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Directional Hearing in Fishes

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1. Introduction

Directional hearing and sound source localization by fishes has several related meanings that arise from our assumptions about localization by human beings and assumptions about the cognitive capacities of fishes. For human listeners, we assume that when we determine the position of a sound source in the space around us, we know in a cognitive sense where the source is located, we can point to it with some accuracy, and we can move directly toward it and remember where the source is. Furthermore, we have the capacity to segregate in perception and locate multiple, simultaneous sources that make up an auditory scene (Bregman, 1990). The quantitative measure of localization for human listeners is the minimum audible angle (MAA), usually defined as the minimum angular deviation (usually in azimuth) required for reliable discrimination between two source locations. In a MAA experiment, we simply assume that not only can we discriminate the difference between two source locations, but that we “know” the direction to both sources in an absolute sense. We also often make the reasonable assumption that most other animal species function the same way: that they too “know” where the sound sources are located.

But how well founded is this assumption in the case of fishes? This question arises for several reasons, including that fishes are thought not to use the same binaural acoustic cues as terrestrial animals, that the underwater environment makes source localization an exceedingly difficult, and sometimes impossible task, and that fishes may have few or any of the cognitive capacities required to “know” anything at all. In addition to these considerations, the history of research on source localization by fishes is contradictory and confusing.

This chapter summarizes the literature on sound source localization in fishes and concludes that the evidence for a localization ability is strong, but that the mechanisms of sound source localization remain a fascinating question and an essential mystery in need of further experimentation and theoretical analysis.

2. Earliest experiments

Sound source localization was first studied in the European minnow (*Phoxinus laevis*), by Reinhardt (1935) in a laboratory tank, and then by Karl von Frisch and Sven Dijkgraaf (1935) in a shallow lake (Lake Wolfgang, Germany). Von Frisch and Dijkgraaf pointed out that the dominant view of human azimuthal source localization was that the determination of minute interaural time differences (ITD - on the order of several microseconds) was required. ITD processing seemed hardly imaginable for fish because effective inputs to the

inner ears are separated by only millimeters, and because sound travels more than four times faster in water than in air. Finally, they emphasized that their minnow *Phoxinus* detects sound pressure indirectly via the swim bladder, a midline structure that fluctuates in volume (vibrates) in response to sound pressure and that would therefore stimulate both ears equally and simultaneously, regardless of source location. They were unable to demonstrate sound source localization by their method and reached the conclusion that it made sense that fish were not be able to locate sound sources for the reasons noted above, even though they thought that this conclusion would be displeasing to biologists. After all, of what use was the great auditory acuity of their fish (*Phoxinus*) if it could not recognize the location of a sound source (see also Pumphrey, 1950)?

3. First re-evaluation

The sound source localization question arose again with the work of Moulton on the directional tail-flip response of goldfish (a species, like *Phoxinus*, having the swimbladder intimately linked to the inner ears via a series of specialized bones – the Weberian ossicles). Moulton and Dixon (1967) conditioned goldfish using food reward to change the preferred direction of a naturally occurring tail-flip response to a sound source. When the saccular and lagenar (auditory) nerve was severed on one side, the conditioned animals flipped their tails as if the sound source was on the side of the intact nerve. Moulton and Dixon concluded that the goldfish behaved as if they had localized the source, and that both ears were necessary for the directional response.

Moulton and Dixon assumed that the directional responses they observed were initiated by the Mauthner cells (M-cells) of the lower brainstem (Furshpan and Furukawa 1962). It now seems questionable that the Mauthner cells, alone, were involved. The M-cells mediate reflex orienting responses (e.g., Canfield and Eaton, 1990), but are probably not responsible for localization capacities that we associate with sound source localization behaviors of the type investigated by von Frisch and Dijkgraaf (1935). Thus, fishes may have at least two pathways for directional hearing; a descending one for reflexive responses and an ascending one possibly mediating more intentional behaviors.

At about this time, Willem van Bergeijk (1964, 1967) had a great influence on this field, and he argued that hearing in fishes should be defined as sound pressure detection (via volume fluctuations of the swim bladder). Since pressure is a scalar quantity, without directionality, and since the swim bladders of most fishes impinge on both ears equally, there would be little or no possibility of directional hearing for fishes. As von Frisch and Dijkgraaf (1935) had argued before him, van Bergeijk reasoned that some other directional sensory system must be responsible for directional orientation behaviors. Van Bergeijk touted the “acoustico-lateralis” hypothesis that the lateral line system and the ears functioned together in hearing, and that only the lateral line was responsible for directional determination.

We now know that the otolith organs of the ears are exquisitely sensitive to oscillatory motion of the head and ears (i.e., acoustic particle motion), with saccular nerve fiber sensitivities to low-frequency displacements as small as 0.1 nanometers, root mean square (e.g., Fay 1984, Fay and Edds-Walton, 1997a). At 100 Hz, displacements of this magnitude accompany a propagating sound wave in the far field at 100 dB re: 1 μ Pa. We now also know that van Bergeijk’s (1967) assumption that ear-mediated hearing in fishes was a matter only of processing the sound pressure waveform using the swim bladder or other gas bubble acting as a pressure-to-displacement transformer, was essentially an error. If van Bergeijk

were correct in his view, sound source localization mediated by the ears in the near- and far-fields would indeed be impossible for fishes. But it is also now widely believed that the otolithic ears of fishes function with great sensitivity in all species as if they were inertial accelerometers (de Vries, 1950; Dijkgraaf, 1960) responding directly to acoustic particle motion in all sound fields.

4. Discrimination experiments

4.1 Directional masking

Chapman (1973), Chapman and Johnstone (1974), and Hawkins and Sand (1977) investigated the effect of signal and masking noise source separation on the signal-to-noise ratio at signal detection threshold for haddock (*Melanogrammus aeglefinus*), and pollack (*Pollachius pollachius*). In general, fish were restrained in a free-field acoustic test range about 21 meters deep, and conditioned to detect tone signals in the presence of a noise masker using cardiac conditioning. Masked thresholds were highest (most masking occurred) when the signal and noise sources were separated by less than 10° azimuth or elevation, but that an 8-15 dB release from masking occurred when the sources were separated by 85° or more (up to 180°). These experiments and results are similar to those on human listeners investigating the binaural masking level difference (BMLD) (Hirsch, 1948) and the “cocktail party effect” (Cherry, 1953), and demonstrate that the directional aspects of hearing operate in fishes as well as human beings, and presumably other terrestrial animals. The peripheral mechanisms underlying these unmasking effects appear to be quite different in fishes and humans, but the consequences for hearing are similar: spatial resolution and filtering that promotes signal detection in noise.

4.2 Minimum audible angles and distance discrimination

A series of “heroic” experiments and theories of sound source localization in fishes were conceived by Hawkins, Chapman, Sand, Schuijf, and their colleagues, mainly in the 1970s (e.g., Schuijf et al. 1972, Chapman 1973, Chapman and Johnstone 1974, Schuijf 1975, Schuijf and Buwalda 1975, Hawkins and Sand, 1977, Schuijf and Hawkins, 1983). In the first psychophysical conditioning experiment on sound source localization, Schuijf et al. (1972) studied the Ballan wrasse (*Labrus berggylta*) using appetitive conditioning in a deep fjord near Bergen, Norway. Two sound sources were separated in azimuth and a conditioning trial consisted of a brief change in which loudspeaker broadcast the 115 Hz tone bursts. Positive responses were rewarded with a piece of food. The discriminations based on source location indicated that the fish detected that the sound came from a different loudspeaker, and this was assumed to result in the perception of a purely spatial change. The authors pointed out, however, that this experiment demonstrated the detection of a spatial change, but did not necessarily indicate that the wrasse correctly determined the locations of the sources. Any difference in the perception caused by switching between the two loudspeakers could have produced these results, and it is only an assumption that the difference in perception was of loudspeakers at different locations. Therefore, this kind of experiment represents a somewhat weak demonstration of sound source localization, and will always be open to alternative interpretations. In other experiments, Chapman and Johnstone (1974) found that azimuthal angular separations of 20° or more were required for the fish to discriminate between sources.

Schuijf (1975) demonstrated that cods could be conditioned to discriminate between different azimuthal source locations with a resolution of 22° , and that two, intact ears were necessary for this discrimination. The minimum audible angle (MAA) of 22° was determined using two- and four-alternative forced choice experiments. Schuijf recognized that the cods could possibly solve this problem by recognizing the identity of each sound projector through timbre difference cues, and solve the problem by associating a correct response location with each projector without being able to determine the actual locations of the sources. Hawkins and Sand (1977) measured the smallest discriminable change in elevation (about 16°). From earlier experiments on the microphonic potentials of the ear, Sand (1974) suggested that two ears seem to be required for azimuthal localization, but that elevation discrimination could be possible using only one ear. This hypothesis has not yet been tested, but is consistent with more recent physiological data on the peripheral encoding of directional information in *Opsanus tau*, the oyster toadfish (e.g. Fay and Edds-Walton, 1997).

These experiments are among the best evidence we have that sound source localization, as we think of it in human experience, is a capacity shared by fish, and additionally, that azimuthal discrimination requires binaural processing. But it must be kept in mind that this conclusion depends on the assumption that fish responded with respect to the actual locations of the sources and not some correlated cues that did not signal actual source location.

Schuijf and Hawkins (1983) studied the question of source distance determination in cod using cardiac conditioning. Two cod were able to discriminate between two sound sources at two distances, at both at 0° azimuth and elevation. This distance discrimination was interpreted to be based on the distance-dependent phase angle between sound pressure and acoustic particle motion within the nearfield of a sound source. It is also possible that the discrimination is based on processing the amplitude ratios between these two acoustic components rather than phase differences. The authors calculated that these ratio differences were less than 4 dB for their sources and that this difference was near the level discrimination threshold for cod, determined previously by Chapman and Johnstone (1974). Thus, this distance discrimination could be based on the processing of simultaneous amplitude ratios between pressure and particle motion. These observations are consistent with the hypothesis that these fish have truly three-dimensional directional hearing, but are not critical experiments in the sense of directly demonstrating that the fish could correctly locate the test sound sources.

5. The 'phase model' of directional hearing

Directional hearing in fishes is thought to depend upon the direct stimulation of the otolithic ears by acoustic particle motion impinging on the head (de Vries 1950, Dijkgraaf 1960). In this case, the axis of motion deflecting on the hair cell cilia could be determined by the pattern of hair cell activation over a population with diverse axes of best sensitivity. Hair cells are morphologically and physiologically polarized to respond best along one particular axis (Flock, 1964, 1965). All three otolith organs of fishes (sacculae, lagena, and utricle) have different orientations in the head in most fish species, and within each organ, hair cells are oriented along various axes (e.g., Popper, 1977). In this way, directional hearing seems to be solved through the assumption that the pattern of neural activity across cell arrays could encode the axis of acoustic particle motion. This idea was called "vector detection" (Schuijf and Buwalda, 1975).

This conception assumed that one end of the axis of acoustic particle motion pointed directly at the sound source, that each auditory nerve fiber received input from only one hair cell or from a group of hair cells having the same directional orientation, and that this mode of stimulation was effective enough to operate at the sound levels usual for the species. The first assumption is valid only for monopole sound sources (e.g., a pulsating source fluctuating in volume), and not for dipoles or higher-order source types. The second assumption was not confirmed until the work of Hawkins and Horner (1981) on the directional response properties of saccular afferents in cod, and more recent work on other species (e.g., Fay 1984, Fay and Edds-Walton 1997, Lu & Popper, 1998). The third assumption of adequate sensitivity was tested indirectly in psychophysical experiments on sound detection by flatfishes without a swim bladder (Chapman and Sand 1974), indicating that displacement detection thresholds were as low as -220 dB re: 1 meter (less than 0.1 nm) at the best frequency of hearing (near 100 Hz). So, it is now thought that the axis of acoustic particle motion can be determined by looking across the population of primary otolith afferents for characteristic spatial patterns.

4.2 The 180° ambiguity problem

The concept of a 'vector detector' immediately suggested an important problem that remained to be solved. That is, while the particle motion axis could be determined by arrays of hair cells, this solution could not determine which end of the axis pointed toward the source or specified the direction of sound propagation. This is known as the "180° ambiguity problem" and has dominated most theoretical and empirical work on directional hearing in fishes since the mid 1970s. Schuijf (1975) and Schuijf and Buwalda (1975) outlined a possible solution to this problem. A determination of the phase angle between acoustic particle motion and sound pressure could resolve this ambiguity. Imagine an axis of particle motion that is from side-to-side. The source could be oscillating from side to side either on the left or right of the receiving animal to produce this axis of particle motion. However, if the sound is propagating from a source at the right, then leftward particle accelerations are coincident with rising pressure and leftward accelerations coincident with a falling pressure. This "phase model" of directional hearing requires that both the sound pressure and particle motion waveforms be encoded at the periphery, and that appropriate central computations take place using useful representations of their phase or timing relations.

Schuijf and Buwalda (1975) evaluated this theory experimentally. They were able to condition cods to discriminate between sound sources directly in front and directly behind the animals, and these directional choices could be reversed by manipulating the phase of sound pressure with respect to the phase of particle acceleration (180° phase shift) of a synthesized standing wave, just as the phase model predicted. This experiment was repeated and extended several times (e.g., van den Berg and Schuijf 1983, Buwalda et al. 1983), and represents the best evidence in support of the phase model for sound source localization by fishes.

A potential weakness of the phase model is its requirement that both sound pressure and acoustic particle motion be encoded separately at the periphery or segregated by central computations. In most unspecialized species with a swim bladder, this could possibly take place through one set of hair cells oriented so as to respond to re-radiated particle motion from the swim bladder (for the pressure-dependent component), and another set shielded from swim bladder signals that responded to direct particle motion stimulation. In Otophysi and other hearing specialist species, the lagena and utricle may also function as auditory

organs (e.g., Wubbles and Schellart 1998) but do not receive swim bladder input (Coombs, et al., 2010). Rather, they respond with great sensitivity to acoustic particle motion as if they were inertial accelerometers (Fay 1984). However, for species without a swim bladder (or equivalent) such as elasmobranchs and flatfish, and for species without specializations for sound pressure detection, this dual encoding assumption is less likely to be valid.

Although not dealing directly with the 180° ambiguity question, Kalmijn (1997) has suggested an ethological explanation for sound source localization in fishes. He pointed out that a fish might not 'know' the location of any sound source, but could reach any sound source successfully simply by swimming in a direction that maintained a constant angle with the local axis of particle motion, which itself need not point to the sound source. Note that for this sort of mechanism to work, the sound source must be assumed to be broadcasting nearly continuously for a relatively long period of time, and that the receiver must be able to decide which direction along the pathway to take in approaching or avoiding the source.

6. Phonotaxis experiments

For many species of fish, males signal their breeding territory locations through advertisement calls that attract females of the species (Fine et al. 1977). It is presumed, and sometimes has been demonstrated, that females are able to localize these sources. Toadfish (family Batrachoididae) are the best studied family (e.g., Fish 1972, Gray and Winn 1961, Winn 1964). McKibben and Bass (1998) presented various continuous sounds mimicking advertisement calls to plainfin midshipman toadfish (*Porchthys notatus*) from one of two loudspeakers near the center of a 4-meter diameter tank (0.75 meter deep) and observed the responses of gravid females released within about 1 meter from the loudspeakers. For continuous tones and harmonic complexes with a fundamental frequency near 100 Hz (at about 130-140 dB re: 1 μ Pa), females were observed to exhibit phonotaxis, or a naturally occurring behavior of approaching the source of these stimuli. These and other (e.g., McKibben and Bass 2001) studies on this species also represent some of the clearest evidence available that fishes are able to locate sound sources. It is not known whether these animals were moving up an intensity gradient (klinotaxis), or approached the source using another search strategy (e.g., the constant-angle mechanism proposed by Kalmijn (1997)), or whether they had determined the source location at the time of initial release in the test arena.

6.1 New phonotaxis experiments on midshipman

Zeddies et al. (2010a) recently presented new phonotaxis observations on midshipman in the same arena used by McKibben and Bass (1998). In this case, the whole sound field was completely and quantitatively measured in terms of sound pressure and acoustic particle motion, and the pathways of approach to the source were videotaped. Female plainfin midshipman fish were collected by hand in the intertidal zone during the reproductive season on the same day as testing. For testing, a US Navy J9 sound projector was suspended from a beam in the center of the tank. An opaque plastic tarp was used as a screen and placed immediately in front of, but not touching, the sound projector to remove any visual cues that might affect sound source localization behavior. The playback signal consisted of a continuous tone at 90 Hz that was similar to the fundamental frequency of the male advertisement call (80-100 Hz; McKibben & Bass, 1998). The tone level at the calibration site was set at 130 dB (re 1 μ Pa).

The behavioral responses of the fish were recorded on videotape using a video recorder and a black-and-white camera mounted approximately 6 m above the tank's testing arena. The video records were digitized using video-to-DVD capture and recording software. The track taken by the fish was reconstructed using a frame-by-frame analysis of the digitized video records. The sound playback experiments were conducted at night between 21:00 and 2:00 h, and the water flow to the test tank was shut off during all tests. Water depth was adjusted to 50 cm for all tests.

Tests began with an individual fish being placed in a 30 cm diameter plastic mesh cylinder positioned approximately 109 cm from the sound source. Fish were then released by manually raising the cylinder. Tests were terminated when the fish swam to the perimeter of the testing arena or when the sound was turned off after a positive phonotactic response. A positive response was recorded when a fish approached the sound source and then directly touched the speaker face or circled in front or under the sound projector. There were no observations of fish returning to the center of the tank after reaching the walls, and rarely, if ever, did a fish remain in the center of the tank once the speaker was turned off.

Pressure measurements were made with an eight-element array of miniature hydrophones forming a cube, 5 cm on a side. This arrangement permitted particle motion to be calculated in the x, y, and z directions by finding the pressure gradient between adjacent hydrophones. Pressure is a scalar quantity consisting of only a magnitude and particle motion (i.e. the displacement, velocity, and acceleration of the media due to an acoustic disturbance) is a vector, having both magnitude and direction. To properly interpret the phonotactic pathways of the fish to the source, quantitative descriptions (maps) of the acoustic pressure and particle motion in the behavioral arena were obtained. Figure 1A shows a contour plot of the sound pressure field, and Fig. 1B is a vector plot of the acoustic particle motion in the arena. Both measurements confirm that the sound projector is essentially a monopole source, with an omnidirectional pressure field, and particle motion axes that point toward and away from the source.

Only gravid females containing ripe eggs showed phonotactic responses to the hum-like playback tone of 90 Hz while spent females containing little or no eggs did not exhibit phonotactic responses. The phonotactic responses of the gravid females consisted primarily of straight to slightly curved tracks to the monopole sound source, as illustrated in Fig. 2A. Once at the sound source, the fish responded unambiguously by either directly touching the speaker face and/or circling in front or underneath the sound projector with prolonged active interest around the sound source. The majority of the tested gravid females (72.5%, 45 of 62) responded to the 90 Hz playback tone and localized the monopole sound source. In contrast, none of the gravid females in the control group ($n = 59$) released with the sound turned off swam toward the sound projector and made physical contact or showed active interest in the silent projector. Thus, these results confirm that gravid females exhibit robust phonotaxis with a high degree of directionality toward the source at initial release, and move along the axis of the particle motion vectors in a monopole sound field.

However, monopole sound sources are a special case, and Kalmijn (1997) has argued that most biological sound sources (such as swimming fish) are dipoles or higher order types. A dipole source is simply modeled as a translating or vibrating sphere that doesn't change shape or volume. The sound field created by a dipole is more complexly shaped than that produced by monopole sources. It is axisymmetric, with a relative sound pressure null at locations in the field that are perpendicular to the axis of source motion. At and surrounding these pressure null locations, particle motion vectors are oriented parallel to the axis of

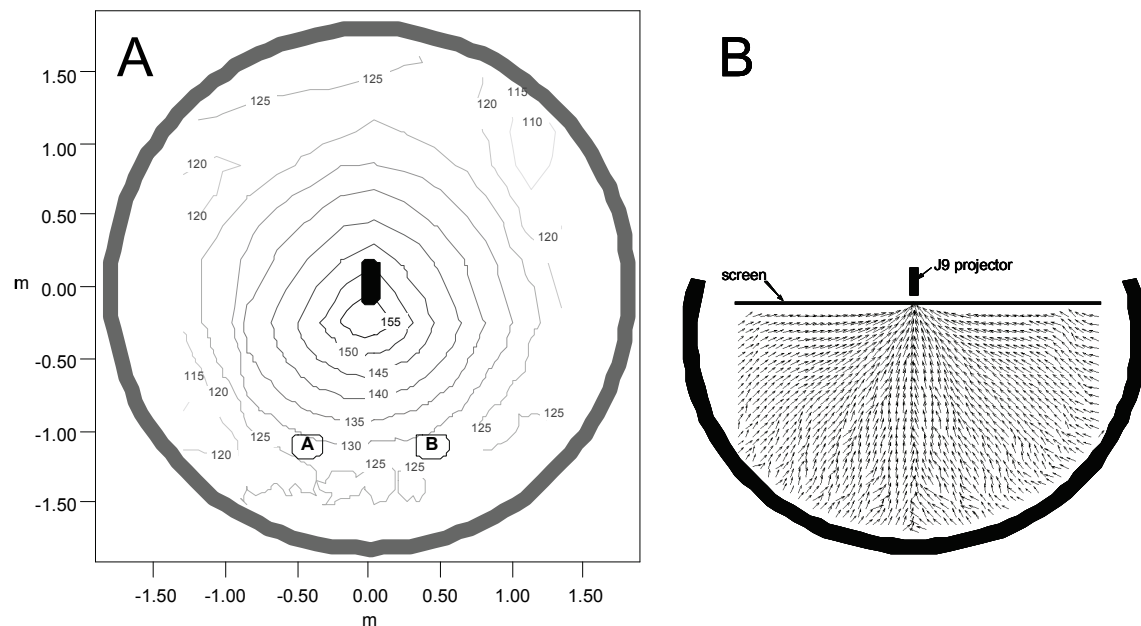


Fig. 1. A. Contour plot of sound pressure field in the test arena. A and B are alternative fish release sites. B. Particle motion field in the test arena calculated from pressure gradient measurements. The arrows on the vectors indicate the direction of increasing magnitude. Modified from Zeddies et al., 2010a.

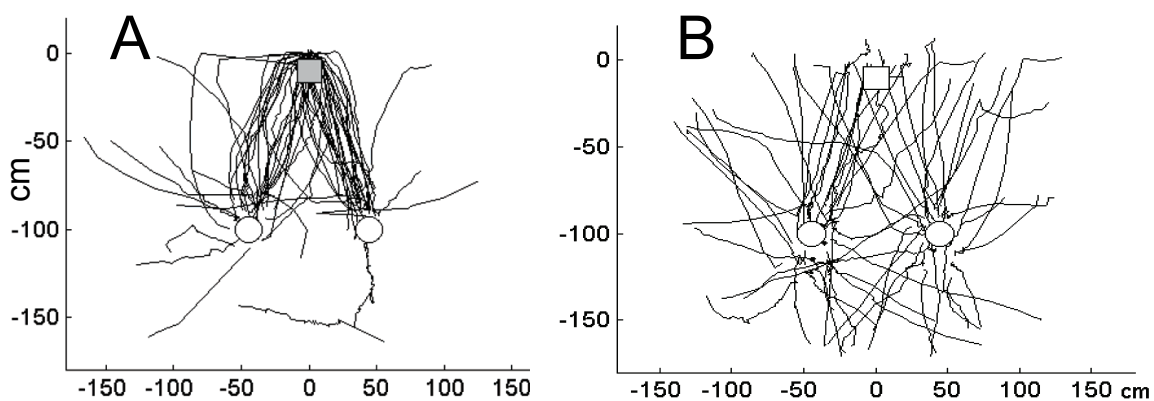


Fig. 2. A. Phonotaxis pathways for 45 gravid females that approached the source. B. Pathways for 59 gravid females without sound. Modified from Zeddies et al., 2010a.

source motion. Only on the axis of dipole vibration do particle motion axes point toward and away from the source. In other words, most particle motion vectors do not point toward and away from the source (as for monopoles), but are oriented at various angles to the axes that pass through the source.

What is the phonotactic response of midshipman fish in a dipole field? In preliminary experiments on this topic (Zeddies et al., 2010b) a dipole source was created using two monopole sources back-to-back, creating a push-pull action. The test tank used and all procedures were essentially identical to the monopole experiments (Zeddies et al, 2010a). After measuring the dipole sound field, the pathways taken by 25 gravid female

midshipman were recorded following release of the fish near the sound pressure null (nearly perpendicular to the source's axis of motion). The results showed that the pathways taken to the source were not straight lines to the source, but rather were curved, essentially following the axes of particle motion as experienced by the fish as it made its way to the source. Some fish initially swam left, and some swam right from the release site, but all of the responding fish swam parallel to the particle motion vectors to the source. Thus for dipole sources, fish can locate the source in the sense that they can eventually arrive at the source, but in this case, they do not and probably could not "know" where the source is. All they seem to know is what the axis of particle motion is at each position in the field in which they find themselves.

These observations on dipole sources add to our understanding of directional by fishes. First, these observations roughly correspond to Kalmijn's ethological scenario for approaching sources, but with the important exception that fish apparently don't use arbitrary but constant angles for approach, but rather seem to select a 0° approach angle with respect to the particle motion vectors. In general, these behaviors correspond to the predictions of the original 'vector detector' notions. Secondly, these observations raise issues with respect to the "180° ambiguity problem." When fish are released near a pressure null where the particle motion vectors are nearly perpendicular to a line to the source, turning right or left is equally effective; there is essentially no 180° ambiguity problem in the sense that there is no response that is more correct than another. As previously mentioned, about 50% of the released fish swim in each of the two correct directions as they approach the source. When released near the axis of dipole vibration, only one directed pathway is correct (taking the fish toward, not away from the source), and the 180° ambiguity problem has to be solved. But what is the difference between these two release sites that necessitates the solution to the problem at one, but not at the other? One possibility is that the particle motion intensity gradient contains information on the direction to the source at the on-axis release site, but not at the release site where the fish experiences a particle motion axis that is perpendicular to the line to the source. In other words, perhaps a detectable intensity gradient contributes to the solution of the "180° ambiguity problem."

7. Physiological studies

Peripheral and central neurophysiological studies of directional hearing in fishes have investigated the encoding of directional information in the primary afferents of the octaval nerve from the ears, and on these directional representations and computations in nuclei of the brainstem. The species investigated have included goldfish (*Carassius auratus*), toadfishes (*Opsanus tau* and *Porchthys notatus*), sleeper goby (*Dormitator latifrons*), rainbow trout (*Salmo gairdneri*), and Atlantic cod (*Gadus morhua*).

7.1 The periphery

Single unit studies on the peripheral encoding of directional information were first reported by Fay and Olsho (1979) and Fay (1981) for goldfish. Hawkins and Horner (1981) measured the first directional response patterns in recordings from the saccular and utricular nerve of the cod in response to whole-body oscillatory accelerations at various axes in the horizontal plane. They found that the response magnitude tended to vary according to a cosine-like function of vibration axis angle. Thus, each afferent studied apparently represented the presumed directionality of a single hair cell or group of hair cells having the same

directional orientation. In other words, each hair cell orientation appeared to have a private line to the brain, a requirement of the notion of “vector detection” assumed by Schuijf (1975) as the first stages of the phase model. For the saccule, the best azimuthal axis of motion corresponded roughly with the horizontal-plane orientation in the head of the saccular organ and otolith. In utricular afferents, best azimuths varied widely, reflecting the diversity of hair cell orientations over the (horizontal) surface of the utriculus. Utricular best sensitivity was similar to that of the saccule, suggesting a possible role for the utriculus in directional hearing. It was noted that the phase angle at which afferents synchronized to the stimulus varied widely among the afferents and did not fall into two groups, 180° out-of-phase with one another. Fay and Olsho (1979) and Fay (1981) also reported a nearly flat distribution of synchronization angles among saccular and lagenar nerve units in goldfish. The phase model (and other related theories of directional hearing in fishes outlined above) assume that pressure and displacement “polarities” would be represented robustly in a bimodal distribution (two modes, 180° out-of-phase) of synchronization angles, as predicted by anatomical hair cell orientation maps for otolith organs (e.g., Dale 1976, Platt 1977, Popper 1977). The fact that phase-locking angles do not cluster in such a way (see also Fay and Edds-Walton 1997 for similar data on *Opsanus tau*) presents a problem for all current theories of sound source localization in fishes: Which neurons “represent” the phases of pressure or displacement waveforms that have to be compared to resolve the “180° ambiguity problem?”

Experiments on directional encoding in goldfish (Fay 1984, Ma and Fay 2002) and toadfish (Fay and Edds-Walton 1997a,b, Edds-Walton et al. 1999) have used a three-dimensional “shaker” system (Fay, 1984) to produce whole-body accelerations in both azimuth and elevation. Figure 3 illustrates typical directional response patterns (DRP) for saccular units of toadfish. These data can be summarized as follows:

1. Most saccular afferents respond in proportion to the cosine of the stimulus axis angle in azimuth and elevation, with a few exceptions (Fay and Edds-Walton 1997a). Thus, each afferent seems to represent the orientation of one hair cell, or a group of hair cells having the same directional orientation (Lu and Popper 1998). Some of the DRPs in Fig. 1 reflect the fact that primary afferents saturate at the highest levels, and therefore tend to loose directionality in these cases (e.g., unit H8 at the highest levels).
2. In the azimuthal plane, most saccular units of the left ear respond best to an axis approximately parallel with the saccular organ’s orientation in the head (about -40°).
3. In the vertical plane, the best elevations among units correspond with the diversity of hair cell morphological polarizations on the saccular epithelium.
4. The best threshold sensitivity for these afferents is high: at 100 Hz, displacement at threshold is about 0.1nm. This is approximately the same amplitude of basilar membrane motion at behavioral detection threshold in mammals (Allen 1996).
5. Intracellular labeling shows that maps of anatomical hair cell orientation do not quantitatively predict physiological directionality (Edds-Walton et al. 1999). This is probably due to the simplifications of constructing two-dimensional maps of three-dimensional structures. Anatomical maps cannot substitute for physiological data in specifying the directional information transmitted to the brain by the octaval nerve.

Since best azimuths for the saccular afferents studied so far tend to cluster about the azimuthal angle in the head of the saccule and otolith (see also Sand 1974), the overall stimulation of the right and left saccules will tend to differ depending on the azimuth of particle motion. Theoretically, azimuth angle can be computed by comparing the summed

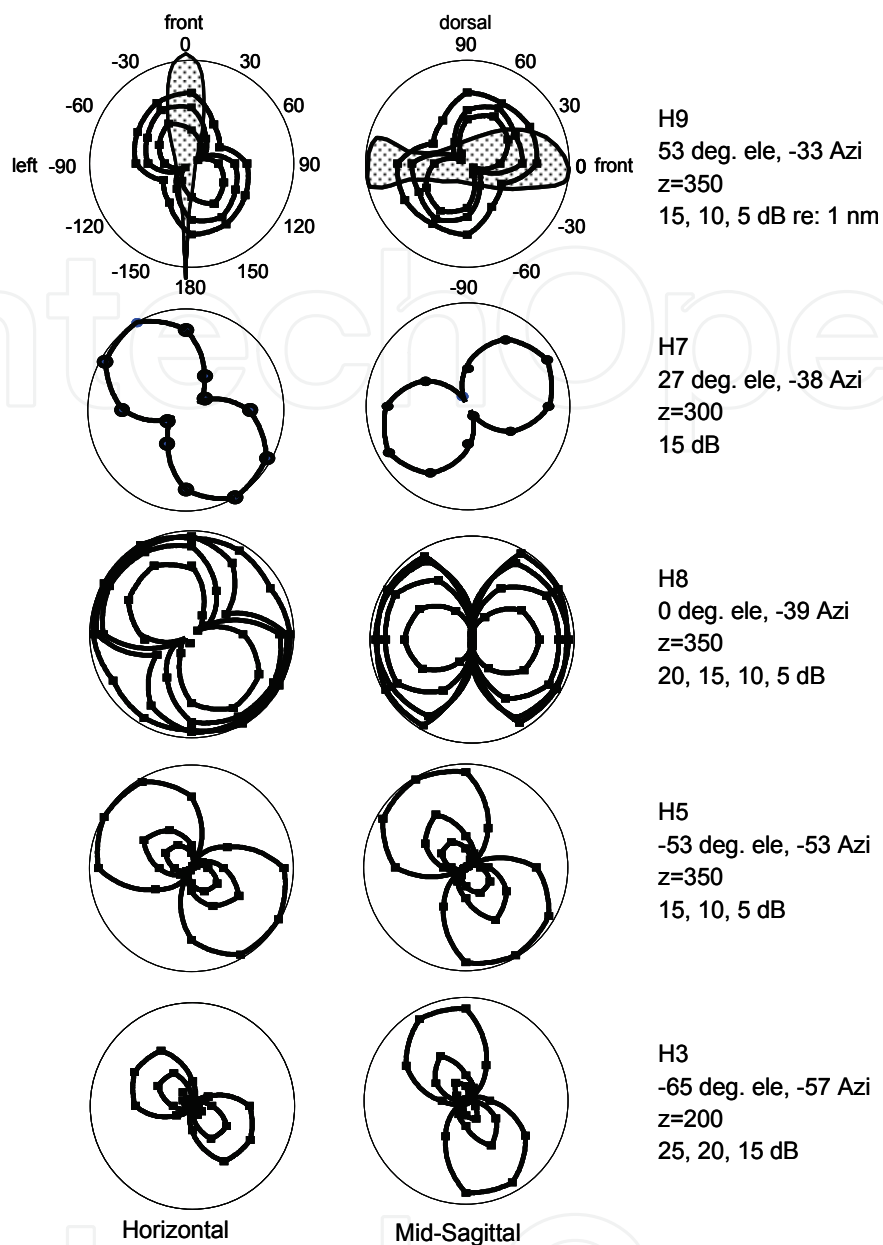


Fig. 3. Representative directional response patterns (DRP) for left the saccule of the oyster toadfish (*Opsanus tau*). The left column shows DRPs in the horizontal plane, and the right column shows DRSs in the mid-sagittal plane. The best azimuths (left) tend to cluster at about -40° . Best elevations (right) vary more widely, covering all elevations.

The keys associated with each pair of DRPs indicate the animal and unit ID, estimates of the best azimuth and elevation, the radial axis represented by the circle for each DRP, and the stimulus levels used.

Modified from Fay and Edds-Walton, 2000.

output of each saccule (e.g., through subtraction or common-mode rejection), but with several ambiguities. Sound source localization in azimuth seems to be a binaural process in fishes as it is in terrestrial animals. Edds-Walton (1998) has identified bilateral projections in a medullar nucleus (descending octaval nucleus), and there is physiological (Edds-Walton and Fay, 2009) and neural labeling data (Edds-Walton, et al., 2009) on *Opsanus tau* indicating

that binaural processing occurs in the medulla. This is consistent with the observations of Moulton and Dixon (1967), Schuijf (1975), and Schuijf and Siemelink (1974) indicating that the information from the two ears is necessary for sound source localization in azimuth. Note, however, that binaural acoustic cues are probably not available to fishes; the binaural information derives from the inherent directionality of the ears that respond directly to acoustic particle motion. Fay and Edds-Walton (1997a) have observed that the phase angles at which the units synchronize to a stimulus vary with the effective stimulus level in non-spontaneous saccular afferents. This means that an interaural phase difference could represent response magnitude, giving rise to a robust interaural timing code for azimuth. Coding for elevation seems to be a different matter, however. The elevation of a sound source is represented within a sensory epithelium as the profile of activity across saccular afferents with different “best elevations” (see Fig. 3). There is a functionally similar hypothesis for determining elevation for mammalian listeners; this is the hypothesis that the spectral profile (pattern of activity over the length of the cochlear epithelium) as shaped by the frequency spectrum as filtered through the head-related transfer function (HRTF) (e.g., Wightman and Kistler 1993). In other words, it is hypothesized for both fishes and mammals, source elevation coded as a monaural profile of excitation over the surface of the sensory epithelium that encodes frequency for mammals, and elevation for fishes.

The directional responses of the auditory nerve have also been investigated for organs other than the saccule. Hawkins and Horner (1981) investigated utricular units in the cod and found them to be most sensitive in the horizontal plane with substantially cosine-like directional response patterns (DRP). Fay (1984) surveyed lagenar and utricular as well as saccular units in goldfish. All three otolith organs had a similar distribution of displacement thresholds (lowest thresholds near 0.1 nm at 140 Hz) and cosine-shaped DRPs. Lagenar and saccular units showed a wide distribution of best axes in elevation with a tendency to cluster in azimuth parallel to the orientation of the respective organs. In the experiments of Lu et al. (2003) on the lagena of the sleeper goby, DRPs deviated significantly from a cosine shape, showing more narrowly shaped DRPs than would be expected from hair cells, and best thresholds that were somewhat higher than saccular afferents from the same species. More broadly shaped DRPs could be explained by excitatory convergence from hair cells having different directional orientations (Fay and Edds-Walton 1997a), but narrowly shaped DRPs cannot be explained at present. The differences in sensitivity between lagenar and saccular units in the sleeper goby could possibly be related to the lagena’s small size in most non-specialized species.

7.2 The auditory CNS

The representations of directional acoustic information in the brain have been studied in *Carassius auratus* by Ma and Fay (2002), *Opsanus tau* by Edds-Walton and Fay, and in *Salmo gairdneri* by Wubbles and Schellart. The major acoustic nuclei of the brainstem are the first-order descending octaval nucleus (DON), the higher-order secondary octaval population (SOP), and the torus semicircularis (TS) of the midbrain. Auditory responses of the SOP, thalamic, and other forebrain auditory nuclei have not been studied with respect to directionality.

Most of the single units recorded in the toadfish DON show simple directional preferences for the axis of whole-body acceleration. The occurrence of directionality in the DON (and

other auditory nuclei) indicates that excitatory convergence from neurons having different directionality probably does not occur in the brain since the directional selectivity of the periphery is maintained by cells throughout the brainstem. The sensitivity, frequency response, and phase-locking of DON units are similar to those of saccular afferents, but the directional response patterns (DRP) of most units tend to be more directionally selective than saccular afferents. This increased selectivity has been termed “sharpening” (Fay and Edds-Walton 1999, Edds-Walton and Fay 2003). Figure 4 shows typically sharpened DRPs from the brainstem of toadfish along with a graphical representation of a simple model mechanism that could account for sharpening (Edds-Walton and Fay, 2003). The hypothesis is that a central cell receives excitatory input from one directional cell, and inhibitory input from another directional cell (possibly from the contralateral ear), both having cosine-like DRPs with different best axes in azimuth or elevation (Fay and Edds-Walton, 1999). This excitatory-inhibitory convergence appears to be a common interaction in the auditory brainstem, and it always results in some degree of directional sharpening, depending on the best axes and weights associated with each input. Recordings from the torus semicircularis (TS) of the midbrain (Fay and Edds-Walton, 2001, Edds-Walton and Fay, 2003) show similar

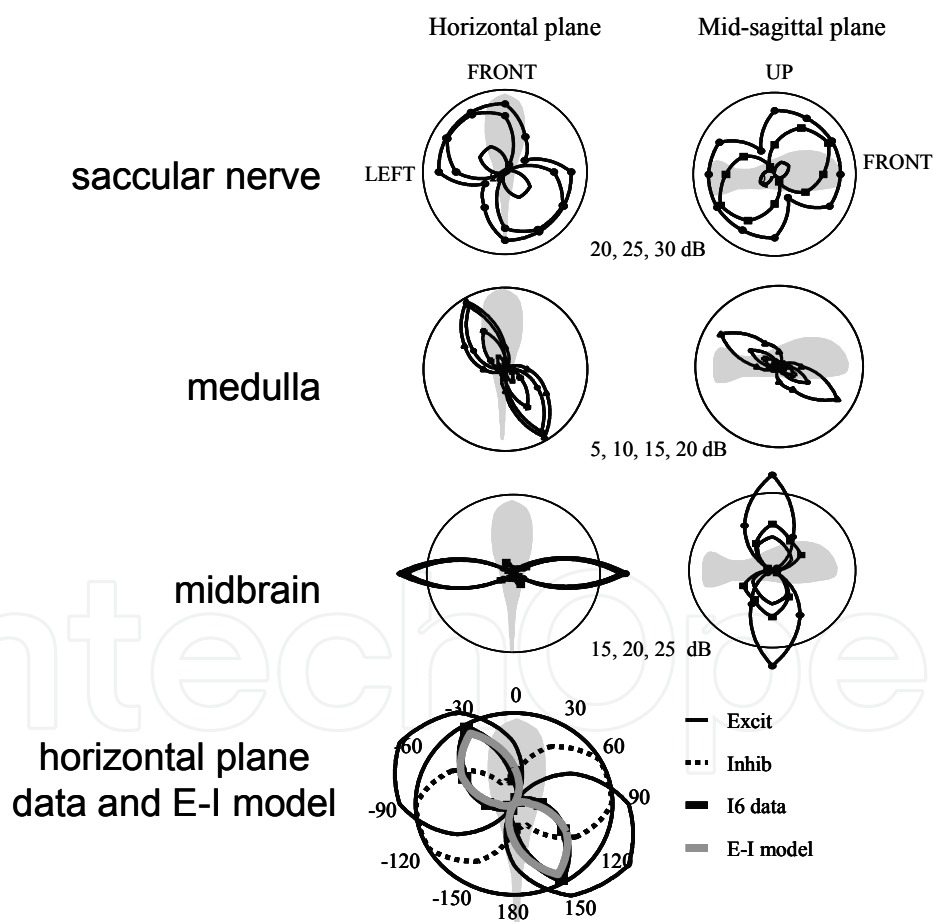


Fig. 4. Directional response patterns (DRP) for three representative cells of the saccular nerve, medulla (DON), and midbrain (TS) for three stimulus levels. Left column – horizontal plane. Right column – mid-sagittal plane (Modified from Edds-Walton and Fay, 200X). At bottom is shown a simple excitatory-inhibitory model for sharpening the DRP along with data from unit I6 (see text) (modified from Fay and Edds-Walton, 2005).

unit sensitivity and frequency response as in the DON, but with dramatically reduced phase-locking, and directional sharpening that is augmented, on average (see Fig. 4). Edds-Walton (1998) has confirmed that binaural projections exist connecting the right and left DONs in the medulla, and Edds-Walton and Fay (2009) have confirmed physiologically that there are binaural interactions among some cells of the DON. In addition, Edds-Walton, et al. 2009 have confirmed that binaural computations involving excitatory and inhibitory inputs take place in the DON using the inhibitory neurotransmitter, GABA.

In the midbrain, directional auditory responses were found both in the nucleus centralis of the torus semicircularis (the “auditory” nucleus), and the nucleus ventrolateralis (the “lateral line” nucleus) in toadfish. In addition, many units recorded in both nuclei showed interactions of auditory and lateral line inputs (excitatory and inhibitory) (Fay and Edds-Walton 2001, Edds-Walton and Fay 2003). It is not known whether such bimodal interactions play a role in sound source localization, but source localization is likely a multimodal function (Braun et al. 2003), and the lateral line system could play an important role close to the source (Weeg and Bass 2002). In general, the best axes for brainstem auditory units are more widely varied in best azimuth and elevation than the same distributions for saccular afferents.

The directional characteristics of TS units also have been studied in goldfish, a species specialized for sound pressure reception (Ma and Fay 2002). Most units recorded responded best to vertical vibration, as predicted by the vertical orientation of saccular hair cells in goldfish and other Otophysi. Thus, excitatory inputs to the TS appear to be primarily from the saccule in goldfish. Nevertheless, deviations from cosine directionality among unit DRPs (i.e., sharpening) were also observed in the goldfish TS, and could be accounted for by simple excitatory-inhibitory interactions as in toadfish. This suggests that sound source localization in Otophysi, if it occurs at all (see Schuijf et al. 1977), may be based on computations taking place elsewhere in the ascending auditory system where lagenar or utricular inputs could be used to help resolve the axis of acoustic particle motion. In any case, the representation of acoustic particle motion appears to be organized quite differently in the midbrains of goldfish and unspecialized species, corresponding to the anatomical differences between their respective saccules (essentially vertically oriented hair cells in goldfish and other Otophysi versus diverse orientations in most other species).

Wubbles, Schellart, and their colleagues have presented a series of studies on directional sound encoding in the midbrain (torus semicircularis or TS) of the rainbow trout (*Oncorhynchus mykiss*). Like the toadfish, this species is not specialized for sound pressure reception but is assumed to receive both direct motion as well as reradiated, pressure-dependent motion inputs from the swim bladder. Fish were stimulated in neurophysiological studies by whole-body acceleration at various angles in the horizontal plane using a vibrating platform that could be rotated to any angle (Schellart et al. 1995). Several important observations on directional representations were made:

1. About 44% of the units recorded were classified as directional (Wubbles and Schellart 1997).
2. Directional units were roughly mapped in the TS with the medial TS containing rostro-caudal orientations and the lateral TS containing cells with many different orientations (Wubbles et al. 1995).

3. The TS has a columnar organization with similar best axes of horizontal motion tending to be constant within vertical columns (Wubbles et al. 1995, Wubbles and Schellart 1998).
4. Some phase-locked units had phase angles of synchronization that did not vary with the stimulus axis angle (except for the expected 180° shift at one angle), while others showed a phase shift that varied continuously with stimulus angle over 360° (Wubbles and Schellart 1997).

Wubbles and Schellart concluded that those and other results strongly supported the phase model. They speculated that the rostro-caudally oriented units of the medial TS were channels activated by swim bladder-dependent motion input, while the diversely oriented units of the lateral TS represented direct motion input to the otolith organs. The utricle was thought to be the otolith organ supplying the direct motion-dependent input because of its horizontal orientation. The authors speculated that the units with synchronization angles independent of stimulus direction represented pressure-dependent swim bladder inputs while the units with variable synchronization phase angles represented direct motion inputs. Wubbles and Schellart (1997) then concluded that "...the phase difference between the(se) two unequivocally encodes the stimulus direction (0-360°)..." (i.e., solves the 180° ambiguity problem). This conclusion would be strengthened by a more clear and detailed explanation for the direction-dependent variation in synchronization angle shown by some units and by a testable theory for the final step that solves the 180° ambiguity.

8. Summary and conclusions

1. There are much data on the acoustical behaviors of several fish species that strongly suggest the capacity directional hearing and sound source localization. Most of these observations indicate the necessity that one or more otolith organs respond to acoustic particle motion.
2. The question of localization in the near- versus far-fields is no longer a critical issue because we now know that near field hearing does not imply that the lateral line system must be involved. The otolith organs respond directly to acoustic particle motion in both fields.
3. Most conditioning and psychophysical studies on the discrimination of sound source location provide evidence consistent with the hypothesis that fishes are able to locate sound sources in a way analogous to localization capacities of human beings and other tetrapods, both in azimuth and elevation. However, most of these studies fail to unequivocally demonstrate that fishes can actually perceive the location of sound sources.
4. An explanation for sound source localization behavior at the level of Mauthner cells and other reticulo-spinal neurons cannot serve to explain conditioning and discrimination learning phenomena with respect to source location.
5. All present accounts postulate that the process begins with the determination of the axis of acoustic particle motion by processing the profile of activity over an array of peripheral channels that directly reflect diverse hair cell and receptor organ orientations ("vector detection").
6. Neurophysiological studies on cells of the auditory nerve and brainstem are consistent with vector detection and show that most brainstem cells preserve and enhance the

- directionality originating from otolith organ hair cells. Goldfish and other Otophysi present a clear problem for this view because there is little or no variation of hair cell directionality in the saccule or at the midbrain. This has led to speculations that Otophysi use other otolith organs (lagena or utricle) in addition to the saccule for vector detection.
7. Vector detection leaves an essential “180° ambiguity” as an unsolved problem (Which end of the axis points to the source, or, in what direction is the sound propagating?). The “phase model” of directional hearing has been moderately successful in solving this ambiguity in theory and experiment. However, the 180° ambiguity is not the only ambiguity for sound source localization throughout the vertebrates. It is not certain that auditory processing, alone, must be able to solve this problem.
 8. Although the phase model is successful in a general sense, it is difficult to apply in several important cases (i.e., for fishes without swimbladders, and for Otophysi) where effectively independent representations of the particle motion and pressure waveforms are required but are not evident.
 9. Additional problems for vector detection and the phase model are that the axis of acoustic particle motion points directly at the source only for monopole sources, and that clear and unambiguous representations of waveform phase that could help in localization have not been observed in auditory nerve units (distributions of phase-locking angles tend to be uniform).
 10. While there are behavioral and electrophysiological observations that are consistent with sound source localization in fishes, there are no examples of localization capacities in a single species that have a comprehensive theoretical explanation. Sound source localization in fishes remains incompletely understood.

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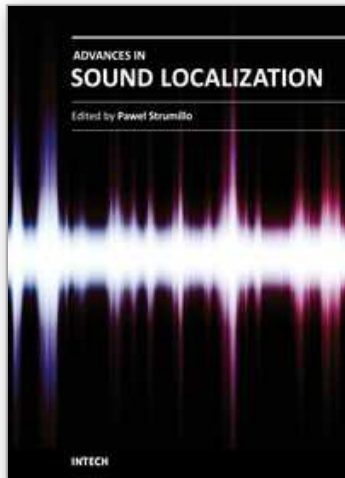
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Sound source localization is an important research field that has attracted researchers' efforts from many technical and biomedical sciences. Sound source localization (SSL) is defined as the determination of the direction from a receiver, but also includes the distance from it. Because of the wave nature of sound propagation, phenomena such as refraction, diffraction, diffusion, reflection, reverberation and interference occur. The wide spectrum of sound frequencies that range from infrasounds through acoustic sounds to ultrasounds, also introduces difficulties, as different spectrum components have different penetration properties through the medium. Consequently, SSL is a complex computation problem and development of robust sound localization techniques calls for different approaches, including multisensor schemes, null-steering beamforming and time-difference arrival techniques. The book offers a rich source of valuable material on advances on SSL techniques and their applications that should appeal to researches representing diverse engineering and scientific disciplines.

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