ABR recording protocol followed that of Kenyon et al. [1998] and Ladich and Yan [1998]. Therefore, only a brief description of the method is given here.

Experimental Setup

Test subjects were secured in a round 11-l plastic tub (33 cm diameter, 13 cm height, 1 cm layer of fine sand) filled with water and adjusted so that the nape of the head was just above the surface of the water, and a respiration pipette was inserted into the subjects' mouth. Respiration was achieved through a simple temperature-controlled (28°C) gravity-fed water circulation system. In order to immobilize animals and to reduce the myogenic noise level they were injected with a curariform agent (galamine triethiodide – Flaxedil). The dosage required was $2\text{--}6 \mu\text{g g}^{-1}$ for *Botia*, *Serrasalmus*, *Agamyxis* and *Pimelodus blochii*, $6\text{--}12 \mu\text{g g}^{-1}$ for *P. pictus* and for *Corydoras* and $3\text{--}4 \mu\text{g g}^{-1}$ for *Platydoras* and *Eigenmannia*. The plastic tub was positioned on an air table (TMC Micro-g 63-540) which rested on a vibration-isolated concrete plate. The entire setup was enclosed in a walk-in sound proof room, which was constructed as a faraday cage (interior dimensions: $3.2 \text{ m} \times 3.2 \text{ m} \times 2.4 \text{ m}$).

Electrodes were pressed firmly against the skin, which was covered by a small piece of Kimwipes tissue paper to keep it moist, in order to ensure proper contact during experiments. Loss of contact immediately resulted in a higher noise level. The contacting point of both electrodes was positioned about 2 mm above the water surface. The recording electrode was placed on the midline of the skull over the region of the medulla. The reference electrode was placed cranially between the nares. The relative position of the two electrodes could be displaced by a few millimeters with no discernible changes in the response waveform and auditory thresholds. Recording electrodes consisted of silver wires (0.25 mm diameter). Shielded electrode leads were attached to the differential inputs of an a.c. preamplifier (Grass P-55, gain $1000\times$, high pass at 30 Hz, low pass at 3,000 Hz). A hydrophone (Brüel & Kjaer 8101, frequency range: 1 Hz – 80 kHz ± 2 dB; voltage sensitivity: -184 dB re 1 V/ μPa) was placed close to the right side of the animals (2 cm apart) in order to determine absolute stimulus SPLs underwater in close vicinity of the subjects. A second custom-built preamplifier (gain $1000\times$) was used to amplify the hydrophone signal. A dual-cone speaker (Tannoy System 600, frequency response 50 Hz – 15 kHz ± 3 dB), suspended in air, was mounted 1 m above the test subject.

ABR Recording Apparatus and Stimulus Presentation

Both sound stimuli presentation and ABR waveform recording were accomplished using a Tucker-Davis Technologies (Gainesville, FL, USA) modular rack-mount system controlled by an optically-linked 200 MHz MMX Pentium PC containing a TDT digital processing board and running TDT 'Bio-Sig' 2.2 Software. Sound stimulus waveforms were constructed using TDT 'Sig-Gen' software, and fed through a DA1 digital-analog converter, a PA4 programmable attenuator, and a power amplifier (Denon PMA 715R) which drove the speaker. The hydrophone preamp output cable was fed to one channel of an AD1 analog-digital converter, while the electrode preamp output was first passed through a PC1 spike conditioner before reaching the AD1.

Both tone bursts and clicks were presented to test subjects. Clicks were 0.1 ms in duration and presented at a rate of 21.1 s^{-1} (to prevent phase locking with any 50-Hz noise). The number of cycles in a tone burst (2–8) was adjusted according to frequency in order to obtain the best combination of stimulus rise time (shorter rise time = greater efficacy at generating ABRs) and peak frequency bandwidth (longer duration = sharper spectral peak) [Silman and Silverman, 1991]. One thousand stimuli at each polarity (90° and 270°) were presented and averaged by the Bio-Sig software. ABR traces form together a 2,000-stimulus trace when averaged. In contrast, averaged sound-pressure waveforms presented at two polarities always cancelled each other out when averaged. Thus stimulus artifact can be eliminated efficiently. At each tested frequency and sound pressure level (SPL) this was done twice and overlaid to examine whether traces were reproducible. SPL was reduced in 4–5 dB steps until the ABR waveform was no longer apparent. The lowest SPL for which a repeatable ABR trace could be obtained, as determined by overlaying replicate traces, was considered the threshold. This method of visual inspection correlation is the traditional means of determining threshold in ABR audiometry [Kileny and Shea, 1986; Gorga et al., 1988; Hall, 1992].

Once the threshold level was determined, the hydrophone recording was analyzed to determine the root mean square (RMS) SPL, based on the method of Burkhard [1984]. Using the capabilities of the Bio-Sig software, cursors were placed 1 cycle apart on either side of the largest (i.e. center) sinusoid of a particular tone burst recording. The software then calculated the RMS of the waveform between the cursors, and calibration factors were applied to determine actual SPL in decibels re $1 \mu\text{Pa}$. Animals were tested at frequencies of 100, 200, 300, 400, 500, 600, 800, 1,000, 1,500, 2,000, 3,000, 4,000 and 5,000 Hz. No thresholds could be determined at 5 kHz for *C. paleatus*.

Only sound pressure measurements were conducted because otophysan fishes primarily detect sound pressure in the frequency range where main energies of sounds were concentrated. Previous studies have demonstrated that *Carassius* and *Ictalurus* are only sensitive to sound pressure above 160 Hz and detect particle motion below 100 Hz [Fay and Popper, 1974, 1975].

Comparison between Audiograms

One threshold point was measured at each frequency for each fish. Threshold values from all individuals as measured at 13 different frequencies were averaged to produce audiograms for each species. Audiograms were compared between species by the General Linear Model two-way ANOVA followed by Bonferroni's multiple comparison procedure. Differences between thresholds at representative frequencies (100, 400, 1,000, 4,000 Hz) were calculated using one-way ANOVA followed by Bonferroni's multiple comparison procedure.

Sound Spectra Determination of Fish Sounds and Comparison with Audiograms

Absolute SPL values of sound spectra were determined by measuring absolute SPL values in dB re $1 \mu\text{Pa}$ and relating them to the relative SPL data gained for each tested frequency by the sound analyzing software.

Sound Pressure Level (SPL) Measurements

SPL-measurements were conducted in a round 11-l tub (except for *Botia*) lined on the inside by acoustically absorbent material (Wetflinger air-filled packing foil) and whose bottom was covered with sand. SPLs were measured using a hydrophone (Brüel & Kjaer 8101) and a measuring amplifier (Brüel & Kjaer 2606, scale 0197 in dB re $1 \mu\text{Pa}$, RMS fast, high pass filter 22.5 Hz, low pass 22.5 kHz). Fish were held about 5 cm away from the hydrophone in the middle of the tank. This distance is partly larger than the distance observed during acoustic communication. Usually fish immediately uttered sound when hand-held. Otherwise they were gently touched on the caudal peduncle.

Sounds uttered when hand-held correspond to those emitted during intraspecific behaviour such as in pimelodids [Schachner and Schaller, 1981] and callichthyids [Pruzsinszky and Ladich, 1998]. SPL-measurements of *Botia* took place in a holding tank during aggressive interspecific interactions. Fishes were typically 5–10 cm away from the hydrophone. SPLs of up to ten sounds were measured for each individual and means were used to calculate the mean SPL-value for each species. All sound recordings took place at temperatures between 25°C and 27°C in a sound-proof chamber.

Sound Spectra Determination and Comparison with Audiograms

Sounds recorded in the course of previous studies were used for sound spectra determination in catfishes [Ladich, 1997b; Pruzsinszky and Ladich, 1998]. Auditory sensitivity and vocalizations were compared independent of size differences between individuals because statistical analysis did not reveal significant differences in hearing sensitivity between size groups (mean size ratio between groups $> 2:1$) in *Botia*, *Platydoras*, *Agamyxis* and *Corydoras*. Furthermore Popper [1970] showed similarity in hearing abilities in different-sized goldfish and Kenyon [1996] demonstrated in an ontogenetic study in damselfish that the final hearing sensitivity developed within the first four weeks of age.

Sound spectra of five to six sounds per individual were averaged by S-Tools, the Integrated Workstation for Acoustics, Speech and Signal Processing developed by the Research Laboratory of Acoustics at the Austrian Academy of Sciences. Relative amplitudes were measured for frequencies used in audiogram determination. The mean relative amplitude was then equated to the absolute SPL-value of sounds as determined by the hydrophone and measuring amplifier (see above).

Generally, a match between the auditory sensitivity and sound spectra in a species was observed when the best auditory sensitivity was found in the frequency range where the main energy of sounds was concentrated.

Results

ABR waveforms were obtained from all species investigated but no vocalizations were recorded from *Carassius* and *Eigenmannia*.

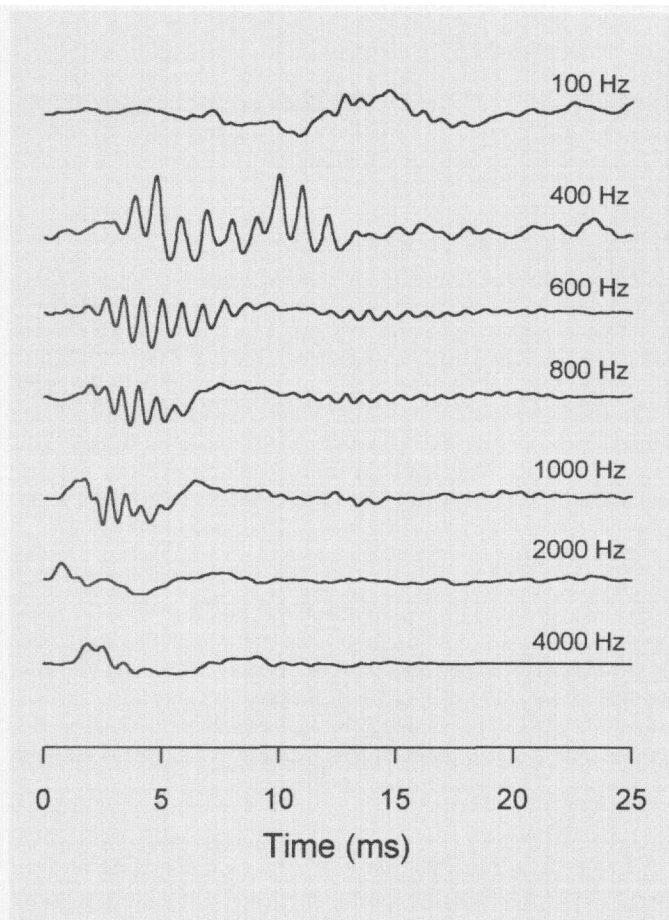


Fig. 1. ABR waveforms from *P. blochii* in response to tone bursts of different frequencies presented at sound pressure levels of 20 dB above hearing threshold. Averaged traces from two different polarities are shown. Note the decreasing onset latency with the increase of frequency.

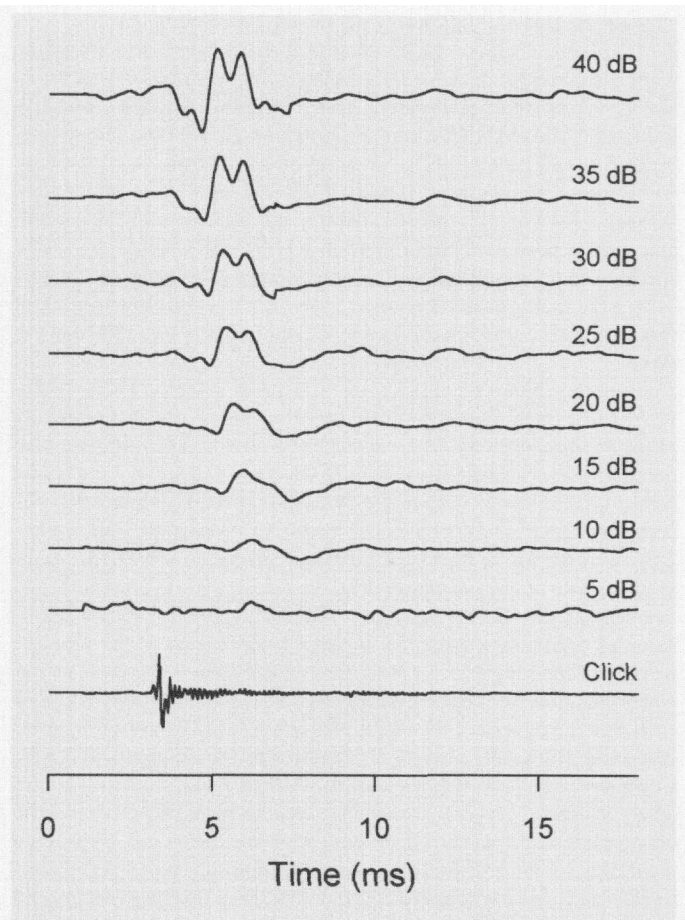


Fig. 2. ABR waveforms from *P. blochii* in response to clicks attenuated in 5 dB steps (0 dB = hearing threshold). Averaged traces (1,000 sweeps each) from two different polarities are shown. Note the increasing onset latency with decreasing SPLs.

ABR Waveforms and Auditory Sensitivity Curves

All otophysans examined showed ABRs to stimulation with click and sinusoid bursts from 100 Hz to 5 kHz (*Corydoras* 4 kHz). A typical suprathreshold ABR consisted of a series of 2–9 rapid downward peaks superimposed over a slow negative deflection lasting approximately 8–11 ms at low frequencies to around 3 ms in response to clicks and high-frequency tone bursts (*Pimelodus blochii* – fig. 1). ABR waveforms showed typical characteristics of auditory-evoked potentials at suprathreshold levels in all nine species. The ABR traces obtained from acoustic stimuli presented at opposite polarities (90° vs. 270°) did not cancel each other out when averaged. The onset latency of the ABR varied with stimulus frequency, ranging from 5.1 ms after stimulus onset at 100 Hz to

as little as 0.5 ms with clicks and 5,000 Hz tone bursts (fig. 1). The onset latency increased with decreasing stimulus amplitude at an average rate of 0.2 ms per 5 dB decrease in click sound level (fig. 2).

All otophysans investigated were sensitive to high-frequency sounds and had sensitivity maxima between 300 Hz and 1,000 Hz (fig. 3, table 2). Two-way ANOVA revealed significant differences between audiograms ($F = 6.94$, $df = 8$, 115 , $p < 0.001$). However, no clear difference between taxa could be observed (table 3). Significant differences were found between representatives of different orders (*Carassius* – *Eigenmannia*, catfishes – *Eigenmannia*), between families within one order (*Pimelodus* – *Corydoras*, *Platydoras* – *Corydoras*) and within the doradid family (*P. costatus* – *A. pectinifrons*) (table 3).

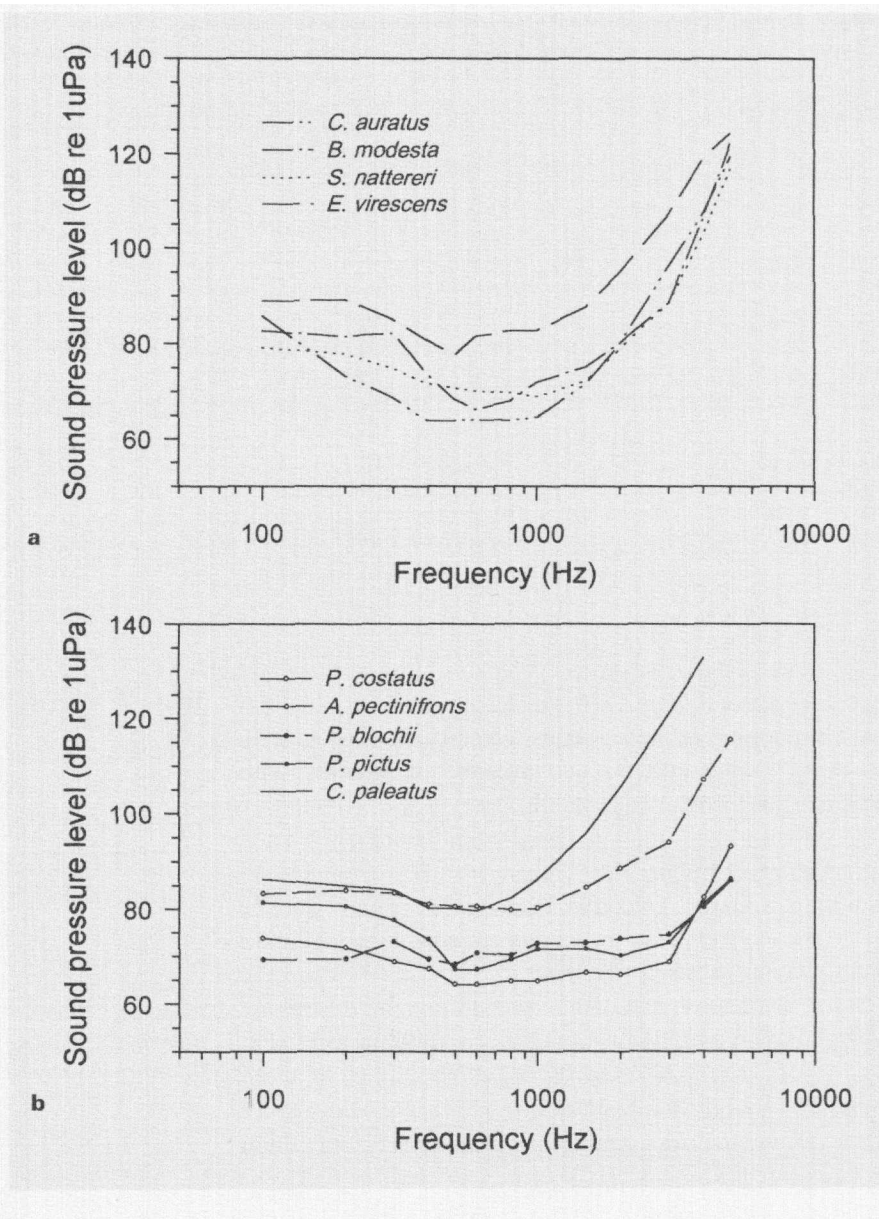


Fig. 3. ABR-audiograms of the otophysan species investigated. **a** Cypriniformes, Characiformes, Gymnotiformes; **b** Siluriformes.

The lowest absolute auditory thresholds were found in the goldfish and the doradid *P. costatus* at 64.0 dB and 63.8 dB (re 1 μ Pa), respectively. *Corydoras* and *Eigenmannia* had the highest thresholds (fig. 3a, b; table 2).

While the hearing thresholds differed maximally by 22–28 dB from 100 to 1,000 Hz among all species, this difference increased rapidly at higher frequencies. At 4 kHz the auditory sensitivity of both pimelodids and the doradid *Platydoras* was more than 50 dB lower than in the callichthyid catfish *C. paleatus* (table 4). A grouping of auditory sensitivities was found in the mid-frequency region (400–1,000 Hz), with *Agamyxis*, *Eigenmannia* and *Cory-*

doras having higher thresholds than the other species investigated. In the high-frequency region (3–5 kHz) both pimelodids and *Platydoras* had the lowest values, with mean thresholds of 86 dB and 93 dB (re 1 μ Pa), respectively (fig. 3b, table 4).

Diversity of Vocalizations

The investigated otophysans emitted three types of sounds. First, pimelodid and doradid catfishes as well as the characid emitted low-frequency drumming sounds produced by swimbladder muscles. These acoustic signals were built up of several harmonics, whereby the fundamental fre-

Table 2. Threshold values for otophysans investigated (dBe re 1 μ Pa). Freq. = Frequency (Hz). n = 9 for *A. pectinifrons* and *P. pictus*, n = 8 for *C. auratus* and *P. costatus*, n = 7 for *P. blochii* and *C. paleatus*, n = 6 for *B. modesta*, *S. nattereri* and *E. virescens*

Freq.	<i>C. auratus</i>		<i>B. modesta</i>		<i>S. nattereri</i>		<i>P. costatus</i>		<i>A. pectinifrons</i>		<i>P. blochii</i>		<i>P. pictus</i>		<i>C. paleatus</i>		<i>E. virescens</i>	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
100	85.8	3.3	82.7	3.7	79.2	3.8	73.9	3.8	83.3	6.0	69.3	4.6	81.4	6.0	86.4	3.9	89.0	9.1
200	73.3	4.3	81.5	4.0	77.8	3.1	71.9	4.9	84.0	5.1	69.5	6.0	80.7	5.9	85.0	2.0	89.3	7.8
300	68.8	3.3	82.2	3.8	74.8	3.2	68.9	5.6	83.4	6.8	73.1	10.3	77.7	4.5	84.1	3.0	85.0	8.0
400	63.9	2.9	73.5	3.4	71.7	2.7	67.5	3.3	81.1	6.7	69.4	9.5	73.7	4.5	80.3	4.9	80.6	4.3
500	64.0	4.0	68.5	3.9	70.8	3.4	64.1	4.1	80.6	6.9	68.3	10.1	67.2	3.8	80.1	4.0	77.7	3.0
600	64.1	4.2	66.3	4.0	70.2	4.3	64.1	3.4	80.7	7.2	70.7	9.9	67.3	5.3	79.7	2.9	81.6	4.9
800	64.0	2.7	68.2	3.1	69.8	3.1	64.9	6.1	79.9	8.4	70.3	12.4	69.3	5.4	82.4	5.4	82.7	6.5
1,000	64.6	3.0	72.0	3.7	69.0	2.8	64.9	3.6	80.2	9.3	72.7	13.4	71.6	8.4	86.3	6.2	82.8	5.2
1,500	71.5	3.1	75.2	2.5	72.2	2.2	66.6	4.3	84.6	8.5	72.9	13.0	71.6	7.2	95.9	6.6	87.7	9.0
2,000	80.0	2.0	80.2	1.8	79.0	2.8	66.3	2.3	88.7	9.6	73.7	13.3	70.2	7.6	105.6	5.3	95.0	6.4
3,000	96.4	4.5	88.7	3.4	88.5	3.8	68.9	3.4	94.0	6.2	74.6	8.4	72.9	7.6	121.1	3.5	107.2	6.2
4,000	107.4	4.3	106.5	5.6	103.0	7.1	82.5	4.5	107.1	6.7	80.4	8.3	81.3	7.5	132.9	4.9	119.2	7.1
5,000	119.5	3.4	122.2	2.5	116.8	4.8	93.1	7.3	115.7	6.3	86.2	5.8	86.4	10.6			124.4	5.0

quency represents the swimbladder muscles contraction rate. The energies of these sounds were mainly concentrated between 100 and 500 Hz and dropped off quickly with increasing frequencies (fig. 4a, c).

Second, loaches emitted broad-band knocking sounds with dominant frequencies below 500 Hz. Contrary to drumming sounds, knocking sounds are much shorter (10–20 ms vs. 100 ms or more) and sound energies of up to several kHz were found (fig. 4b).

Third, catfishes produced – in addition to drumming sounds – series of broadband pulses by rubbing their pectoral spines in a groove of the shoulder girdle. In these stridulatory sounds dominant frequencies ranged between 1 and 4 kHz without possessing a low-frequency maximum (fig. 4c).

Relationship between ABR-Audiograms and Sound Spectra

There were no clear differences in auditory sensitivity between vocal and nonvocal species. Among cypriniforms the sound-producing cobitid *B. modesta* and the nonvocalizing cyprinid *C. auratus* had similar hearing thresholds (mean overall difference: 3.4 dB). Similarly, the overall difference between the goldfish and the characid *S. nattereri*, which produced drumming sounds, was 1.5 dB (fig. 3a). No pronounced low-frequency hearing sensitivity was observed in the loach and the piranha although in both species mean energy of sounds were concentrated below 400 Hz (fig. 5a, b).

In catfishes stridulation sound spectra match the flat hearing curves, except for *C. paleatus* (fig. 5c–g). This cal-

Table 3. Interspecific differences between audiograms (dB) calculated by the General Linear Model (two-way ANOVA) and pairwise multiple comparison procedure (Bonferroni's method). All other differences between species were not significant ($p > 0.05$)

	Diff. of means \pm SE	p
<i>P. costatus</i> – <i>A. pectinifrons</i>	-17.8 ± 4.9	<0.05
<i>P. costatus</i> – <i>C. paleatus</i>	-24.9 ± 5.0	<0.001
<i>P. costatus</i> – <i>E. virescens</i>	-23.0 ± 4.9	<0.001
<i>P. blochii</i> – <i>C. paleatus</i>	-21.6 ± 5.0	<0.001
<i>P. blochii</i> – <i>E. virescens</i>	-19.7 ± 4.9	<0.001
<i>P. pictus</i> – <i>C. paleatus</i>	-20.6 ± 5.0	<0.01
<i>P. pictus</i> – <i>E. virescens</i>	-18.7 ± 4.9	<0.01

lichthyid species had the poorest hearing ability of all catfishes investigated (fig. 3b). Auditory sensitivity decreased rapidly above 800 Hz, and the main energies of sounds were concentrated between 1 and 2 kHz (fig. 5g). Interestingly, similar stridulation sound spectra did not result in similar high frequency hearing abilities in catfishes (fig. 3b). None of the pimelodid and doradid species, which produce two types of sounds, did possess two auditory sensitivity maxima (fig. 5c–g).

Sound energies of both types of sounds were 20–40 dB above the hearing thresholds in the larger catfish species such as *P. costatus*, *Pimelodus* and the loach *B. modesta* (fig. 5a, c, e, f). Acoustic signals of these four species were clearly audible without a hydrophone to human listeners. In

Table 4. Significant interspecific differences (Diff.) of means at representative frequencies tested using one-way ANOVA for each frequency and pairwise multiple comparison test (Bonferroni's method). Statistically significant differences following adjustment to the number of frequencies tested ($p < 0.0036$). Positive threshold differences mean a higher auditory threshold of the first species of a pairing at this particular frequency

100 Hz	Diff. (dB)	400 Hz	Diff. (dB)	1,000 Hz	Diff. (dB)	4,000 Hz	Diff. (dB)	4,000 Hz (continued)	Diff. (dB)
<i>Ca-Pc</i>	11.8	<i>Ca-Ap</i>	-17.2	<i>Ca-Ap</i>	-15.6	<i>Ca-Pc</i>	24.9	<i>Sn-Cp</i>	-29.9
<i>Ca-Pb</i>	16.4	<i>Ca-Cp</i>	-16.4	<i>Ca-Cp</i>	-21.7	<i>Ca-Pb</i>	26.9	<i>Sn-Ev</i>	-16.2
<i>Bm-Pb</i>	13.3	<i>Ca-Ev</i>	-16.7	<i>Ca-Ev</i>	-18.2	<i>Ca-Pp</i>	26.0	<i>Pc-Cp</i>	-50.4
<i>Pc-Cp</i>	-12.6	<i>Pc-Ap</i>	-13.6	<i>Sn-Cp</i>	-17.3	<i>Ca-Cp</i>	25.5	<i>Pc-Ev</i>	-36.7
<i>Pc-Ev</i>	-15.1	<i>Pc-Cp</i>	-12.8	<i>Pc-Ap</i>	-15.3	<i>Bm-Pc</i>	24.0	<i>Ap-Pb</i>	26.7
<i>Ap-Pb</i>	14.0	<i>Pc-Ev</i>	-13.1	<i>Pc-Cp</i>	-21.4	<i>Bm-Pb</i>	26.1	<i>Ap-Pp</i>	25.8
<i>Pb-Pp</i>	-12.1	<i>Ap-Pb</i>	11.7	<i>Pc-Ev</i>	-17.9	<i>Bm-Pp</i>	25.2	<i>Ap-Cp</i>	25.7
<i>Pb-Cp</i>	-17.1					<i>Bm-Cp</i>	26.4	<i>Pb-Cp</i>	-52.4
<i>Pb-Ev</i>	-19.7					<i>Sn-Pc</i>	20.5	<i>Pb-Ev</i>	-38.8
						<i>Sn-Pb</i>	22.6	<i>Pp-Cp</i>	-51.5
						<i>Sn-Pp</i>	21.7	<i>Pp-Ev</i>	-37.9

Ap = *A. pectinifrons*; *Bm* = *B. modesta*; *Ca* = *C. auratus*; *Cp* = *C. paleatus*; *Ev* = *E. virescens*; *Pb* = *P. blochii*; *Pc* = *P. costatus*; *Pp* = *P. pictus*; *Sn* = *S. nattereri*.

the smaller species sounds are much fainter. In *A. pectinifrons* the energy maxima were 10–15 dB above thresholds, while a clear mismatch between dominant frequencies of stridulatory sounds and best frequencies of hearing existed in *C. paleatus* (fig. 5d, g).

Discussion

The present study demonstrates that ABRs could be elicited between 100 Hz and 5 kHz in every representative of all four otophysan orders – Cypriniformes, Characiformes, Siluriformes and Gymnotiformes. Previous observations of ABRs in chondrichthyes, basal osteichthyan groups such as osteoglossiforms and polypteriforms [Corwin, 1981; Corwin et al., 1982], as well as in several perciform families (Belontiidae, Cichlidae, Centrarchidae) gave evidence that auditory evoked potentials (AEP) can be picked up in all fishes similarly to higher vertebrates [Kenyon et al., 1998; Ladich and Yan, 1998]. Furthermore, the ABR waveforms in all otophysans examined showed features typical for AEPs such as (1) no cancelling out of traces evoked by tone bursts of opposite polarities, (2) increase in the onset delay with decreasing frequency and sound pressure levels and (3) decrease in duration of the ABR waveform with increasing frequency. This consistency in waveform characteristics together with the similarity of ABR- and behavioral audiograms in the goldfish [Jacobs

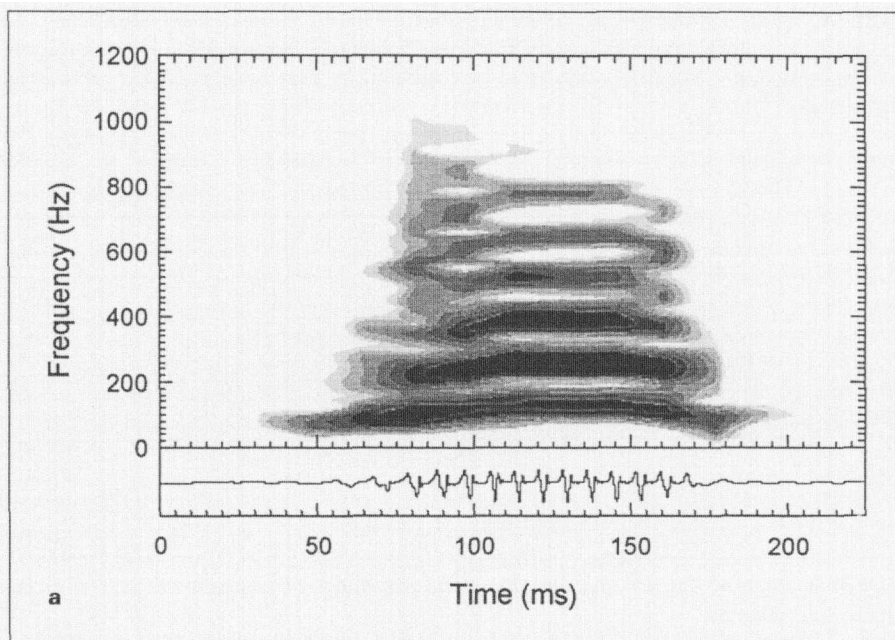
and Tavolga, 1967; Popper, 1971; Kenyon et al., 1998] indicates that the ABR-recording technique is a reliable method for comparing auditory sensitivity among otophysines.

Interspecific Differences of Hearing Thresholds and Comparison with Other Otophysans

All otophysans examined have enhanced hearing abilities and showed high-frequency sensitivity maxima between 300 Hz and 2,000 Hz. These data generally agree with audiograms obtained in other cypriniforms, characiforms and siluriforms [Fay, 1988], except for the marine catfish *Arius felis*, which possesses an unusual low-frequency hearing ability [best hearing sensitivity: 200 Hz, upper hearing limit 1,000 Hz; Popper and Tavolga, 1981]. This pronounced low frequency sensitivity seems to be related to differences in inner ear morphology in aridiids, which have an enlarged utricle.

Detailed comparisons between audiograms gained by different methods are limited because thresholds differ in even the same species under different conditions. Discrepancies of 30–60 dB at particular frequencies were found in several species including the cod *Gadus morhua* and the goldfish *C. auratus* [Hawkins, 1981], the bullhead catfish *Ictalurus nebulosus* [Poggendorf, 1952; Weiss et al., 1969] and the blue gourami *Trichogaster trichopterus* [Saidel and Popper, 1987; Ladich and Yan, 1998]. These differences could be attributed partly to varying ambient noise levels, near field conditions (air loudspeaker vs. underwater

Fig. 4. Sonogram and oscillogram of (a) a drumming sound of *S. nattereri* (sampling frequency 4 kHz, filter bandwidth 30 Hz, time frame 32 ms, 50% overlap), (b) a knocking sound of *B. modesta* (sampling frequency 16 kHz, filter bandwidth 250 Hz, time frame 4 ms, 50% overlap) and (c) a drumming (arrow) and a stridulatory sound of *P. blochii* (sampling frequency 16 kHz, filter bandwidth 400 Hz, time frame 2.5 ms, 50% overlap). Note that difference in the graphic presentation (sonogram) of drumming sounds in *Serrasalmus* and *Pimelodus* are due to the different filter bandwidth used.



speaker), different conditioning techniques (heart rate, food reward), surgery (saccular microphonics) and probably stimulus duration (e.g. continuous pure tone versus short tone bursts) [Hawkins, 1981; Popper et al., 1973; Kenyon et al., 1998; Ladich and Yan, 1998].

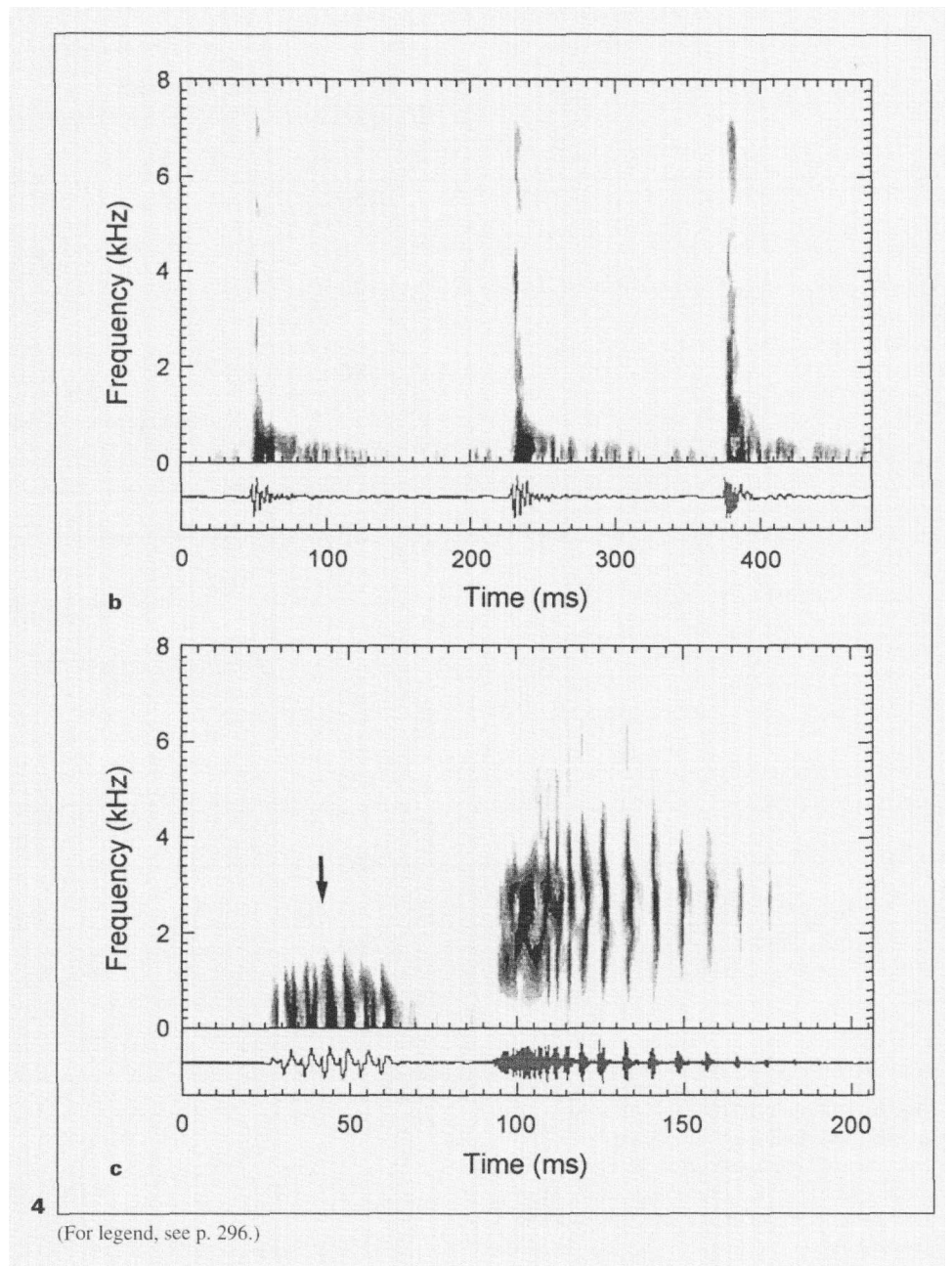
In the piranha *S. nattereri*, behavioral thresholds gained from avoidance conditioning experiments, where fin movements were taken as a response to pure tones of 8–10 s duration, differed by 3 to 18 dB from ABR thresholds [Stabentheiner, 1988]. Behavioral thresholds were lower below 1,000 Hz and increased rapidly above 1 kHz. No behavioral thresholds could be obtained above 1,500 Hz. Nevertheless, it is assumed that *Serrasalmus* detects sounds up to several kHz because ABRs – and thus a response of the whole auditory pathway – could clearly be recognized above 1,500 Hz. *Astyanax*, a related characid, perceived sounds up to 7.2 kHz [Popper 1970].

In general, it is assumed that ABR-audiograms differ from behavioral curves in giving lower thresholds with increasing frequencies mainly due to differences in sound stimuli presented [Kenyon et al., 1998]. The ABR-recording technique is a suitable method for comparing the auditory sensitivities among representatives of a large taxon because it allows measurements under identical acoustical conditions, independent of limitations of training different species.

The ABR-audiograms revealed major differences in auditory sensitivity among otophysans. Overall differences between hearing curves showed lowest auditory thresholds

in both pimelodids and one doradid catfish, while poorest sensitivity was observed in *A. pectinifrons*, *C. paleatus* and *E. virescens*. Both cypriniforms – *C. auratus* and *B. modesta* – as well as the characid *Serrasalmus* possess intermediate auditory sensitivities. Significant differences were also observed at all representative frequencies tested and were especially pronounced at high frequencies (3–5 kHz). While in the mid-frequency region cypriniforms and the characid were similarly sensitive as *Pimelodus* and *Platydoras* their auditory sensitivity decreased above 2 kHz clearly. These differences reflect neither the systematics of otophysans nor the ability to communicate by sounds. The nonvocal goldfish revealed auditory sensitivities similar to the vocalizing loach and the piranha. Additionally, the worst hearing abilities could be found in sound-producing as well as nonvocal species (*C. paleatus* vs. *E. virescens*).

Similarity between audiograms was found in closely related (*P. blochii* and *P. pictus*) as well as distantly related fishes (cypriniforms and the characid), and significant differences existed within the doradids. Audiograms of representatives of one genus measured by the same technique are sometimes almost identical such as in *Eupomacentrus* [Myrberg and Spires, 1980] or are very similar [*Astyanax* – Popper, 1970; *Trichopsis* – Ladich and Yan, 1998]. Different hearing abilities in closely related genera are rarely sufficiently explained by differences in accessory hearing structures or inner ear morphology except in the holocentrids. In this group auditory capacities apparently increase



with decreasing distances between swimbladder diverticula and the inner ear based on improved coupling between air-filled chambers and the inner ear [Coombs and Popper, 1979]. In labyrinth fishes, differences are thought to be caused by the different-sized suprbranchial chambers, an air-breathing cavity dorsally of the gills; it lies close to the hearing organs and thus enhances sound perception at its resonance frequency [Ladich and Yan, 1998; Yan 1998].

Among catfishes the rather poor hearing ability of *Corydoras* might be explained by its small swimbladder, and the fact that it is also encased in bone [Chranilov, 1929]. The

reduction and encapsulation of the swimbladder in this genus may be an adaptation to its air-breathing habits. It might reduce buoyancy in these bottom-dwellers due to the air-filled vascularized hindgut. On the other hand, the unusual high-frequency hearing ability of certain catfishes cannot currently be explained on the basis of morphological specializations.

Correlation between Sound Production and Hearing

Comparing the auditory sensitivity and sound spectra in otophysan fishes might yield information on the constraints

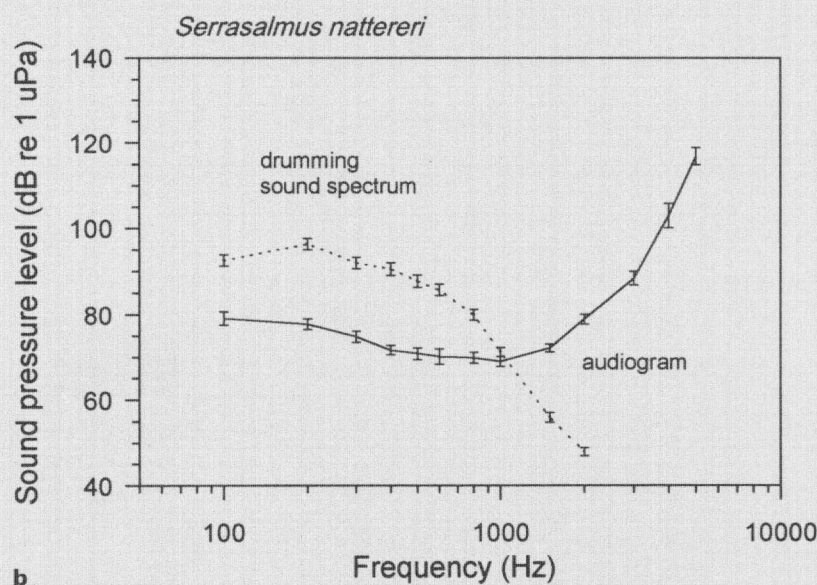
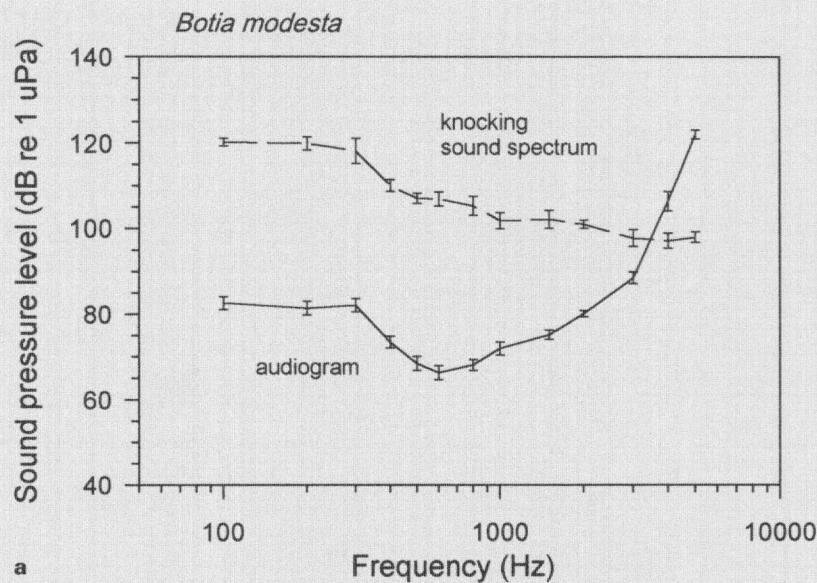


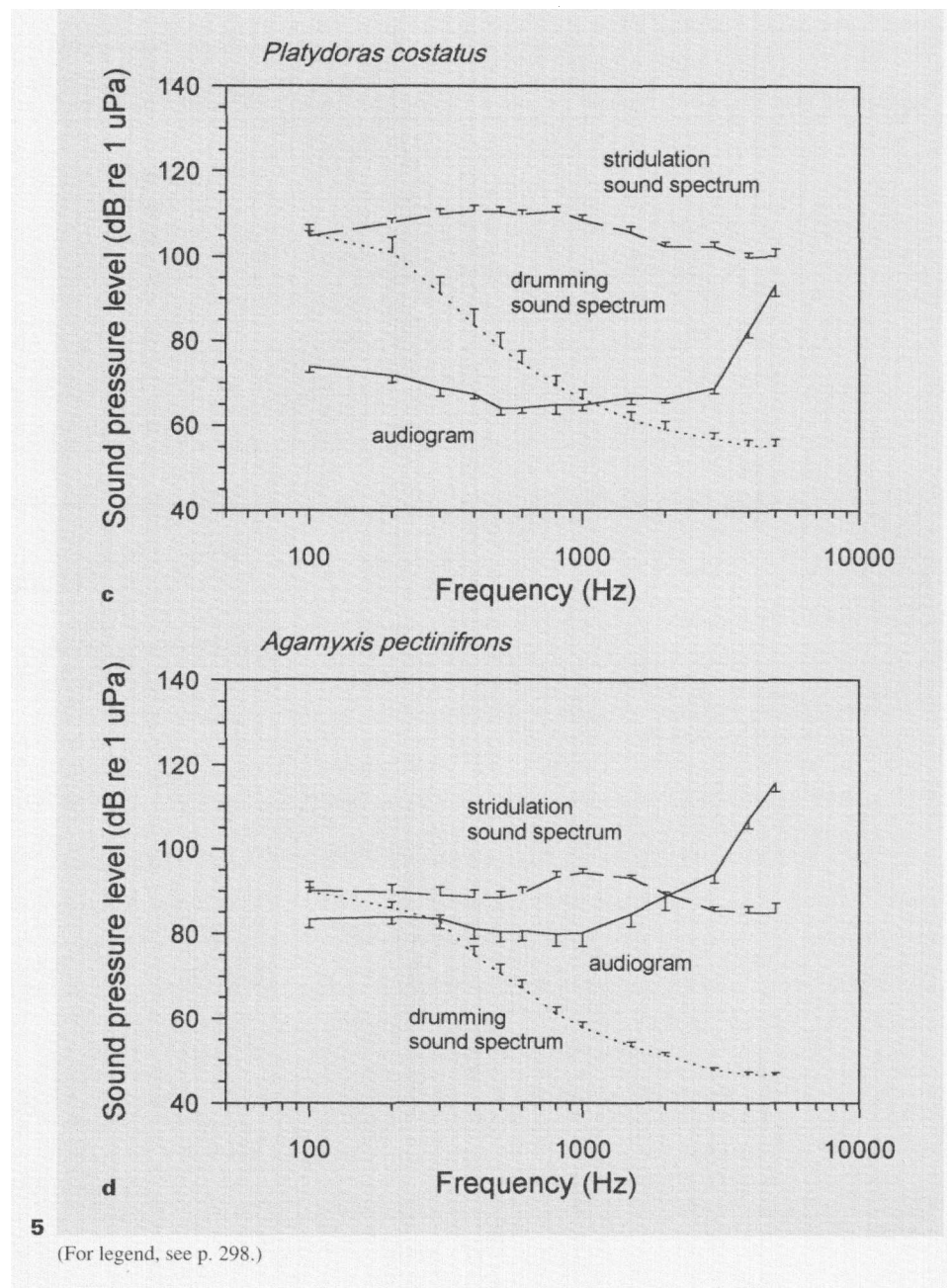
Fig. 5a-g. Audiograms (means \pm SE) of investigated otophysans in relation to spectral and intensity characteristics of sounds. In species emitting two types of sounds, error bars are only drawn in one direction to avoid overlapping.

involved in the evolution of hearing specializations. Such comparison must also include nonvocalizing species in order to determine whether these species underlie different selective pressures and thus develop other auditory sensitivities.

The present study provides evidence that the hearing curves of nonvocalizing species do not significantly differ from sound-producing fish. The audiogram of *Carassius* does not differ in any frequency from the cobitid *Botia*, which emits loud broad-band knocking sounds or from the

characid *Serrasalmus*, which utters low-frequency drumming sounds. The hearing sensitivity in the nonvocal knife-fish *Eigenmannia* differs from only three out of seven vocalizing species. The development of sound-generating (sonic) mechanisms in several otophysans did not seem to selectively improve hearing abilities in species utilizing the acoustical channel for communication.

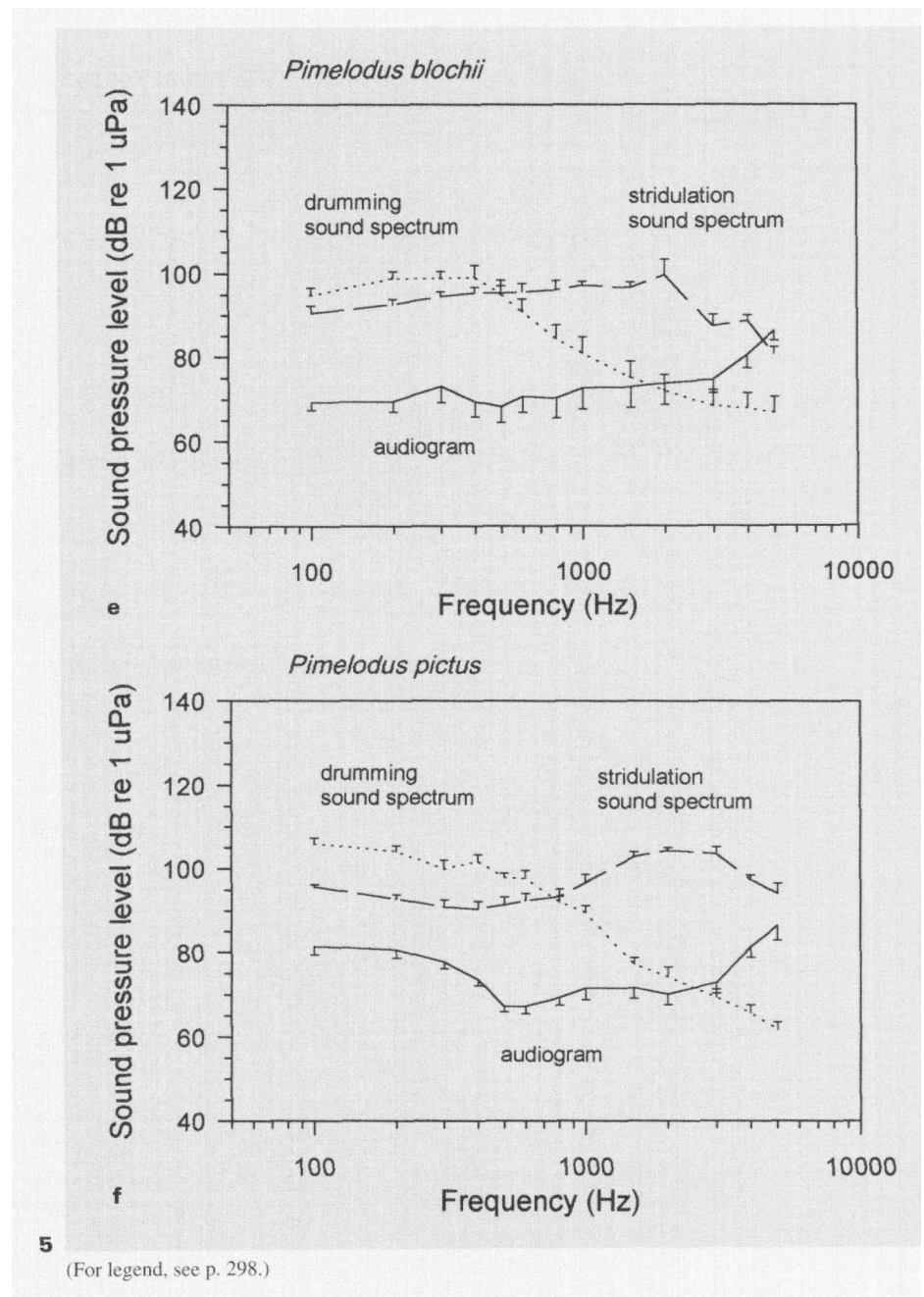
Comparison of whole audiograms and total spectra of sounds revealed that species emitting low-frequency sounds did not possess a pronounced low-frequency hearing sensi-



tivity nor did all species emitting high-frequency stridulation sounds reveal low auditory thresholds at higher frequencies. However, this lack of a match does not necessarily imply that fishes cannot detect conspecific sounds, because the difference between hearing thresholds and sound pressure levels must be considered. Specifically, communication distances in *Agamyxis* are limited because SPLs are maximally 8–15 dB above hearing thresholds at particular frequencies. On the other hand, acoustic signals can easily be recognized in species emitting high-amplitude

sounds such as the green loach (40 dB above threshold) despite the fact that dominant frequencies of sounds are outside the best auditory sensitivity. Additionally, the above comparisons cannot provide any information about which sound characteristics (spectral, temporal, intensity) are exploited by otophysan fishes [Myrberg et al., 1978].

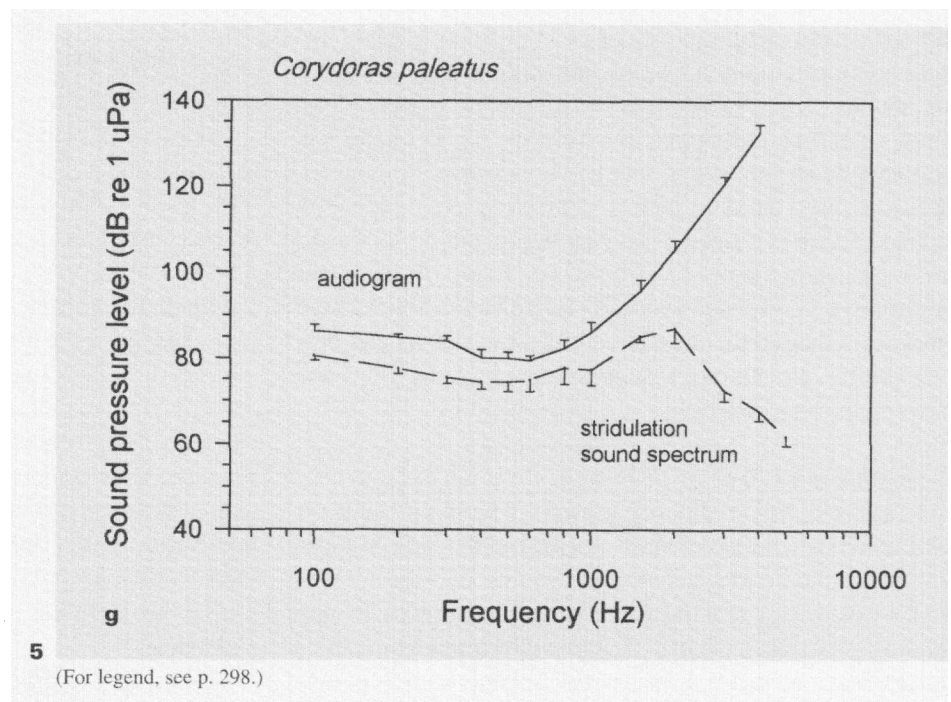
Differences in sound pressure levels between species cannot be sufficiently explained by communication distances. During agonistic interactions, for example, contestants emit sounds when they are very close to each other,



typically 0–5 cm, independently of SPLs [Ladich et al., 1992; Ladich, 1997b; Ladich and Yan, 1998]. Different loudness might indicate different efficiencies of sound-generating organs or sound transmission characteristics of the environment, different communicative purpose of acoustic signals, or ecological constraints such as predation risks. A positive correlation between both curves, which means a concentration of sound energies in a frequency region with low auditory sensitivity, might limit acoustic communication while increasing the risk of interception by predators

or intraspecific interceptors [Myrberg, 1981]. In the otophysans investigated, however, no limitation of acoustical communication exists because they communicate over short distances (<10 cm) under laboratory conditions. This is also assumed for *Corydoras*, because males typically vocalize at distances less than 1 cm from the female during courtship [Pruzsinszky and Ladich, 1998].

The mere perception of conspecific sounds does not imply that sound production evolved in correlation with auditory sensitivity in a particular species. Especially the



fact that the most sensitive hearing range does not coincide with dominant frequencies in any species investigated contradicts this assumption. No pronounced low-frequency hearing sensitivity exists in species emitting swimbladder drumming sounds or even knocking sounds. Flat hearing curves occur only in species emitting stridulatory sounds, such as pimelodids and the doradid *Platydoras*, but the stridulating catfish *Corydoras* have a very poor high-frequency hearing sensitivity. Finally, none of the catfish species producing two types of sounds has two auditory sensitivity maxima.

In summary, when comparing hearing curves of vocalizing and nonvocalizing species as well as audiograms of species emitting drumming sounds to those producing stridulatory sounds or knocking sounds, no clear relationship can be found between sound spectra and the auditory sensitivity. Therefore, acoustical communication does not seem to be the major force for the evolution of hearing specializations (Weberian apparatus) in otophysan fishes.

Correlation between Hearing and Sound Production in Other Teleosts

The lack of correlations between main energies of sounds and best hearing sensitivities in otophysans contradict data gained in other vocal teleosts. However, all other studies were limited to one species or representatives of one genus [Cohen and Winn, 1967; Myrberg and Spires, 1980; Stabentheiner, 1988; Ladich and Yan, 1998]. Schellart and

Popper [1992] statistically compared the geometric mean of the bandwidth of the sonogram in 15 species with that of the audiogram as published by various authors [Fay, 1988] and found a 'moderate but significant' correlation.

Is the generation of certain sound types related to particular hearing abilities? The development of the diverse swimbladder muscles is clearly not limited to certain hearing abilities, environmental or systematic constraints. Low-frequency drumming sounds are generated by hearing specialists such as catfishes, characids [present study; Markl, 1972] and mormyrids [Crawford and Huang, in press] as well as by numerous hearing generalists such as cods [Hawkins and Rasmussen, 1978; Hawkins, 1993], triglids [Tavolga and Wodinsky, 1963], toadfishes [Cohen and Winn, 1967; Fish and Offutt, 1972; Fine, 1981; Brantley and Bass, 1994] and drums [Ono and Poss, 1982; Connaughton and Taylor, 1996]. Knocking sounds, a short broad-band sound with energy maxima below 500 Hz, were also found in hearing specialists such as loaches (present study) as well as in generalists such as the sculpin *Cottus gobio* [Ladich, 1989]. Broad-band high-frequency sounds (>500 Hz), on the other hand, are mainly known from groups having enhanced hearing abilities such as mormyrids [Rigley and Marshall, 1973], cyprinids [Ladich, 1988], catfishes [Rigley and Muir, 1979; Ladich, 1997b; present study], and gouramis [Ladich and Yan, 1998], although they have also been described in hearing generalists, for example centrarchids [Ballantyne and Colgan, 1978], damselfish [Spanier, 1979; Myrberg et

al., 1993] and cichlids [Lanzing, 1974]. Hearing generalists probably detect only a limited frequency range of all types of sounds. Even sound energies of low-frequency drumming sounds cannot be perceived above 200 Hz by the hearing generalist *Porichthys notatus* [Cohen and Winn, 1967]. Because most studies lack a detailed analysis of whole sound spectra it is unclear to what degree sound production matches hearing in these vocal species. Based on our current knowledge a correlated evolution has to be assumed in some species, although the distribution of sonic organs and hearing abilities among otophysans and other teleost fishes does not support this generally.

Evolution of Hearing in Fishes

The similarity of auditory sensitivity between vocalizing and nonvocalizing otophysan species and the lack of a clear relationship between hearing curves and sound spectra leads to the assumption that the Weberian apparatus evolved prior to or mostly independently from the development of sound-generating mechanisms. This notion appears to be supported by a phylogenetic analysis of the sound producing mechanisms within this group of teleosts. According to Fink and Fink [1996], cypriniforms are the most primitive group among the otophysans with Characiphysi (characiforms and Siluriphysi) being its sistergroup. Interestingly, only a few representatives of the large order of cypriniforms are known to be vocal [Stout, 1963; Ladich, 1988; Valinsky and Rigley, 1981] and in no case was there a sonic/vocal organ described. This indicates that sound generating structures are less specialized within Cypriniformes. Highly specialized sonic organs such as swimbladder drumming muscles clearly only evolved in its sistergroup Characiphysi. Many characids (jaraqui, piranha) as well as numerous catfish families possess extrinsic swimbladder muscles [Schaller, 1967; Markl, 1971; Ladich and Bass, 1998]. Phylogenetic analysis revealed that the Weberian apparatus and thus enhanced hearing abilities seem to be the main feature of all otophysans [Fink and Fink, 1996] while sound production evolved occasionally in Cypriniformes and on a regular basis in Characiphysi.

Which environmental constraints might have caused the ancestors of otophysans to enhance their hearing abilities? Freshwater environments are generally much quieter than marine habitats due to the smaller influence of wind and coastal surf. Additionally, most of the sound energy that propagates in shallow freshwater habitats is of higher frequency [Hawkins and Myrberg, 1983; Schellart and Popper, 1992]. Lowering the hearing threshold and extending the frequency range would improve the chance of survival during attacks by predators and/or enable better prey detection

[Canfield and Eaton, 1990; Eaton et al., 1995; Canfield and Rose, 1996]. Markl [1972] observed that piranhas attacked prey items accompanied by splashing noise significantly more often than those presented silently. These advantages help explain the success of this taxon. The otophysans contain about 6,500 species; this is equivalent to 27% of all known fish species and about 64% of freshwater species [Nelson, 1994].

Predator avoidance through development of hearing may largely explain the evolution of ultrasonic hearing in numerous nocturnally active, flying insects including moths, crickets, praying mantises, beetles and katydids [Hoy, 1992]. Although no such clear relationship between hearing and predator vocalization has yet been described in fishes, some data indicate that such an adaptation also evolved underwater. Mann et al. [1997] demonstrated that clupeid fish can detect ultrasound (25–130 kHz) and respond to echolocating pulses of dolphins in playback experiments by escape behaviour.

Based on the results of the present study it appears that the major selective pressures involved in the evolution of the Weberian apparatus are predator avoidance and/or prey detection in quiet freshwater habitats and less so the optimization of acoustical communication.

Acknowledgements

I thank Art Popper for critically reading the manuscript and for discussion on this topic, and two anonymous reviewers for their suggestions, which improved the manuscript. Furthermore I thank Barbara Gereben-Krenn and Axel Schmid for providing *C. paleatus* and *E. virescens*, subsequently. This study was supported by the Austrian Science Fund (FWF grant No. 12411-BIO).

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