Chapter 3
Evolution of the Understanding of Fish Hearing

Olav Sand, Arthur N. Popper, and Anthony D. Hawkins

3.1 Introduction

Fishes have no external auditory structures. Nevertheless, several thousand years before the first formal studies of fish audition in the late nineteenth century, a number of observers, including fishers, became aware that fishes can hear. Information on the very earliest observations on fish bioacoustics can be found in several reviews written by some of the leading twentieth-century researchers on fish hearing, including Parker (1918, 1903), von Frisch (1936, 1938a), Kleerekoper and Chagnon (1954), and Moulton (1963). Translations of several of the earlier papers are found in a volume compiled by Tavolga (1976). This chapter focuses on the origin and evolution of the current understanding of the mechanisms of hearing and the hearing capabilities of fishes based upon experiments starting in the nineteenth century.

A related topic of considerable interest and importance, with a similar long history, is sound communication by fishes, but the topic is beyond the scope of this chapter. However, those interested in it are directed to papers by (among others) Moulton (1963), Tavolga (1971, 1977), and Hawkins and Myrberg Jr (1983).

Two other areas, the anatomy of the auditory central nervous system (CNS) and the physiology of the CNS in fishes, are not covered in any depth in this chapter because much of the work has been performed since the late 1970s. For those interested in the anatomy of the CNS, there are excellent reviews by Northcutt (1980)

O. Sand (✉)
Department of Biosciences, University of Oslo, Oslo, Norway
e-mail: olav.sand@ibv.uio.no

A. N. Popper
Department of Biology, University of Maryland, College Park, MD, USA
e-mail: apopper@umd.edu

A. D. Hawkins
Loughine Ltd, Kincraig, Blairs, Aberdeen, UK

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and by McCormick (1992, 1999). A paper by Walton et al. (2017) reviews both the anatomy and physiology of the CNS.

3.2 Anatomical Studies of the Inner Ear

Early in the nineteenth century, the German physiologist Ernst Heinrich Weber (1795–1878) published a seminal study of the auditory system of fishes. In his study, Weber (1820) illustrated not only the inner ears of the carp (*Cyprinus carpio*), a close relative of the goldfish (*Carassius auratus*), but also described a series of bones between the swim bladder and the inner ear (Fig. 3.1). Moreover, Weber rightly suggested an auditory function of this bony chain, later termed the Weberian ossicles[1] (see Sect. 3.6.3). Fishes that possess Weberian ossicles are referred to as *otophysans* (or ostariophysans).

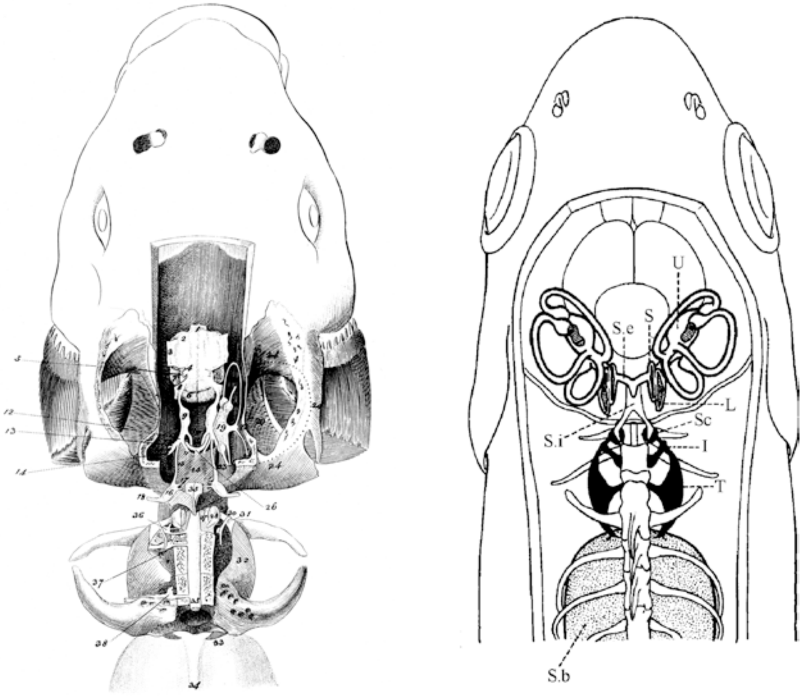

Fig. 3.1 The Weberian ossicles. Left: Original drawing by Weber (1820). Right: Schematic illustration by von Frisch (1936). Labels: I—intercalarium; L—lagena; S—saccule; Sc—scaphium; S.i—sinus impar; S.e—sinus endolymphaticus; S.b—swim bladder; T—tripus; U—utricle

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[1] A copy of Weber (1820) can be found at: https://archive.org/details/b22007374/page/42. This includes the complete text (in Latin) and all of the figures.

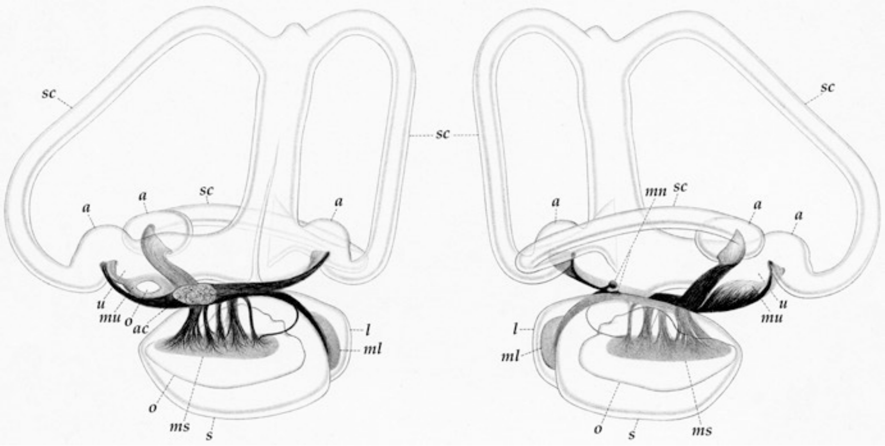

Fig. 3.2 Drawings of the ear of the Atlantic salmon, *Salmo salar*, from plate XIV of Retzius (1881). Left is a medial view (anterior to the left). Right is a lateral view (anterior to the right). Labels: a—ampullae; l—lagena; ml, ms, and mu—epithelia (maculae) of otolith organs; mn—macula neglecta; o—otoliths; r—rami of the eighth cranial nerve to various ear parts; s—saccule; sc—semicircular canals; u—utricle

In the later nineteenth century, the Swedish physician and anatomist Gustaf Retzius (1842–1921) published a set of volumes in which he beautifully illustrated the detailed structure of the ears in many vertebrate species from lampreys to mammals (Retzius 1881). Of these, 48 species were elasmobranchs (cartilaginous fishes) or teleosts (bony fishes) (Fig. 3.2) showing details of the anatomy of fish ears that are of immense value even today. Retzius illustrated the major otolith organs (the saccule, lagena, and utricle), the semicircular canals, and their innervation. He also showed the presence of another organ, the macula neglecta, which consists of two patches of sensory tissue overlain by a gelatinous cupula (mn in Fig. 3.2). The macula neglecta is diminutive in bony fishes and terrestrial vertebrates, but is much larger in many elasmobranch species. In these species, it may be involved in hearing (Tester et al. 1972; Fay et al. 1974; Corwin 1977, 1981).

The morphology of the ear was examined in detail by other investigators in the first part of the twentieth century, with a focus on comparative morphology (de Burlet 1931), although some early workers also asked questions about function of the inner ear in hearing (e.g., Werner 1926). Whereas the earlier workers only had access to studies with the light microscope for anatomical studies, the advent of electron microscopy allowed for ultrastructural examination of the ear in the mid-twentieth century. One of the earliest workers to do this was the Swedish physiologist Åke Flock, who used transmission electron microscopy (TEM) to investigate the structures of the sensory epithelia in the burbot, *Lota lota* (e.g., Flock and Wersäll 1962; Wersäll and Flock 1965; Flock 1970). Flock and his colleague Jan Wersäll demonstrated the structure and the morphological polarization of the ciliary bundle of hair cells, with a single true cilium, the kinocilium, at one end of a bundle

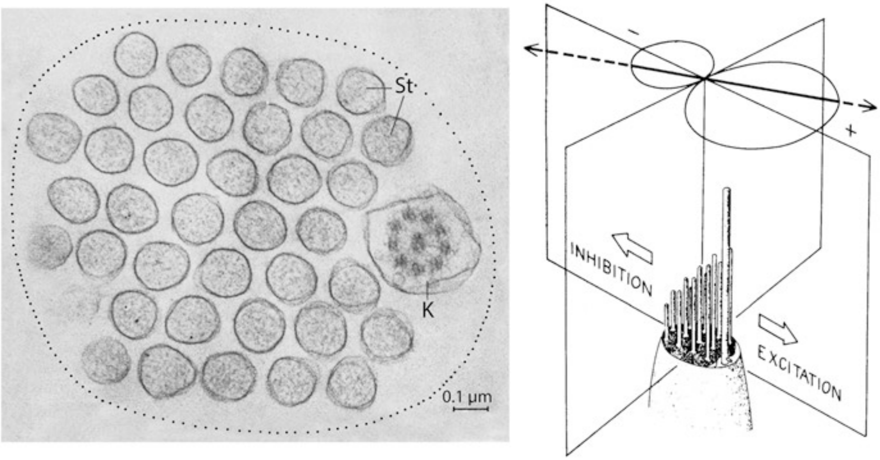

Fig. 3.3 Left: Morphological polarization of the ciliary bundle of hair cells (also see Fig. 3.4). Cross-section TEM of a sensory hair bundle showing a single kinocilium (K) at one end of a bundle of stereocilia (St). Dotted line (inserted using Photoshop) indicates the circumference of the apical surface of the hair cell. (From Flock and Wersäll 1962, with permission). Right: Physiological polarization of hair cells. When the ciliary bundle is bent toward the kinocilium, the hair cell depolarizes and the firing rate from the afferent nerve fiber increases. The hair cells hyperpolarize when bending is in the opposite direction. As indicated by the polar coordinate sketch, the magnitude of the depolarization exceeds hyperpolarization at equal bending in opposite directions. (From Flock 1971, with permission)

of stereocilia (Fig. 3.3 left and Fig. 3.4). He also demonstrated that there was a distinct hair cell orientation pattern in each of the otolith organs, though the saccular data, based on TEM, were shown to be inaccurate in later studies using scanning electron microscopy (SEM) (Popper 1981). Finally, Flock demonstrated that the sensory hair cells of fishes are not only morphologically polarized but also physiologically polarized, meaning that their electrical response is dependent on the bending direction of the ciliary bundles (Fig. 3.3, right) (Flock 1964, 1971). Thus, Flock demonstrated that sensory hair cells are directionally sensitive, a feature of crucial importance regarding the ability to discriminate between sound directions (Sect. 3.8).

Whereas these earlier workers suggested that the hair cell polarization in the ear was important, this was finally demonstrated in physiological studies on the goldfish by the Japanese investigator Taro Furukawa and colleagues (e.g., Furukawa and Ishii 1967; Ishii et al. 1971; Furukawa et al. 1972) and reviewed in an historical context by Furukawa (2002). In the first of a series of papers, Furukawa and Ishii (1967) recorded from single fibers of the eighth nerve to the saccule and demonstrated that different epithelial regions along the saccular epithelium responded to different frequencies. This was the first experimental evidence of a peripheral place mechanism for frequency discrimination in fishes. However, a possible role of such a mechanism in fishes is still largely unexplored.

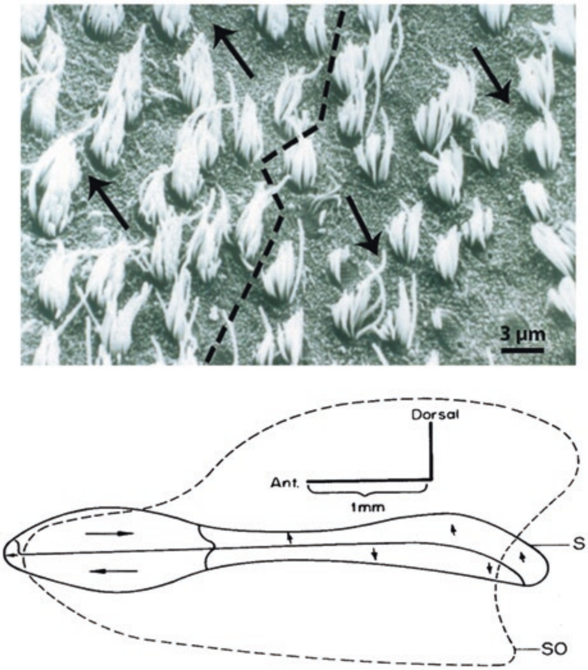

Fig. 3.4 Upper: Hair cell orientation patterns in fishes. Scanning electron micrograph from a lizardfish (*Sardia* sp.). Hair cell orientation is defined as the direction from the center of the bundle of stereocilia and toward the kinocilium. Hair cells to the left of the dashed line are oriented to the upper left, whereas those to the right are oriented in the opposite direction. Lower: The saccular hair cell orientation pattern in the lake whitefish. The saccular (S) macula is partially overlain by otolith (SO), represented by dashed line. Arrows indicate the orientation of the ciliary bundles in each region, with different orientation groups separated by solid lines. (From Popper 1976, with permission)

Furukawa and Ishii (1967) also showed that the hair cells with opposing orientations responded to different phases of the signal, a finding that was later further confirmed in the goldfish (Piddington 1972; Fay 1974b). Furukawa and colleagues also did a series of studies on synaptic function in the ear of goldfish as well on the ultrastructure of sensory hair cells in fishes (e.g., Hama 1969; Hama and Saito 1977).

3.3 Ideas About Fish Hearing Prior to 1900

In his *History of Animals* (Peri ta zôia historiôn), the Greek philosopher Aristotle (384–322 BCE) declared that fishes can hear, although he could not identify any organs of hearing. Some 400 years later, the Roman author and naturalist Pliny the Elder (23–79 CE), in his *Natural History* (Naturalis Historia), also concluded that fishes do not appear to have a hearing organ but can still hear. Later, several Roman authors confirmed the assumption that fishes can hear by presenting anecdotal evidence, as demonstrated by Claudius Aelianus (175–235 CE):

> Those who live by the lake of Marea catch the Sprats there by singing with the utmost shrillness, accompanying their song with the clash of castanets. And the fishes, like women dancing, leap to the tune and fall into the nets spread for their capture. And through their dancing and frolics the Egyptians obtain an abundant catch.[2]

Claudius Aelianus also described dense calcareous objects, later termed otoliths, in several species and linked these structures to hearing. This impressive speculation was not explored further until Casserius (1609) discovered that fishes possess internal ears.

Much later, Izaak Walton (1593–1683), an English writer and avid angler, wrote the most famous of all books on angling, *The Compleat Angler or the Contemplative Man's Recreation* (Walton 1653), which is still in print in a somewhat updated edition (Walton and Cotton 1861). Walton noted:

> And this reason of Sir Francis Bacon has made me crave pardon of one that I laughed at for affirming that he knew Carps come to a certain place, in a pond, to be fed at the ringing of a bell or the beating of a drum. And, however, it shall be a rule for me to make as little noise as I can when I am fishing…

By the eighteenth century, it was well known that the critical organs of hearing in man and other terrestrial vertebrates resided in their inner ears. Consequently, the presence of inner ears in fishes was considered firm evidence for the ability of fishes to hear. For example, Hunter (1782) stated:

> As it is evident that fish possess the organ of hearing, it becomes unnecessary to make or relate any experiment, made with live fish, which only tends to prove this fact.

This view was generally accepted by all the leading physiologists during the nineteenth century, as reviewed by Parker (1903). However, toward the end of the nineteenth century, it became increasingly clear that the inner ear of terrestrial vertebrates has the dual sensory function of hearing and balance (*equilibrium*, i.e., sensitivity to various types of acceleration). Because no traces of the complex structures of the inner ear responsible for hearing in terrestrial vertebrates (e.g., basilar papilla, cochlea) were evident in the fish labyrinth (defined as all parts of the inner ear) (Platt 1983), it soon became a general assumption that the ear was a sense organ only for balance (Lee 1898). This new understanding caused a shift in the common assumption that fishes can hear, and the pendulum quickly swung away to the opposite conclusion. Critical scrutiny of previous reports of hearing in fishes revealed mainly anecdotal evidence, and it was proposed that the observed responses to presumed auditory stimuli may instead have been elicited by visual cues (e.g., Kreidl 1896). This uncertainty catalyzed numerous experiments aimed at clarifying whether fishes can hear.

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[2] http://www.attalus.org/translate/animals6.html#30 (see section 30), from AELIAN: ON THE NATURE OF ANIMALS, book 6

3.4 Experimental Studies Demonstrating Hearing in Fishes

The first controlled experimental study on fish hearing was probably performed by the American physiologist G. H. Parker (1903), who developed a method to test hearing in fishes. He built an apparatus he referred to as a "sounding board" attached to the outer wall at one end of a large aquarium. A bass violin string was stretched on the board in such a way that the 40 Hz sound generated by the string's vibrations was transmitted into the aquarium. The study used the mummichog (referred to by Parker as the green killifish), *Fundulus heteroclitus*, a hardy marine species common along the US east coast.

Parker examined innate behavioral responses of mummichogs to the sound from a violin string and found that the fish consistently responded to the sound with rapid movements of their pectoral fins. Whereas this suggested hearing, Parker was concerned that the whole tank was being vibrated by the string, and that this could have resulted in the fish responding to alternative, non-acoustic stimuli. To test this idea, Parker prevented movement of the tank walls by using a tuning fork vibrating at 128 Hz as a source and found that the mummichog again responded to the sound, leading him to conclude that he had demonstrated hearing. He also performed a series of experiments on fish with impaired inner ears and lateral line systems, and the results supported the idea that the fish detected sound via the ears (see Sect. 3.6).

At that time, researchers working on several other species doubted that fishes could hear because no innate responses to sound were observed. However, the German investigator Karl von Frisch (later awarded the Nobel Prize for his work on the dance language of bees) pointed out that observation of innate responses may be an unreliable method for studying sensory abilities in animals. Therefore, von Frisch (1923) questioned the quality of previous studies of hearing in fishes and developed his own method that involved training a fish to behave in an unambiguous manner when it detected a particular sound. Training paired a conditioned stimulus (sound) with an unconditioned stimulus to which the fish responded without training. In the first study employing this method, von Frisch (1923) trained blinded catfish (brown bullhead, *Ameiurus nebulous*) to respond whenever he whistled, by pairing the sound with food. The fish learned to respond quite quickly and were very consistent in their response.

3.5 What Fishes Hear?

Although the studies by Parker (1903) and von Frisch (1923) demonstrated that fishes can hear, the frequency range (bandwidth) of sounds they could hear was still not known. Later, von Frisch and his students addressed this question using a conditioning technique. Indeed, many of the present ideas on fish hearing were first explored by von Frisch, his Dutch student Sven Dijkgraaf and many of Dijkgraaf's students, including Arie Schuijf (Sect. 3.8). Dijkgraaf provided fundamental thinking about both fish hearing and the role of the lateral line, as discussed in Sect. 3.6.

Several of the early studies revealed that responses to sound were evoked most readily in otophysan species (reviewed by von Frisch 1936, 1938a). However, later studies showed that the audible frequency ranges of several species within some non-otophysan taxa are similar to those of some otophysan species (see Sect. 3.5.1.2).

3.5.1 Auditory Frequency Range and Sensitivity

3.5.1.1 Otophysans

The conditioning studies by von Frisch were continued by his student H. Stetter (1929) on two otophysans, the brown bullhead and the European minnow (*Phoxinus phoxinus*). Stetter explored both the frequency range of hearing (using tuning forks) and auditory sensitivity (using a whistle). He demonstrated that the brown bullhead could detect frequencies up to about 13 kHz and as low as 16 Hz, whereas European minnows could hear pure tones up to 5–7 kHz.

In order to examine auditory sensitivity (the lowest sound level detectable by the subject), Stetter used a whistle generating a fundamental tone of 660 Hz and then lowered the sound level until the fish failed to respond. The actual level of the auditory threshold was not established, but when Stetter and von Frisch submerged individual colleagues and students into a large aquarium to compare their ability to detect the same sounds as the European minnow (Fig. 3.5), they concluded that the minnow could hear as well as humans underwater.

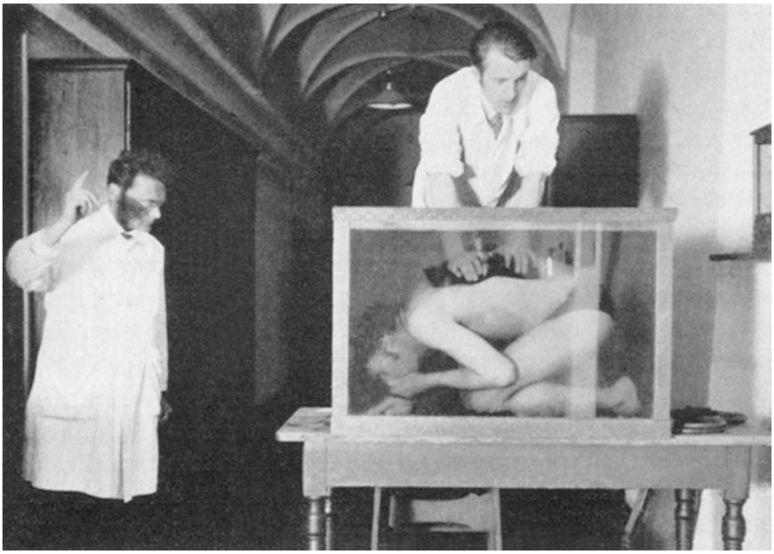

Fig. 3.5 Arrangement for comparing the hearing sensitivity of European minnow to that of a submerged human. Stetter is pushing on the person and von Frisch is overseeing the experiment. (From Stetter 1929, with permission)

Later, von Frisch and Stetter (1932) combined conditioning experiments with ablation of various structures assumed to play a role in sound detection in fish, in order to reveal the sensory components that actually are involved in hearing. This is discussed in Sect. 3.6 and in von Frisch (1936).

3.5.1.2 Non-Otophysan Species with Gas-Filled Chambers Associated with the Ear

A common feature of a number of non-otophysan taxa (which lack Weberian ossicles) including, but not limited to, the Mormyridae (elephant-nosed fishes), Anabantidae (labyrinth fishes), and Clupeiformes (e.g., Clupeidae, the herring family), is close contact between the ears and gas-filled compartments. The anatomy of such couplings and their presumed auditory roles are discussed in Sect. 3.6.3.

The hearing ability of a mormyrid, *Pollimyrus isodori*, was studied by Grete Diesselhorst (1938) who reported high auditory sensitivity with an upper frequency cutoff of about 3.1 kHz. This work was continued by Elisabeth Stipetić, who tested the hearing ability of another mormyrid, *Marcusenius macrolepidotus* (Stipetić 1939), with results almost identical to those for *Pollimyrus isodori*. Stipetić also studied the anatomy of the mormyrid ear in great detail.

Soon after, Hiltrude Schneider (1942) found that several anabantid species had hearing matching that of the mormyrids, with audible frequency ranges up to about 4.7 kHz. Diesselhorst, Stipetić, and Schneider were all students of von Frisch.

The first audiogram for a clupeid, the Atlantic herring (*Clupea harengus*), was reported by the Norwegian physiologist Per S. Enger (1967), based on neurophysiological recordings from the brainstem. The recordings revealed sensitive hearing with an upper frequency limit of about 4 kHz.

A bit earlier, William N. Tavolga and Jerome Wodinsky (1963), working in the Bimini Bahamas marine lab of New York's American Museum of Natural History (Tavolga 2002), examined hearing in several marine species. They found that the hearing ranges of two closely related squirrelfish species, *Holocentrus adscensionus* (longjaw squirrelfish) and *Holocentrus vexillarius* (dusky squirrelfish), differ greatly. Interestingly, both species have anterior projections of the swim bladder in close proximity to the ear, and both make similar sounds that they use in various, and similar, behavioral contexts. However, *H. adsensionus* can detect sound frequencies up to almost 3 kHz whereas *H. vexillarius* only detects sounds to about 1.2 kHz and with poorer sensitivity. The difference in hearing capabilities may be related to differences in the specific distance from the swim bladder to the ear in the two species (Nelson 1955). The relationship between the position of the anterior part of the swim bladder and hearing was further demonstrated in squirrelfish in a study on *Myripristis kuntee*, in which the swim bladder is in intimate contact with the ear. Hearing range and sensitivity were greater in *M. kuntee* than in the aforementioned species, supporting the notion that close proximity between the swim bladder and the ear improves hearing (Coombs and Popper 1979).

3.5.1.3 Non-Otophysan Species Without Gas-Filled Chambers Associated with the Ear

Diesselhorst (1938) also studied the hearing ability of the European eel (*Anguilla anguilla*) and Atlantic mudskipper (*Periophthalmus barbarus*) and found that they could only detect frequencies below 650 Hz. This agrees with later studies revealing an upper audible frequency cutoff usually below 1000 Hz in many of the non-otophysan species studied to date (reviewed by Popper et al. 2003). However, there is substantial variation in hearing ability among non-otophysan species, which is likely related to a possible auditory function of a swim bladder (see Sect. 3.6.3). Moreover, it must be recognized that there are hearing data for only just over 100 of the more than 34,000 species of fish (reviewed in Ladich and Fay 2013).

3.5.1.4 Other Investigations of Fish Hearing

Much of the work on fish hearing in the first half of the twentieth century was done in Europe, except for the studies by Parker and his students. In the second half of the twentieth century, several scientists from the United States entered the fish hearing research scene. Most notably, Tavolga, a biologist, and Wodinsky, a psychologist, approached the question of fish hearing from the perspective of modern psychoacoustics (see Sect. 3.5.1.2).

Basing their designs on the system developed by comparative psychologist M. E. Bitterman and his group (Wodinsky et al. 1962), Tavolga and Wodinsky used a shuttle box (Fig. 3.6) to train fish to perform a conditioned response whenever it heard a sound in order to avoid a weak electric shock (see Tavolga 2002 for an autobiographical history). Tavolga and Wodinsky (1963) combined this method with a “staircase” approach (explained in the legend to Fig. 3.6, lower) to determine hearing sensitivity in nine species of marine fishes. However, they were not able to determine whether the fishes were responding to sound pressure or particle motion (Tavolga and Wodinsky 1965).

Conditioning based on negative reinforcement (electric shock), rather than feeding, proved to be a very efficient method for obtaining sensory thresholds. The most common techniques in later studies have been respiratory conditioning (e.g., Fay 1969) (Fig. 3.7, top) and cardiac conditioning (e.g., Chapman and Hawkins 1973). In such studies, restrained fish are exposed to a sound followed a few seconds later by a mild electric shock. Normal unconditioned awareness or fright responses in fish are reduced heart and respiratory rates. After a few trials, the heart and respiratory rates change if the fish hears the sound, before receiving the shock, thus indicating detection of the sound.

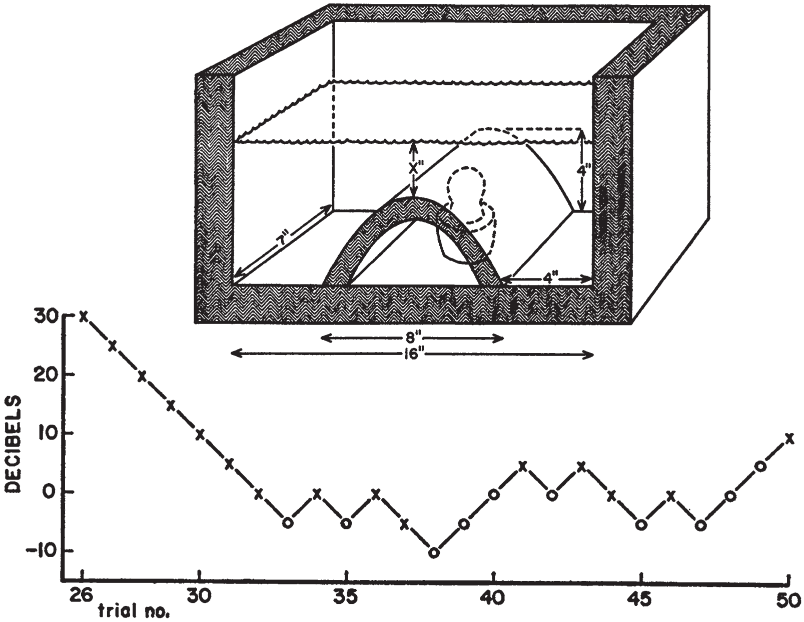

Fig. 3.6 Upper: Shuttle box used by Tavolga and Wodinsky (1963) to test hearing sensitivity in fishes. The box was partially divided into two chambers by a barrier, under which was an underwater speaker. Using electric shock as an unconditioned stimulus, fish were trained to cross the barrier whenever they heard a sound. If the fish heard the sound it would cross the barrier before shock onset, thus avoiding getting a shock. Lower: An example of the staircase method used in the same study to determine auditory thresholds. Data are for the longjaw squirrelfish at 1600 Hz. At the highest sound levels, the fish learned the task. Thereafter, the sound level was lowered for each successive trial resulting in a positive response (indicated by an "x"), until the animal did not respond (o). It then received a shock, and the sound was raised for the subsequent trial. Following the next positive response, the sound level was again lowered, and so on. The threshold was finally estimated as the sound level giving 50% probability for a positive response. In the depicted example, the threshold at 1600 Hz was −1.25 dB re 1 μbar, which, using today's terminology, would be 98.5 dB re 1 μPa. (From Tavolga and Wodinsky 1963, with permission)

3.5.2 Auditory Discrimination

The first published study of frequency discrimination in fishes was done by F. Westerfield (1922) in the United States. She worked with mud minnows (*Umbra limi*) that she trained to discriminate between two sounds with different frequencies produced by a ukulele, one sound meant food and the other a noxious stimulus. Fish were able to discriminate between the sounds, as demonstrated by different behavioral responses to the two sounds. However, the work was rather limited and does not provide full insight into frequency discrimination by fishes.

This was followed by a more extensive study by Stetter (1929), who was the first to systematically explore auditory frequency range, sensitivity, and frequency discrimination in a fish. Stetter trained European minnows to respond to one sound

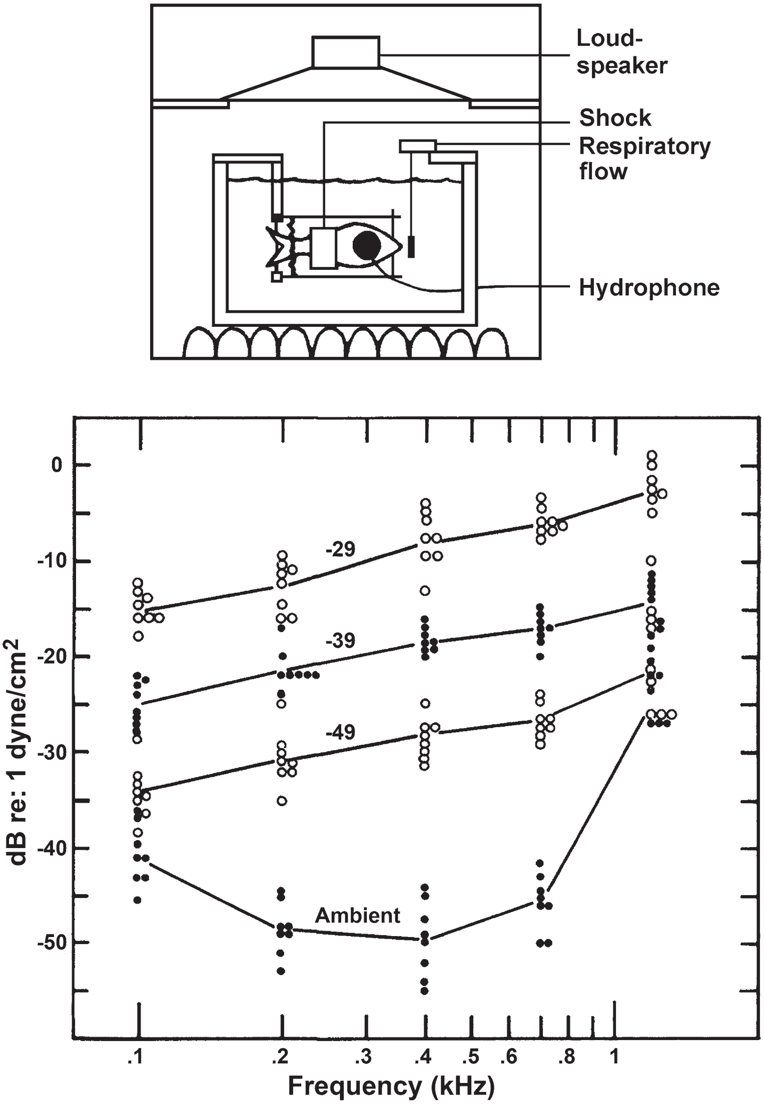

Fig. 3.7 Upper: Arrangement for studying auditory masking in goldfish. Auditory thresholds of submerged, restrained fish were obtained using respiratory conditioning (see Sect. 3.5.1.4). The fish was fitted with shock electrodes and the respiration frequency was recorded by detecting water flow across the mouth. Lower: Sound pressure thresholds from four goldfish determined at four noise conditions (ambient, −29, −39, and −49 dB re1 dyne/cm^2/Hz) as a function of the frequency of the test tone. The applied noise was uniform, and the bandwidth was 50–2,000 Hz. Lines connect the means at each noise level. Filled and open symbols separate data obtained at different noise levels. Overlapping points are displaced to the right. Within the tested frequency range, the masking effect was independent of frequency, and 10 dB noise increment elevated the threshold by about 10 dB. (Modified from Fay 1974a, with permission)

with a food reward and then punished, with a tap from a glass rod, responses to another sound that differed significantly in frequency (called the warning sound) from the feeding sound. After a number of trials, the fish learned to respond only to the feeding sound. Stetter then moved the frequency of the warning sound closer to that of the feeding sound until the minnows also started to respond to the warning sound, indicating that the fish failed to detect a significant difference between the two sounds. He found that all minnows could discriminate between frequencies separated by one octave, and that the two best performing animals could discriminate between 290 and 345 Hz.

One problem with Stetter's study, however, was that the sounds to be discriminated were presented 15 min apart, thus requiring memory of the first sound to make the discrimination. In contrast, another student of von Frisch, Th. Wohlfahrt (1936a), examined frequency discrimination in the European minnow by presenting sounds in rapid succession. He showed a much finer discrimination of about six percent difference between tone frequencies.

However, whereas the studies by Stetter (1929) and Wohlfahrt (1936a) demonstrated discrimination between tones, the authors did not control the differences in tone intensity. Thus, it is possible that the animals were discriminating between intensities rather than frequencies.

It was not until the discrimination studies by Jacobs and Tavolga (1967, 1968) that it became clear that fishes can discriminate between both intensity and frequency. Jacobs and Tavolga tested frequency discrimination, using their shuttle box and operant conditioning, applying the concept of the just noticeable difference (JND), or the smallest difference between two signals (e.g., frequency or intensity) that could be discriminated. In these studies, fish were constantly presented with pulsed sounds of the same frequency or same intensity. At some point, the standard pulse was alternated with a pulse of different amplitude or frequency. The fish were trained to respond when they detected any alternation in the signal. The two sounds were then brought closer and closer together until the fish failed to respond, thus indicating that the difference between the sounds had become less than the JND. Results showed a sound intensity JND of about 5 dB from 100 to 1,0000 Hz and a frequency discrimination JND of 4–5 % in the same frequency range (Jacobs and Tavolga 1968). However, studies were restricted to the goldfish, and so applicability to other species, and in particular to non-otophysans, remained an open question.

Tavolga, again cognizant of critical aspects of hearing in terrestrial vertebrates, was the first to examine the focal questions of masking and critical bands in fishes to better understand the function of the hearing mechanisms and capabilities of goldfish, using a modification of the operant conditioning paradigm (Tavolga 1967, 1974). The only other behavioral studies of masking and critical band have been in goldfish (Enger 1973; Fay 1974a; Popper and Clarke 1979), Atlantic cod (Buerkle 1969; Hawkins and Chapman 1975), and Atlantic salmon (Hawkins and Johnstone 1978). Typically, fishes respond to masking by showing an increase in auditory threshold that is related to the level of the masker above threshold, as demonstrated by Fay (1974a) (Fig. 3.7).

It is interesting, from a historical perspective, that Jacobs and Tavolga (1967) were the first since Bigelow (1904) to study hearing in the goldfish. Subsequently, also in the United States, Richard R. Fay measured goldfish hearing using respiratory conditioning (Fig. 3.7) (Fay 1969), followed by a decades long series of studies that considered broad questions about goldfish hearing, from stimulus generalization (Fay 1970) to soundscape analysis (Fay 2009). The extensive data on hearing in goldfish provided by Fay serve as an invaluable basis for comparison with terrestrial species as well as with other fishes (reviewed in Fay and Megela Simmons 1999; Yost et al. 2020).

3.6 The Quest for the Hearing Organ(s)

3.6.1 The Function of the Labyrinth

As noted in Sect. 3.3, the understanding at the end of the nineteenth century that fishes completely lack the labyrinthine structures responsible for hearing in mammals (e.g., a cochlea) undermined the general assumption that fishes could hear. Hence, in parallel with the experiments discussed in Sect. 3.4, that demonstrated that fishes are definitely able to hear, other experiments were performed in order to reveal the sound detecting organs.

Kreidl (1895) was the first to explore experimentally the function of the teleost labyrinth. He supposedly removed the complete labyrinth in goldfish using forceps and observed that equilibrium was greatly disturbed while there was no change in responses to sound. Kreidl concluded that the sense of balance in goldfish resides in the labyrinth, whereas sound is detected by mechanoreceptors in the skin or the lateral line. Kreidl's conclusion was supported by Frederic Lee (1898), who stated, in a paper reviewing the sensory functions of the ear and lateral line, that the sole function of the fish labyrinth is equilibrioception. Similar observations were made by the English geneticist William Bateson (1890) as part of a review of the literature on fish sensory systems and baitfish.

The conclusions by Kreidl, Lee, and Bateson were contradicted by Parker (1903), who disabled the labyrinths in mummichog killifish by cutting the nerves innervating the ears (cranial nerve VIII). Subsequently, the fish had disturbed balance and a complete loss of responses to sound. Parker concluded that the labyrinth serves as a sense organ for both balance and sound and that both the skin and the lateral line are insensitive to sound.

Parker doubted that the very different findings between his study on killifish and the study by Kreidl (1895) on goldfish could be explained by species differences. This inspired Henry Bryant Bigelow to repeat Kreidl's experiments. Bigelow (1904) found that cutting cranial nerve VIII in goldfish rendered the fish insensitive to sound, as Parker (1903) had reported for the killifish. Attempting to find the cause of the discrepancy between his and Kreidl's results, Bigelow carefully repeated

Kreidl's surgical method, by which he removed the semicircular canals and the attached parts of the labyrinth. Following the operation, the goldfish exhibited greatly disturbed balance, but eventually recovered their normal posture, which Bigelow explained by compensatory mechanisms based on sight. The treated fish then displayed normal responses to sound, in agreement with Kreidl's results. However, closer examination showed that this method only removed the semicircular canals and the utricle (together often referred to as the pars superior), whereas the saccule and lagena (the pars inferior), being more deeply embedded in the skull in cyprinids (members of the carp family), were left behind. Hence, Bigelow concluded that the hearing ability in goldfish probably depends on the saccule and the lagena.

Later, Parker and Van Heusen (1917) studied the relative roles of the labyrinth, the lateral line, and the skin for sound detection in the brown bullhead. They impaired the labyrinths by cutting cranial nerve VIII. They also surgically destroyed the lateral line canal organs and desensitized the skin senses with an aqueous solution of magnesium sulfate.

It is interesting to note the technical requirements adopted to achieve well-defined auditory stimuli in these experiments in 1917. At the time, sounds for hearing experiments were often created by bumping objects into the aquarium wall, dropping items into the water, clapping of hands, etc. More refined experiments applied tones from musical instruments, which include harmonics, or pure tones generated by tuning forks. Parker and Van Heusen (1917) were the first to attempt to generate relatively pure tones using electricity. In their experiments, seven frequencies from 43 to 2752 Hz were produced using a series of seven AC-current generators sharing a common shaft driven by a 10 hp (7.5 kW) electric motor. The total construction weighed "not far from half a ton" (450 kg). To avoid vibrations from the apparatus reaching the test site, they placed the generators in a separate basement room about 40 m from the aquarium. The AC-currents drove a submerged telephone with a tight rubber cover, whereas airborne sounds evoking clear responses in normal fish were produced by blowing a whistle.

Parker and Van Heusen (1917), extirpating various tissues that could be involved in sound detection, concluded that airborne sound, entering the water, is only detected by the labyrinth, which is also sensitive to sounds from a submerged source, whereas the skin and the lateral line respond only to the lowest underwater frequencies. It was thus assumed that the lateral line organs are stimulated by low-frequency water vibrations, and that these organs resemble primitive ears. Parker and Van Heusen also reported that the brown bullhead can detect sounds with the labyrinth up to 688 Hz, but not to higher frequencies.

Bigelow's (1904) experiments were the first to show that the various otolith organs may have different functions linked to hearing and the sense of balance. This important conclusion was not, however, tested and verified until Manning (1924) used the same method to remove the semicircular canals and the utricle as did Kreidl (1895) and Bigelow (1904). However, a similar procedure was not feasible for extirpating the lagena and the saccule, which, in goldfish, are closely linked to one another and embedded in the skull just beneath the brain (see Platt 1977 for a comprehensive description of the goldfish auditory system). Rather than cutting the eighth cranial nerves, which would also disconnect the utricle, Manning surgically destroyed the saccular and lagenar otoliths in situ. Using the same equipment for generating underwater sound as Parker and Van Heusen (1917) (see above), Manning observed responses of normal and operated goldfish to frequencies from 43 to 2752 Hz. He concluded that the utricle was responsible for hearing from 43 to 688 Hz, whereas the saccule and lagena, and especially the lagena, were responsible for higher frequency hearing. The results were essentially in agreement with Parker's (1903) and Bigelow's (1904) conclusion that the sense of balance depends on the utricle, whereas the lagena and saccule are the main sound detectors. However, Manning's results also indicated that the utricle, the skin, and the lateral line might all be sensitive to the lowest frequencies tested.

von Frisch and Stetter (1932) later studied the effects of extirpation of the different components of the labyrinth, using the ability of the European minnow to respond to various sound frequencies. Removal of the utricle and semicircular canals only affected equilibrium, whereas hearing remained normal. Moreover, through very delicate and skillfully performed surgery, von Frisch and Stetter (1932) succeeded in removing the saccule and the lagena without damage to other parts of the labyrinth. These fish displayed completely normal postural reflexes, while frequencies above about 150 Hz failed to elicit a response. The fish still responded to lower frequencies with less sensitivity, but at 16 Hz the sensitivity was the same as before the operation. In addition, surgical impairment of the lateral line canal organs along the trunk and on the head did not reduce the sensitivity to the lowest frequencies. Therefore, it was assumed that such low frequencies were detected by sensitive tactile sensors in the skin, and not the lateral line. However, it should be noted that the free neuromasts on the body surface were not considered, and no attempts were made to impair this component of the lateral line system. Furthermore, the utricle was not removed, and so the possibility that the utricle might detect very low frequencies, in addition to controlling balance, was not ruled out.

Subsequently, von Frisch (1938b) applied an even more refined surgical technique and selectively removed either the saccule or the lagena in European minnows (Fig. 3.8). After bilateral removal of the lagena, the hearing sensitivity remained normal for all frequencies tested, as was the case after selective removal of the saccule on both sides. Hence, both saccule and lagena were thought to serve as sensitive sound detectors in the minnow. The study was then extended to juvenile specimens of the Ide (*Leuciscus idus*), another otophysan, confirming the conclusions from the minnow studies.

So far, all the studies on the function of the different components of the inner ear in fishes, from Bigelow's (1904) pioneering study to the refined experiments by von Frisch (1938b), were performed on otophysans. In order to explore if the reported functional organization of the labyrinth might be an exclusive otophysan feature, Dijkgraaf examined the effects of removing either the pars superior or the pars inferior on postural reflexes and hearing in two non-otophysan species, the rock goby (*Gobius paganellus*) (Dijkgraaf 1950) and the black goby (*Gobius niger*) (Dijkgraaf 1952). The experimental approach was to train the gobies to respond to the sound of

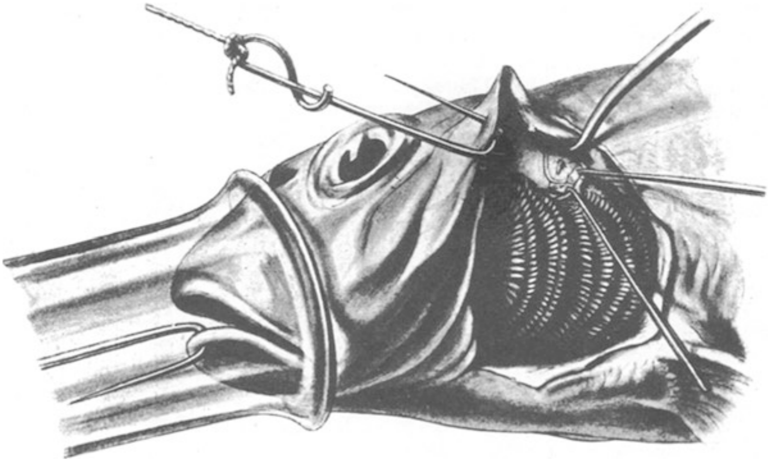

Fig. 3.8 Surgical arrangement for extirpating the lagena and the saccule (pars inferior) in the European minnow. (From von Frisch and Stetter 1932, with permission)

tuning forks using the conditioning method introduced by von Frisch (1923). In both species, bilateral removal of the pars superior abolished all postural reflexes, whereas these were intact after removal of the pars inferior. However, perception of sound was impaired by bilateral elimination of the pars inferior, although the fish showed normal sensitivity to frequencies at and below 100 Hz, which presumably were detected by the skin or lateral line.

The studies on both otophysans and non-otophysans did indicate a general division of labor between the pars superior and pars inferior in teleosts, the former being responsible for the sense of balance and the latter for hearing. Yet, there are probably numerous exceptions to this rule. For example, it now appears that the utricle detects sound up to at least a few hundred Hz in several teleost species, as suggested first by Manning (1924), and may be involved in directional hearing (e.g., Lu et al. 2004; Rogers and Sisneros 2020), and in ultrasound detection in some clupeids (Plachta et al. 2004). Furthermore, in elasmobranchs, all three otolith organs respond to both gravitational stimuli (Lowenstein and Roberts 1949) and low-frequency vibrations up to 120 Hz (Lowenstein and Roberts 1951).

3.6.2 Sound Stimulation of Otolith Organs

Although Parker and his students showed that sound can be detected by otolith organs in fishes, the actual detection mechanism was not understood at the time. It was known that the mass density of soft body tissue is about the same as that of water, whereas the mass density of otoliths and otoconia (found in all non-teleost fishes and terrestrial vertebrates) is much higher. This enables otolith organs to detect gravitation and linear acceleration in all vertebrates. However, it was not obvious that sensitivity of fishes to sound might depend on a related mechanism. In 1950, the Dutch physicist Hessel de Vries and the English zoologist Richard Julius Pumphrey independently pointed out that in a sound field, the fish body will follow the particle motion in the surrounding water. The inertia of the denser otoliths then causes these to lag behind—thus creating relative movements between the otoliths and the sensory maculae.

de Vries (1950) measured the mechanical properties of otolith organs in isolated heads of several fish species. He mounted the heads on a tilting or rotating board with attached X-ray film and measured the otolith movements induced by various acceleration forces (Fig. 3.9). de Vries (1950, 1956) modeled the otolith organs as critically damped, simple harmonic oscillators, and he presented the equations describing the motions of such systems. At frequencies below the natural frequency of the system, the deflection of the otolith relative to the sensory epithelium follows the acceleration of the organ, and the model indicates a working range of otolith organs reaching from zero Hz to the upper frequency limit of hearing. Hence, de Vries concluded that detection of gravity, linear locomotory acceleration, and forced acceleration of a fish in a sound field occurs by the same mechanism and that the transition between these functions is seamless. de Vries' groundbreaking description of the mechanical properties of otolith organs in fishes ought to have been the foundation of later studies of this subject, but was poorly understood at the time.

de Vries (1950) also attempted to calculate the minimum perceptible energy of an otolith organ, but erroneously based the estimation on the assumption that the minimum detectable acceleration is similar to that of the human labyrinth. At the time, it was not known that the labyrinth in fishes is nearly four orders of magnitude more sensitive to linear acceleration than the human labyrinth (Sand and Karlsen 1986). Thus, when very low auditory thresholds were reported during the following two decades, scientists lost confidence in de Vries' model for hearing in the acoustic far field (see below).

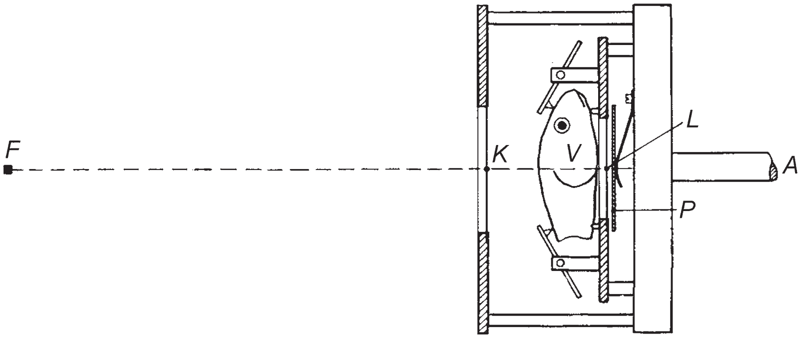

Fig. 3.9 De Vries' arrangement for measuring otolith mechanics. A—rotation axis; F—X-ray tube; K and L—cross wires for alignment; P—photographic plate; V—fish head clamped in holder. (From de Vries 1950, with permission)

The concepts of acoustic near and far fields were introduced to marine bioacoustics by Americans Gerard G. Harris and Willem van Bergeijk (Harris and van Bergeijk 1962; Harris 1964; van Bergeijk 1964). The acoustic near field is the region in which particle motions caused by movements of the sound source and incompressible flow are larger than those caused by the sound pressure-induced compression and rarefaction of the medium. The acoustic far field is the region beyond, in which the sound pressure-induced particle motions dominate. Both investigators (who often collaborated) assumed that far field hearing in fishes was only possible in species possessing a swim bladder produced by that transforms sound pressure into sufficiently high particle motion to stimulate the otoliths (see Sect. 3.6.3). However, Chapman and Sand (1974) later utilized the properties of a free sound field in the ocean to demonstrate that two teleost species without a swim bladder, the flatfishes dab (*Limanda limanda*) and plaice (*Pleuronectes platessa*), detect particle motion and not sound pressure. Stimuli with different ratios between sound pressure and particle motion were obtained by varying the distance to the sound source within the acoustic near field (Fig. 3.10). The lowest auditory thresholds in the flatfishes were below 0.1 nm particle displacement, or close to 10^{-5} m s^{-2} particle acceleration, which allows detection of normal sound intensities in the far field. Later, Hawkins and MacLennan (1976) achieved similar stimulus control using a standing wave acoustic tube fitted with a sound projector at each end and confirmed that the plaice is sensitive only to particle motion.

3.6.3 The Swim Bladder as an Accessory Hearing Organ

As discussed in Sect. 3.5.1.1, early twentieth-century investigators noted that otophysans are generally more sensitive to sound than most non-otophysan species, thus supporting the assumption of an auditory role of the Weberian ossicles as proposed by Weber (1820) (Fig. 3.1). The physical basis for this notion is that a volume of gas pulsates when exposed to oscillating pressure (Alexander 1966a, b). Therefore, when exposed to sound, the surface of a swim bladder may display larger radial motion amplitudes than the water particles in the absence of a gas-filled bladder. The amplified motions may then be transferred to the inner ear via the Weberian ossicles, thus providing an auditory gain and making the intact fish sensitive to sound pressure, though the otolith organs remain sensitive to particle acceleration.

As an extension of the experiments described in Sect 3.6.1, von Frisch and Stetter (1932) were the first to test this hypothesis experimentally. They found that surgical removal of the swim bladder in the European minnow increased the auditory thresholds by up to 20–30 dB. Similar results were obtained for the goldfish by Fay and Popper (1974). An alternative approach to demonstrate an auditory function of the swim bladder would be to explore if the fish is sensitive to sound pressure rather than particle motion. This strategy was followed in Germany by Autrum and Poggendorf (1951) and Poggendorf (1952, in translation in Tavolga 1976) for the brown bullhead.

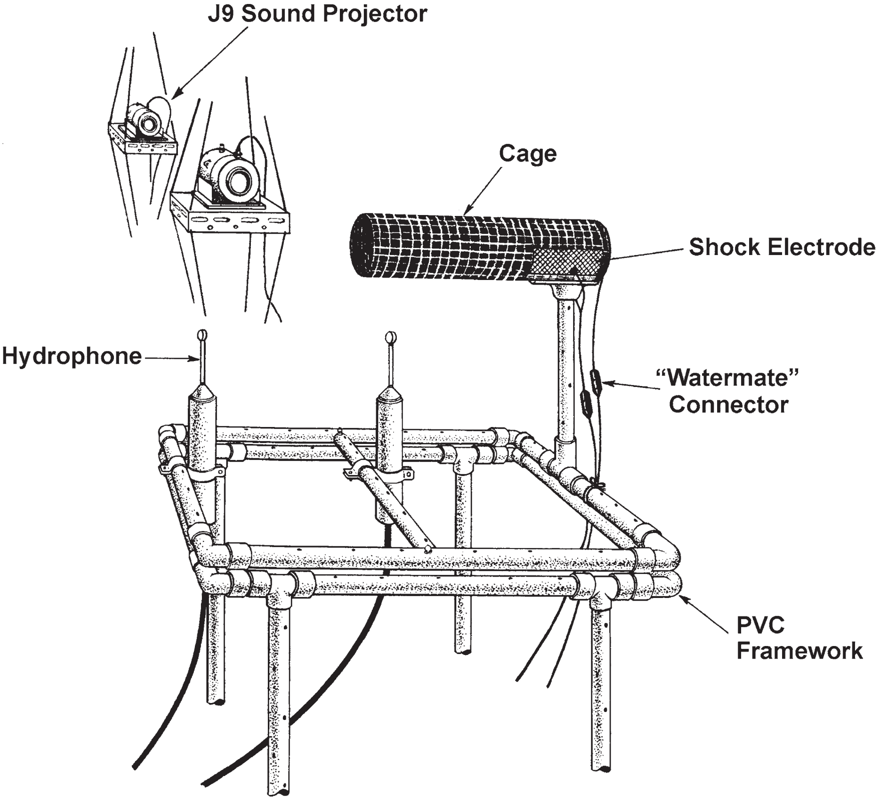

Fig. 3.10 Setup for bioacoustic field experiments under virtually free field condition. The top of the underwater framework with the fish cage was 15 m below the surface, 6 m above the bottom, and 100 m from the shore. (From Chapman and Hawkins 1973, with permission)

Poggendorf used an acoustic tank in which the ratio between sound pressure and particle motion varied between regions. The central part of the tank bottom consisted of an oscillating piston (Fig. 3.11, left), and the fish cage was positioned at various depths above the piston. For the first time in a fish bioacoustic study, sound pressure under water was measured using a hydrophone (a modified piezoelectric microphone), and particle motion was estimated from measurement of the pressure gradient. For a given piston amplitude, sound pressure was lowest close to the surface and increased with depth, whereas the opposite was true regarding particle motion. By employing the conditioning technique introduced by von Frisch (1923), Poggendorf found that the sound pressure thresholds were independent of depth. Hence, he concluded that sound pressure is the relevant stimulus parameter at threshold level, and that the swim bladder has an auditory function in the brown bullhead.

The importance of the Weberian ossicles for the auditory function of the swim bladder was demonstrated by surgical disruption of the chain, thereby increasing

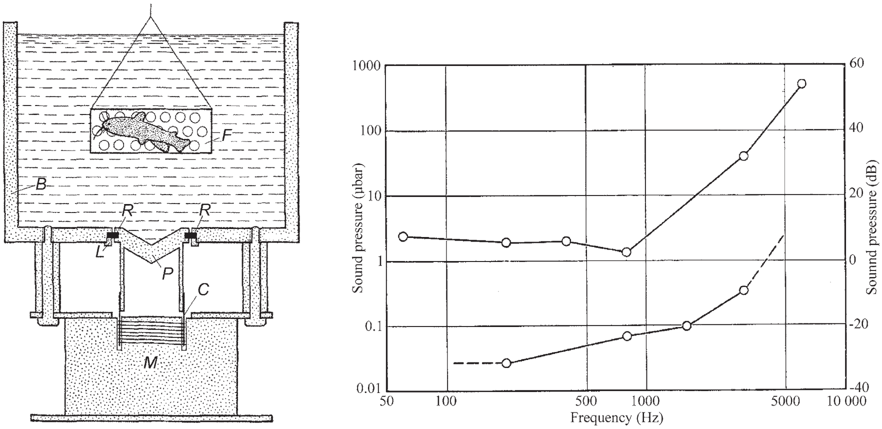

Fig. 3.11 Left: The acoustic tank used by (Poggendorf 1952) to obtain regions with different ratios between sound pressure and particle motion. Labels: B—brass wall; C—coil; F—fish cage; L—lock ring; P—piston; M—magnet; R—rubber washer. Right: Lower audiogram presents mean threshold values from two normal brown bullheads. The upper audiogram shows mean thresholds from the same fish after surgical impairment of the Weberian ossicles. (Both panels modified from Poggendorf 1952, with permission)

auditory thresholds by 30–40 dB (Fig. 3.11, right). However, the fish were still sensitive to sound pressure at threshold levels. Based on this observation, Poggendorf (1952) was the first to suggest that the swim bladder may also be important for the hearing ability of non-otophysan species.

Between 1959 and 1966, British scientist Robert McNeill Alexander published a series of papers on the physical properties and the various physiological functions of the swim bladder in several species of fish. Regarding its auditory role and the mechanical properties of the Weberian ossicles, the most relevant results are reviewed in Alexander (1966a). Alexander also concluded that the very presence of a swim bladder may aid hearing, but without an efficient mode of transmission, the gain will fall off in proportion to the square of the distance to the ear. He suggested that the extra gain at resonance would be modest, due to heavy damping of the swim bladder oscillations. Later, Sand and Hawkins (1973) confirmed this heavy damping by measuring swim bladder resonance in intact, submerged Atlantic cod at different depths.

Alexander also studied the function of the Weberian ossicles in detail. Based on anatomical measurements, he suggested that the mechanical arrangement of ossicles and ligaments in the chain (Fig. 3.1) might provide a considerable amplification of the radial movements of the swim bladder surface. Unfortunately, later researchers have not further explored and tested this assumption.

In Sect. 3.5.1.2, it was noted that some non-otophysan species display audible frequency ranges similar to many otophysans. A common characteristic of these species is the existence of gas-filled chambers in close contact with the ears. For example, in the clupeids, narrow, tubular extensions from the swim bladder end in a gas-filled bulla close to each utricle (Wohlfahrt 1936b; O'Connell 1955). Mormyrids also possess swim bladder-derived, gas-filled chambers in close contact with the ears (von Heusinger 1826; Stipetić 1939; Popper 1981). In anabantids (labyrinth fishes), the gas chamber is an accessory respiratory organ in the form of an air-filled cavity in the head, the labyrinth organ (Das 1928), which is filled with air by the fish gulping air at the surface.

The broad hearing bandwidth in the non-otophysan species referred to above did indicate an auditory role of gas-filled chambers in close contact with the ears and also in the absence of Weberian ossicles, but direct evidence for this hypothesis was lacking. Comparison of the hearing ability with and without gas in the chambers could have provided more direct evidence, but such experiments are difficult in both clupeids and mormyrids due to complex morphologies. However, in the anabantids, such experiments are relatively simple to perform, because the fish fills the labyrinth organ with air by gulping air at the surface. Schneider (1942) took advantage of this feature and compared the hearing ability of four species of labyrinth fish with and without air in the labyrinth organ. Air depletion caused the upper audible frequency cut-off to drop from up to about 4.7 kHz to below 700 Hz (see also Saidel and Popper 1987).

Following these studies, it was still an open question as to whether a swim bladder, with the primary role to provide buoyancy, might improve the hearing ability also in non-otophysan species. Such a function had been suggested by Poggendorf (1952), de Vries (1956), and Alexander (1966a), but was not tested until Enger and Andersen (1967) performed experiments indicating that the Atlantic cod was sensitive to sound pressure in the upper range of its audible frequencies. They recorded microphonic potentials from the inner ear and utilized the properties of the near field of a free sound field in the ocean to alter the ratio of particle motion to sound pressure (see Sect. 3.6.2). Their conclusion was later supported by Chapman (1973) and Chapman and Hawkins (1973) who used cardiac conditioning to determine hearing thresholds in a number of species, including the Atlantic cod, under virtually free field condition in a Scottish loch, using sound projectors positioned at various distances from the fish (Fig. 3.10) (reviewed in Hawkins and Chapman 2020). They showed that four species of Gadidae (the cod family) were sensitive to sound pressure in the upper part of their audible frequency range. In particular, the Atlantic cod responded to sound pressure at threshold level for all frequencies between 50 Hz and about 500 Hz, the highest audible frequency, whereas the thresholds were related to particle motion at lower frequencies.

Evidence of an auditory function of the swim bladder in the Atlantic cod was also provided by Sand and Enger (1973), who recorded microphonic potentials from the same fish with and without gas in the swim bladder. Emptying the swim bladder lowered the upper frequency cutoff and reduced the hearing sensitivity by more than 20 dB in the optimal frequency range (200–300 Hz). However, the sensitivity was not altered at frequencies below 100 Hz. In contrast to this, Chapman and Sand (1974) fitted the flatfish dab, which lacks a swim bladder, with an artificial "swim bladder" in the form of a small rubber balloon placed exterior to the fish just beneath its head. This arrangement shifted the upper frequency cutoff from about 200 to about 350 Hz. The hearing threshold was lowered by about 20 dB at 200 Hz, but by only 3 dB at 30 Hz.

The results from the field experiments discussed above are in agreement with theoretical considerations by Sand and Hawkins (1973), who pointed out that the swim bladder pulsations exceed the free field particle motions only above a certain frequency. Thus, the gain provided by a swim bladder is frequency dependent. Below a certain frequency, which depends on both swim bladder volume and depth, the swim bladder provides no auditory gain.

The evidence supporting an auditory role of the swim bladder in the Atlantic cod is convincing. However, in this species, anterior projections from the swim bladder bring its rostral end rather close to the ear, and it is still a matter of discussion to which degree other non-otophysan species may utilize the swim bladder as an accessory hearing organ. This question can be elucidated by studying the diversity in ear structure and hearing range within single taxa, which has been explored most extensively in the squirrelfishes (Holocentridae). Within this family, the hearing ability correlates clearly with the distance between the swim bladder and the ears. Species with the closest proximity between these structures have a hearing range similar to that of the otophysans, whereas species with a greater distance between the swim bladder and the ear have a hearing range closer to that of the Atlantic cod (Tavolga and Wodinsky 1963; Coombs and Popper 1979). These and other similar results support the argument that adaptations to utilize the swim bladder to enhance hearing have evolved multiple times in fishes (Popper et al. 2003).

3.7 The Lateral Line System

Before the middle of the nineteenth century, the leading view was that the lateral line system in fishes comprised an arrangement of mucous glands. However, based on anatomical evidence, Leydig (1868) proposed that the lateral line system constituted a hitherto unknown sensory system—a “sixth sense.” This assumption was demystified by Schulze (1870), who discovered that free neuromasts possess a cupula that is moved by weak water currents. He suggested that both water currents and low-frequency sounds are relevant stimuli for these organs.

The idea that the lateral line system is primarily an accessory hearing organ for detection of low-frequency sound soon became generally accepted (Mayser 1881), and prevailed well into the twentieth century. Major reasons for this view were the similar anatomical features and the common embryological origin of the sensory cells in the lateral line system and the labyrinth, and it has been suggested that the ear arose from an invagination of the cephalic lateral line early in the evolution of fishes (Pumphrey 1950; van Bergeijk 1967).

This acousticolateral hypothesis was originally proposed by Ayers (1892), who argued that the ear and lateral line system develop from the same embryonic placode, and that their innervation arises from the same region of the brain. This notion prevailed for many decades, but later studies, using modern neuroanatomical tracing methods, demonstrate a clear distinction in innervation between the ears and the lateral line system (reviewed in Northcutt 1997; McCormick 1999). The intriguing early history of lateral line research has been thoroughly reviewed by Parker (1903) and Coombs and Bleckmann (2014).

Between the early 1930s and the late 1970s, there was a controversy between two of the leading fish bioacoustics scientists at the time, Sven Dijkgraaf and Willem A. van Bergeijk, regarding the possible function of the lateral line as an accessory hearing organ. Dijkgraaf explained his view in a classical review (Dijkgraaf 1963), whereas van Bergeijk reviewed his a few years later (van Bergeijk 1967).

Although both agreed that the lateral line is stimulated by water motion, they disagreed about the nature of effective stimuli. Based on recordings of microphonic potentials from the lateral line in the mummichog killifish in response to an adjacent, vibrating sphere, Harris and van Bergeijk (1962) argued that the lateral line would be an acoustic detector of water motion within the whole extent of the near field. This view led van Bergeijk (1967) to conclude:

> *…the lateral line organs are organized in a system that is … capable of near-field hearing…*

At the time, the majority of scientists in this field of research embraced van Bergeijk's view. Within the acoustic near field, the lateral line took care of the low frequencies, while the inner ear responded to the higher frequencies (e.g., Tavolga and Wodinsky 1963). In the acoustic far field, only fishes possessing a swim bladder were assumed able to detect propagating sound waves (van Bergeijk 1964).

Contrary to this view, Dijkgraaf (1963) emphasized that the long wavelengths of the relevant frequencies (15 m at 100 Hz) would cause an almost neutrally buoyant fish and its surrounding water to vibrate with virtually the same phase and amplitude within almost the whole near field of a sound source. Hence, no relative motions would occur between the fish surface and surrounding water, which is the relevant stimulus for the lateral line. Later, the insensitivity of the lateral line system to such sound stimuli was confirmed experimentally (Sand 1981).

Dijkgraaf argued that the lateral line can detect moving and vibrating objects at close range, surface ripples somewhat farther from the source, the turbulent wake of moving objects long after they have passed, and stationary objects at close range. The latter was termed "distant touch" and depends on distortion of the self-generated flow field around a moving fish. The British scientists Eric Denton and John Gray were the first to confirm experimentally that the lateral line may only be stimulated within the innermost part of the acoustic near field, generally within a range of just a few centimeters from the source (Denton and Gray 1982). Coombs and Janssen (1990) later confirmed this finding in the mottled sculpin (*Cottus bairdi*). Denton and Gray (1982) also emphasized that the limited distance range of lateral line sensation protects against masking by the high levels of low-frequency ambient noise in the oceans. The inner ear, on the other hand, is sensitive to such background noise, which is an essential component of the aquatic acoustic environment. The various aspects of lateral line sensation, which is a sensory modality distinctly different from hearing, are reviewed in Sand (1984) and Sand and Bleckmann (2008), and the division of labor between the lateral line system and the auditory system is discussed in Braun and Sand (2014).

3.8 Directional Hearing

Determining the location of a sound source at some distance from an animal is important for locating predators, prey, mates, rivals, etc. Indeed, Pumphrey (1950) suggested that detection of the direction of sound propagation is a fundamental property of hearing and should be included in its very definition. However, whereas terrestrial vertebrates possess this ability, it is not yet fully clear whether fishes are able to determine the direction to a sound source from a distance.

Early experiments on directional responses of fishes to sound were carried out in a small laboratory tank by Parker (1912). During the continuous production of repetitive underwater sounds, several fish species gradually moved away from the sound source, leading Parker to suggest that sound could influence the direction of fish locomotion.

Later, von Frisch and Dijkgraaf (1935) carried out behavioral studies on European minnows at the edge of a lake. The fish were rewarded with food when they came close to a sound projector. However, there was no definite orientation of the fish toward the sound source and it was not possible to establish whether this species was able to locate sound sources beyond a few body lengths. Reinhardt (1935), after conducting experiments in a tank, also concluded that the European minnow and the brown bullhead lacked a directional acoustic sense for sounds or vibrations.

Despite these indeterminate results, the American physiologist Donald Griffin (1950) concluded that fishes may be attracted to or repelled by a sound source. Subsequently, Kleerekoper and Chagnon (1954) observed that creek chub (*Semotilus atromaculatus*) were able to locate a source of vibration, most likely oriented by the intensity gradient, in an experimental tank.

Still, van Bergeijk (1964), in a very influential paper, concluded that fishes were not likely to be able to determine sound directions using the mechanisms employed by terrestrial vertebrates, such as detection of differences in the intensity, time of arrival, and phase at the two ears. He argued that, in fishes, the differences in the binaural cues used for localization in air would be miniscule because their ears are very close together and the speed of sound is about 4.3 times faster in water than in air. van Bergeijk also assumed that hearing by fishes in the acoustic far field involved the detection of sound pressure, utilizing the swim bladder, and that this single sound pressure detector would stimulate both ears simultaneously and equally. Because he assumed that the information conveyed to the two ears would be identical in fishes, he concluded that only the lateral line system was able to locate sound sources, operating only in the acoustic near field. However, as pointed out by Dijkgraaf (1963) and as discussed in Sect. 3.7, the lateral line may only detect acoustic near field motions at a distance of just a few centimeters from the source.

Subsequent experiments supporting the existence of directional hearing in fishes were carried out in the sea by Olsen (1969) and Schuijf et al. (1972). Discrimination between sounds coming from different directions was confirmed by Chapman and Johnstone (1974) and by Schuijf (1975) (Fig. 3.12), who showed that some teleost species could detect changes in the propagation direction of sound in the horizontal plane. Chapman and Johnstone (1974) also showed that the degree of masking of a pure tone by broadband noise from a separate sound projector became reduced as the angle between the two sound projectors was increased. It was later shown that the Atlantic cod can discriminate between spatially separated sound sources in the median vertical plane (Hawkins and Sand 1977), between frontally incident and caudally incident sounds (Schuijf and Buwalda 1975), and even between diametrically opposed sound sources in both the median vertical and transverse vertical planes (Buwalda et al. 1983).

Obviously, these field experiments contradict van Bergejk's hypothesis that fishes lack a directional auditory sense in the acoustic far field. Pumphrey (1950) and de Vries (1950) had suggested earlier that the otolith organs effectively detect particle motion, a vector quantity with both magnitude and direction, and Dijkgraaf (1960) later proposed that the otolith organs are inherently directional in their response to sounds. This suggestion was ultimately supported by anatomical studies (Sect. 3.2) showing that the individual hair cells within the otolith organs are directionally orientated and organized in patterns in which the direction of the axis of

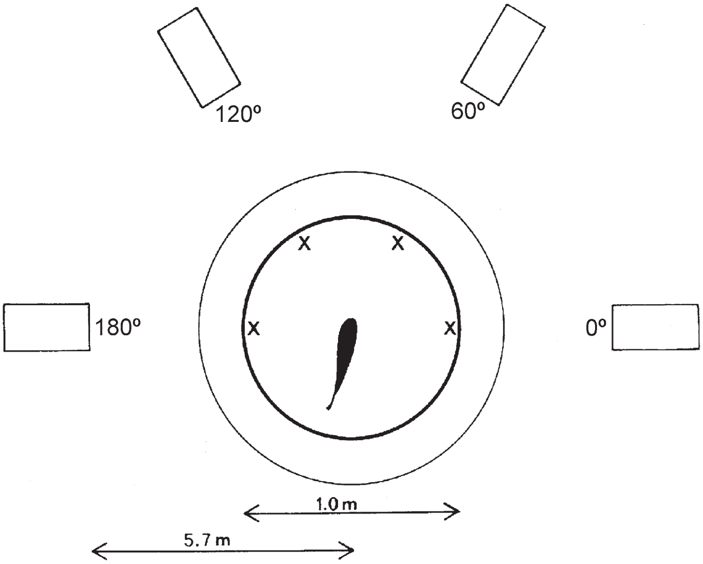

Fig. 3.12 Example of behavioral testing of directional discrimination. The fish moved within a netting cage and was trained to orient toward the food dispenser (x) in line with the active sound transducer. However, this approach cannot unambiguously demonstrate that the fish perceives the actual location of the sound source. (Redrawn from Schuijf 1975, with permission)

optimal sensitivity varies along the macula (e.g., Dale 1976; Enger 1976; Popper 1976). Thus, the fish brain may determine the direction of particle movements of the incident sound by vectorial weighing of the input from different regions of the sensory maculae. This was the underlying hypothesis that motivated both the SEM studies of the ultrastructure of fish ears discussed in Sect.3.2, and the electrophysiological studies of regional differences in directional sensitivity of otolith organs described below. All current models of directional hearing in fish are based on such a mechanism. See Popper et al. (1988) and Rogers et al. (1988) for a discussion of vectorial weighing.

When the hypothesis of directional hearing based on vectorial weighing of inputs from different populations of hair cells emerged, it seemed difficult to provide experimental support, due to the inevitably complex sound fields in small laboratory tanks described by US physicist Antares Parvulescu (1964). However, Enger et al. (1973) eliminated the problem of making directionally well-defined stimuli in small tanks by vibrating the fish in air, which simulates the effect of the kinetic sound component in water. They recorded microphonic potentials as the fish was vibrated in different directions (Fig. 3.13) and confirmed that the otolith organs of the haddock (*Melanogrammus aeglefinus*) were directionally sensitive. Later, the vibration method was refined and used by others (e.g., Sand 1974; Hawkins and Horner 1981; Fay 1984), and recordings from afferent nerve fibers from different parts of the ear showed regional differences in directional sensitivity within the sensory maculae.

Piddington (1972) reported that the goldfish can discriminate between compressions and rarefactions in a sound field. Soon after, Schuijf (1976) pointed out that

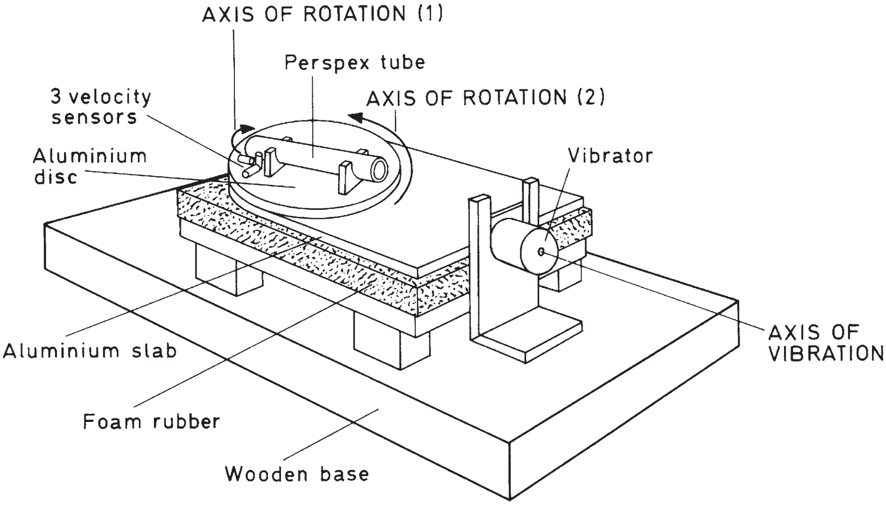

Fig. 3.13 The first vibration table used to simulate the kinetic sound component by vibrating the fish in air. The direction of vibration was altered by rotating the tube with a fish in the horizontal plane. More refined designs were later used in numerous studies of directional hearing in fish. (From Enger et al. 1973, with permission)

information about propagation direction of sound may be obtained by comparing the phase of particle motion with the phase of sound pressure sensed via the swim bladder.

Later, Buwalda et al. (1983) confirmed that phase relationship could be used for resolving sound direction. In this study, the phase relationship was controlled by using pairs of opposing sound projectors to generate standing waves in the ocean. In an additional study, Schuijf and Hawkins (1983) showed that Atlantic cod could even discriminate between sound sources at different distances, as the phase difference between particle motion and sound pressure varies with distance.

The emerging picture based on the phase model of directional hearing is that species with a swim bladder may have an acoustical sense of space. However, experiments have yet to demonstrate that fishes are able to perceive the actual location of a sound source from a distance without moving through the sound field, unlike mammals. Instead, the behavioral studies have only revealed that some species of fish are able to *discriminate between* sounds from different directions. Kalmijn (1997) suggested that a moving fish may still locate a source, although not instantaneously, by keeping a constant angle between its body axis and the incident particle motion detected by the inner ear. This strategy will guide the fish to all types of sound sources, i.e., monopoles, dipoles, and combinations including higher order sources.

The field of directional hearing in fish is more comprehensively reviewed by Sand and Bleckmann (2008), Rogers and Zeddies (2008), and Hawkins and Popper (2018). Despite the numerous experimental and theoretical studies on directional hearing in fish for more than 100 years, the mechanism by which fishes localize sound sources is still one of the great enigmas of fish hearing.

3.9 Conclusions

The intent of this chapter is to highlight the history of work on fish hearing, with primary emphasis on a substantial number of papers from the nineteenth century and the first 75 or so years of the twentieth century. The selected papers are not only formative (as well as informative), but they often are also germane to current thinking on fish bioacoustics. Many of the issues raised, the answers provided, and the thinking about the results directly address current research areas, including hearing thresholds, directional hearing, masking, effects of anthropogenic sound, and so on.

Furthermore, it is clear that the earlier investigators recognized technical problems that we are still dealing with today, including how to do hearing measures, tank acoustics, and various other methodological issues. Most of these topics are discussed in detail by Popper et al. (2019). Numerous current questions that need to be addressed to better understand fish bioacoustics rest on understanding many of the earlier studies discussed in this historical review.

Acknowledgments We dedicate this chapter to mentors and close friends and to present and future researchers in the fascinating field of fish bioacoustics. We also dedicate this chapter to (in chronological order of their initial contributions): G. H. Parker, K. von Frisch, S. Dijkgraaf, P. S. Enger, W.N. Tavolga, A. Flock, W. A. van Bergeijk, and R. R. Fay. We are grateful to Dr. Darlene Ketten for her excellent editing and suggestions that substantially improved this chapter.

Compliance with Ethics Requirements Olav Sand declares that he has no competing interest. Anthony Hawkins declares that he has no competing interest. Arthur Popper declares that he has no competing interest.

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