6
Orientation to Auditory and Lateral Line Stimuli

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1. Introduction

1.1 Underwater Acoustics

The reader of this chapter should have basic knowledge of underwater acoustics, and is referred to other texts for a thorough discussion of the topic in a biological context (e.g., Harris 1964; van Bergeijk 1967; Kalmijn 1988). In short, sound has a dualistic nature and consists of both a pressure component and a kinetic component. Far from the sound source, particle motions associated with the pressure fluctuations constitute the kinetic component. These motions can be expressed as particle displacement, particle velocity, or particle acceleration. The ratio between sound pressure and particle velocity is constant far from the source, and defines the acoustic impedance of the medium. In addition to generating propagating sound, a vibrating sound source produces hydrodynamic flows in its vicinity. These particle motions are independent of the elastic properties of the medium, and decay very steeply with distance from the source. Consequently, particle motions close to the source are composed of both hydrodynamic flows and motions associated with the propagating sound. The attenuation of the sound pressure and the associated particle motions follow $1/r$ under free-field conditions (in a homogeneous medium far from any boundaries), where r is the distance from the source. The hydrodynamic particle motions (which dominate close to the source) attenuate much more steeply, following $1/r^2$ for a monopole source, which pulsates in volume, and $1/r^3$ for a dipole source, which vibrates with constant volume. The distance at which hydrodynamic and pressure-associated particle motions have equal amplitude is $1/2\pi$ of the wavelength for an ideal monopole source. Closer to the source the hydrodynamic particle motions dominate, and this region is commonly termed the acoustic nearfield. The region beyond, where the sound pressure-associated particle motions dominate, is then called the acoustic farfield. The nearfield is frequency-dependent and expands towards lower frequencies, and is also more extensive for a dipole source.

In the pure farfield, the particle motions are normal to the wave front, and for a monopole the particle motions are radial to the source also in the nearfield. However, for a dipole sound source the nearfield particle motions are more complex and may have any direction relative to the vibration axis of the source (see Section 2.3 and Fig. 6.6).

1.2 Physical Considerations and Historical Background

The ears of terrestrial vertebrates are sensitive to sound pressure, which is a scalar quantity, and directional information cannot be mediated via a single pressure detector. Thus, directional hearing in terrestrial vertebrates is based on the analysis of differences in sound intensity, phase, and time of arrival at the two ears. The ratio between the speed of sound in water and air is approximately 4.5, making the differences in both phase and arrival time at the two ears correspondingly less for a fish than for a comparable animal in air. Further, sound passes through the body of a fish with negligible reflective loss, minimizing the intensity differences between the two ears, while the body of terrestrial animals may constitute an effective sound barrier causing sound shadows that maximize such intensity differences. Moreover, in many teleosts a gas-filled swimbladder acts as a single sound pressure detector by transforming sound pressure into particle motion (Braun and Grande, Chapter 4).

The physical considerations mentioned in the preceding text seem to indicate unfavorable conditions for directional hearing in fish, in accordance with the ambiguous results from the initial investigations of this ability in teleosts. It is technically more difficult to conduct controlled experiments on directional hearing than to test the general hearing sensitivity, and during the first half of the previous century only three studies specifically addressed directional hearing in fish (Reinhardt 1935; von Frisch and Dijkgraaf 1935; Kleerekoper and Chagnon 1954). The first two of these papers concluded that fish cannot localize sound sources, whereas the third reached the opposite conclusion.

In spite of the scanty experimental data available at the time, van Bergeijk published a tremendously influential theoretical paper on directional hearing in fish in 1964. His analysis (van Bergeijk 1964) was based on the following assumptions:

- Hearing in the acoustic farfield is strictly a detection of sound pressure, and is based on the swimbladder acting as a transformer between pressure and particle movement.
- Within the acoustic nearfield, the lateral line may detect the incident particle movements at considerable distance (at least many body lengths) from the source.
- Biologically significant sounds have fairly high frequencies (at least several tens of Hertz), making sound detection in the farfield a dominant aspect of hearing in fish.

Later, all these assumptions were shown to be erroneous, but based on this shaky foundation van Bergeijk formulated his theory of directional hearing in fish:

- A single pressure detector (the swimbladder) cannot be used to localize a sound source, and fish behave according to their physical limitations: They do not detect the sound direction in the farfield.
- The lateral-line system amply satisfies the minimum requirements for localization of a sound source in the nearfield. Consequently, fish are capable to localize sound sources in the nearfield only.

Among his fellow scientists working on hearing in fish, van Bergeijk was unique in his physical and mathematical approach, and van Bergeik's authority was unprecedented. He was respected to such a degree that for several years his theoretical considerations hampered further progress in this field of research. However, for scientists mainly studying shark behavior, van Bergeijk's theory did just not fit their observations, and the idea that he might be wrong slowly evolved. In particular, Nelson and Gruber (1963) and Myrberg et al. (1969) concluded, based on their field observations, that sharks can detect and orient to sounds in the acoustic farfield. These important studies showed that a swimbladder is not required to detect farfield sound of normal intensities, and that sharks may react to such sounds with directed responses. Chapman and Sand (1974) showed that flatfish, which also lack a swimbladder, are sensitive to particle motion, and that the lowest auditory thresholds are less than 0.1 nm, measured as particle displacement. Recordings from primary afferent neurons from otolith organs in the goldfish (*Carassius auratus*) revealed similar low thresholds for whole-body vibrations (Fay 1984). Such sensitivity enables fish to detect farfield sounds of normal intensities even in the absence of a swimbladder.

Schuijf et al. (1972) were the first to show that teleosts may discriminate between sounds of different directions at approximate farfield conditions. Several behavioral experiments, which are reviewed in Section 3, have confirmed and extended this observation. Thus, both sharks and teleosts can discriminate between sounds of different directions, but what are the physiological mechanisms behind this ability? Further, how are fish able to not only discriminate between sounds from different directions, but also to locate the sound sources? In the following, we discuss different models for directional hearing in fish, and to which degree these models are supported by behavioral observations. The directional fast-start escape responses (startle responses), which are elicited by high intensity acousticolateral, somatic, and visual stimuli activating reticulospinal neurons, are treated in a separate section. We also include a section on the role of lateral line organs in directed responses, although these organs are insensitive to propagating sound (see review by Sand 1984).

2. Models for Directional Hearing

2.1 Vectorial Analysis of Particle Motions

Soft fish tissue has nearly the same acoustic properties as water, and will vibrate with the same phase and amplitude as the surrounding water during exposure

to sound. In contrast, the otoliths have a mass density three times larger than that of the neighboring tissue, and will lag behind the motions of the hair cells when the fish oscillates in a sound field. This creates shear movements of the sensory hairs in close contact with the otoliths (Fay and Edds-Walton, Chapter 3). Otolith organs are thus accelerometers, as outlined by de Vries (1950), and the inner ear of fish is inherently sensitive to the kinetic sound component (particle acceleration). The hair cells are directionally sensitive displacement detectors (Flock 1965; Hudspeth and Corey 1977), and in the otolith organs the hair cells are organized in patterns where the direction of the optimal sensitivity axis varies along the maculae (see review by Popper and Coombs 1982). It is therefore reasonable to suggest that the fish brain may calculate the direction of particle movements of the incident sound by vectorial weighing of the input from different regions of the sensory maculae, and *all current models of directional hearing in fish are based on this idea*.

In the acoustic farfield, the particle motions are radial to the source (normal to the wave front), simplifying the computation of sound direction. However, in the nearfield the situation may be more complex, as discussed in Section 2.3. Another complicating factor is the auditory function of a swimbladder. The advantage of a swimbladder in lowering auditory thresholds may be at the expense of acute directional hearing, because the amplified vibrations reradiating from the swimbladder may mask the incident particle motions. This issue is discussed further below.

At the time 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 (Parvulescu 1967). However, because a fish in water is nearly acoustically transparent and vibrates with the same phase and amplitude as the surrounding medium, vibration of the fish in air simulates the kinetic sound component in water. Such an approach eliminates the problem of making directionally well defined stimuli in small tanks (Enger et al. 1973; Sand 1974). In retrospect, this seems rather obvious, but at the time it was a mental leap. Nearly all later neurophysiological studies of directional hearing in fish have employed variations of this stimulation technique. The only exception is a study by Buwalda and van der Steen (1979), who employed a standing wave controlled by pairs of opposing sound projectors to investigate the directionality of saccular microphonic potentials in the Atlantic cod (*Gadus morhua*). This stimulation technique is described in detail by Buwalda (1981).

In the experiments by Sand (1974), microphonic potentials were recorded from various positions along the saccular macula and from the lagena in perch during whole body vibration in air. For vibrations in the horizontal plane the angular response pattern was the same for all electrode positions along the sacculus, and showed a cosine function with maximal amplitude of the microphonic potentials at an angle of about 20° relative to the long axis of the fish (Fig. 6.1A). The angle between the optimal axes for the two ears was thus about 40°, which corresponds to the mean angle between the saccular otoliths in this species.
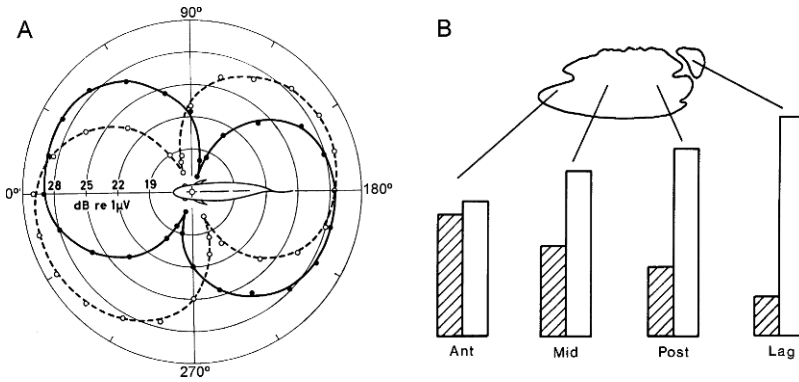
FIGURE 6.1. (**A**) Polar diagram of microphonic potentials recorded from the right (•) and left (o) sacculus in perch as a function of the horizontal vibration angle. Maximal microphonic responses were evoked by vibration directions deviating about 20° from the long axis of the fish, which corresponds to the mean angle of about 40° between the sacculi in this species. (**B**) Comparison of mean ratios between the microphonic sensitivity to vertical (open columns) and optimal horizontal (hatched columns) vibrations at 200 Hz for the anterior (Ant), mid (Mid), and posterior (Post) parts of the sacculus, and for the lagena (Lag). The lagena and posterior part of the sacculus are predominantly sensitive to vertical vibrations, whereas the anterior part of the sacculus is equally sensitive to horizontal and vertical vibrations. (From Sand 1974.)

Consequently, the saccular microphonic response is greatest when the relative otolith movements are along the main orientation axis of the sacculus in the head. Since the paired sacculi have different orientations in azimuth, the output from the right and left sacculus will be different (except for sources in the mid sagittal plane), although the incident particle motions are virtually the same at both ears. It was thus concluded that fish might determine the azimuth of a sound source by comparing the output from the two ears. Fish would then be similar to terrestrial vertebrates in utilizing interaural response differences as the basis for computation of azimuth. In agreement with this hypothesis, Schuijf and Siemelink (1974) found that the ability of Atlantic cod to discriminate between horizontal sound directions was lost after unilateral severing of the auditory nerve. Further, binaural interactions have been demonstrated by recordings from single units in both the acoustical lobes of the medulla oblongata and in the mesencephalic torus semicircularis in Atlantic cod (Horner et al. 1980), and Edds-Walton (1998) has provided anatomical evidence for binaural processing in the toadfish.

Figure 6.1B shows the relative microphonic responses to vertical and horizontal vibrations for the different recording positions in perch. The lagena and the posterior part of the sacculus were relatively more sensitive to vertical vibrations than the anterior part of the sacculus, in agreement with the pattern of saccular and lagenar hair cell orientation in this species (Enger 1976), and it was suggested that input from only one ear might provide sufficient information

to estimate the elevation of a sound source. It was also concluded that the ability of the fish to determine the elevation of a sound source should be at least as good as the resolution of azimuth. The latter suggestion was later confirmed in behavioral experiments (Section 3).

The experiments by Sand (1974) provided the first electrophysiological data supporting a vectorial weighing mechanism for directional hearing in fish. However, recordings from afferent fibers from different parts of the ear give more refined information about regional differences in directional sensitivity of the sensory maculae, and reveals directly the directional information conveyed to the next level in the auditory pathway. Such experiments were first performed by Fay and Olsho (1979), who recorded responses from saccular and lagenar afferents in the hearing specialist goldfish during head vibrations in three orthogonal directions. The vibration directions of optimal sensitivity in the horizontal and sagittal planes were then calculated, and found to correspond roughly with the hair cell orientation maps. Polar diagrams of the directional sensitivity to primary auditory afferents in fish were first presented by Hawkins and Horner (1981), who recorded from the saccular and utricular branches of the auditory nerve in Atlantic cod during whole-body vibrations in the horizontal plane. The saccular units showed a narrow angular distribution of their optimal axes of vibration, with a mean optimal angle of 6° relative to the long axis of the fish (Fig. 6.2A).
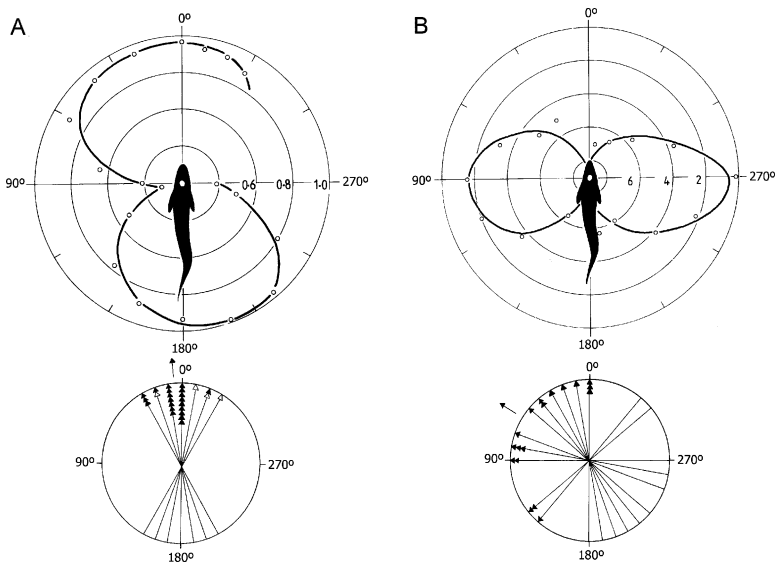

FIGURE 6.2. (**A**) Polar diagram of the spike frequency recorded from a primary afferent neuron from the left sacculus in cod as a function of the horizontal vibration angle. Lower panel: Distribution of the optimal horizontal vibration angle of afferent neurons from the left sacculus. Closed arrows represent units from the anterior ramus, and open arrows are from the posterior saccular ramus. (**B**) Comparable diagrams for primary afferent neurons from the left utriculus in cod. (From Hawkins and Horner 1981.)
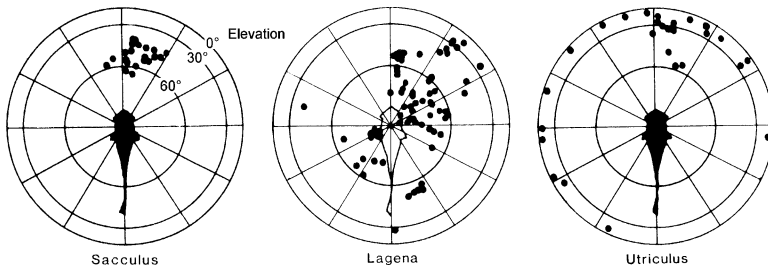
FIGURE 6.3. Distributions in spherical coordinates of the optimal vibration axes of single afferents from the right sacculus, lagena, and utriculus in the goldfish. The ear is depicted in the center of a globe, and the position of the symbols on the northern hemisphere shows the location at which the optimal axis would penetrate the surface of the globe. (From Fay 1984.)

In contrast, the utricular units displayed a wide angular distribution, with some optimal sensitivity axes even perpendicular to the long axis of the fish (Fig. 6.2B).

Soon after, Fay (1984) studied the responses in branches of the auditory nerve innervating all three otolith organs in the goldfish. The stimulation system was designed to produce whole-body accelerations along any axis in space, and the directional sensitivity of saccular, lagenar and utricular units was determined in three dimensions (Fig. 6.3). The optimal vibration axes of saccular units were tightly grouped in space, in agreement with the notion that the sacculus is mainly stimulated by reradiated swimbladder motions in otophysan species (which possess Weberian ossicles, Braun and Grande, Chapter 4). Lagenar units were more widely scattered in elevation, but with azimuth roughly grouped around 60°. The optimal axes of utricular units covered a wide range in a nearly horizontal plane, corresponding to the horizontal orientation of the utricular macula.

The most sensitive units responded to vibrations down to 0.1 nm at 140 Hz, which corresponds to the auditory particle motion thresholds previously obtained in behavioral experiments on flatfish (Chapman and Sand 1974). There were no major differences in sensitivity between units from the different branches of the auditory nerve, indicating that all otolith organs may be involved in hearing.

Following these pioneering studies, similar recordings from primary, auditory afferents have also been performed in toadfish (*Opsanus tau*; Fay and Edds-Walton 1997, 2000; Edds-Walton et al. 1999), sleeper goby (*Dormitator latifrons*; Lu and Popper 1998, 2001; Lu et al. 1998, 2003, 2004), and plainfin midshipman (*Porichthys notatus*; Weeg et al. 2002). Based on all the electrophysiologcal studies on the peripheral auditory organs in fish, the following main conclusions related to directional hearing may be drawn:

- Primary auditory afferents tend to have directional response patterns similar to the cosine directional response function of a single hair cell, indicating that each afferent contacts a population of hair cells with the same directional orientation.

- Afferents from all otolith organs are sufficiently sensitive to respond to particle motions associated with sounds of normal intensity, indicating that the brain may use information from all otolith organs in its computation of sound direction.
- Strong phase locking to the stimulus is a common feature of the neural responses in primary auditory afferents. Information about stimulus phase is thus conveyed to the central nervous system.
- The optimal axes of saccular and lagenar afferents display a wide scatter in elevation, but with azimuths grouped along axes coinciding with the physical orientation of the maculae. Optimal axes of utricular afferents are mainly in the horizontal plane, and show a wide scatter in azimuth. These patterns are compatible with the mainly vertical orientations of the saccular and lagenar maculae, and the horizontal orientation of the utricular macula in most species (with clupeids as the major exception). In otophysan species, the optimal axes of saccular units are more tightly grouped than in hearing non-specialists, in agreement with the tight link between the sacculus and the swimbladder.
- The distribution of the optimal axes of primary afferents suggests that information from one ear might suffice for computation of sound source elevation, while information from both ears might be required for computation of azimuth. Thus, the peripheral auditory apparatus of a fish appears capable of three-dimensional detection of sound direction.

If the directional information conveyed to the central nervous system via the primary afferents is utilized in the control of behavior, there should exist central auditory nuclei where the sound direction is represented in a manner appropriate for decision-making. The torus semicircularis (TS) in the mesencephalon, which is homologues to the inferior colliculus in mammals, is a likely candidate for such functions. TS receives input from major auditory areas in the medulla oblongata (McCormick and Hernandez 1996). Further, single-unit recordings from the TS in the Atlantic cod have demonstrated binaural interactions, and sound may induce both excitation and inhibition of neurons in this area (Horner et al. 1980).

The directional sensitivity of TS neurons has been studied in three species: rainbow trout (*Oncorhynchus mykiss*; Wubbels et al. 1995; Wubbels and Schellart 1997, 1998), goldfish (Ma and Fay 2002), and toadfish (Edds-Walton and Fay 2003, 2005a). The data from rainbow trout and toadfish showed that the directionality of the primary afferents was not only preserved in the TS, but various degrees of sharpening of the directional responses were also observed. The sharpening has been tentatively explained via a combination of excitatory and inhibitory inputs to the same neuron (Ma and Fay 2002; Edds-Walton and Fay 2003, 2005a). In the rainbow trout, directional sensitivity was studied only in the horizontal plane, where the optimal vibration directions of the TS units displayed a wide distribution covering any vibration angle (Fig. 6.4A). Thus, the TS in rainbow trout seems well equipped for determination of sound direction, at least in the plane studied.
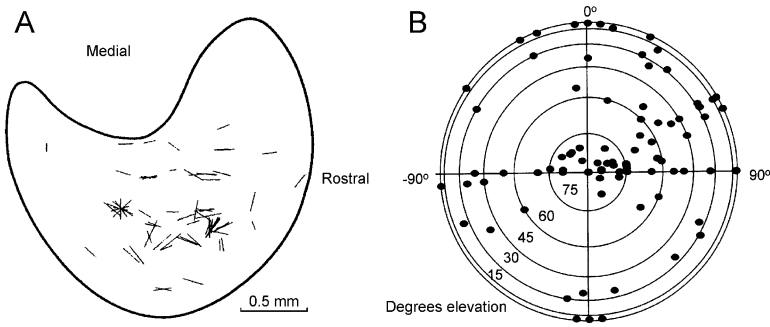
FIGURE 6.4. (**A**) Dorsal view of location of directional sensitive units in the right torus semicircularis in the rainbow trout. The center of each line represents the location of the unit (mean depth about 300 μm below the surface of TS), the length denotes its directional sharpness, and the orientation shows its optimal direction of vibration in the horizontal plane. The distribution of optimal directions covers any vibration angle. (From Wubbels and Schellart 1998.) (**B**) Distribution in spherical coordinates of the optimal vibration axes of directional single units in the left TS in toadfish. The fish is in the center of a globe, and the position of the symbols on the northern hemisphere shows the location at which the optimal axis would penetrate the surface of the globe. The optimal axes are widely distributed in space, covering any azimuth and elevation. (From Edds-Walton and Fay 2003.)

In the toadfish, the three-dimensional directional responses of TS single units have been studied in great detail (Edds-Walton and Fay 2003, 2005a). Most units were directionally sensitive, with a sharpened directional response compared to primary afferent neurons. The optimal vibration axes were arrayed widely in spherical space, covering all azimuths and elevations (Fig. 6.4B). Interestingly, some TS neurons seemed to be bimodal, responding both to whole body acceleration and to stimuli that presumably activated the lateral line system (Edds-Walton and Fay 2003, 2005b). The distribution of optimal vibration axes in toadfish TS is much wider than the comparable distribution of optimal axes of saccular afferents in this species (Edds-Walton et al. 1999). This discrepancy could be due to input from other otolith organs than the sacculus, which is commonly considered the main auditory end organ in fish, or to computations based on the directional properties of saccular afferents from both ears. In either case, the data indicate that all axes of acoustic particle motion around the fish are represented in the TS.

Recordings from the TS in the hearing specialist goldfish (Ma and Fay 2002) show a strikingly different picture than the data from the hearing nonspecialists rainbow trout and toadfish. The optimal vibration axes of directional goldfish TS units were tightly grouped in space (primarily vertical), in a similar fashion as the distribution of optimal vibration axes of saccular afferents (Fig. 6.3). The wide scatter of best axes of lagenar and utricular afferents was thus not reflected in the properties of TS neurons. The authors discussed if the lack of diverse optimal axes of TS units indicates poor directional hearing in goldfish (and other

hearing specialists), or is due to inadequate sampling of higher order auditory neurons. It would be remarkable if the seemingly useful directional information conveyed by lagenar and utricular afferents is not utilized in these species.

The electrophysiological data on directional sensitivity obtained by vibrating the fish in air exclude pressure stimulation via the swimbladder. It is still not understood how the directional information in the incident particle acceleration is protected against masking by the amplified secondary particle motions radiating from the swimbladder. Stimulation of the otolith organs via the swimbladder is likely to be identical for symmetrical parts of the two ears, and also independent of sound direction. In agreement with this notion, Buwalda and van der Steen (1979) observed that whereas the saccular microphonic responses in Atlantic cod showed a cosine relationship to the axis of particle motion in a standing wave with a high ratio between particle motion and pressure, the responses became omnidirectional when this ratio was inverted. However, the incident particle motion input to the otolith organs will generate different responses in symmetrical elements of the ears (except for sources in the midsagittal plane). Consequently, information about the direction of the incident particle motion may be obtained by subtracting the responses from the two ears (common mode rejection), whereas adding the responses from the two ears will emphasize the sound pressure waveform (which are common to both ears). The existence of such mechanisms lacks experimental verification. However, parallel detection of incident particle motion and sound pressure is a prerequisite for the phase model for directional hearing, which is discussed in the next section.

2.2 The Phase Model for Directional Hearing

As outlined in the previous section, the otolith organs in fish are inertial motion detectors directly stimulated by the particle accelerations of a sound wave, and fish may use these organs to determine the three-dimensional directionality of the incident sound. However, detection of the direction of the particle motion is in itself not sufficient to determine the direction to the sound source, since the particle motion in the farfield is alternately either away from or toward the source. Consequently, there is an inherent bidirectionality or 180° ambiguity in the response of a simple particle motion detector, making it impossible to discriminate between opposing sound sources (180° apart).

This inherent 180° ambiguity is solved by the phase model for directional hearing in fish (Schuif 1975, 1976, 1981). The model is based on the fact that the direction of farfield particle motion and wave propagation coincides during acoustic compression, while these directions are opposite during rarefaction. The model was inspired by Piddington's (1972) observation that goldfish can discriminate between sounds of inverted polarity. In species with a swimbladder, the model assumes that the fish is able to simultaneously detect the direction of the incident particle movements and the sound pressure—via the swimbladder (Fig. 6.5). By decoding the phase difference between these components, fish may be able to discriminate between opposing sound sources. In the previous
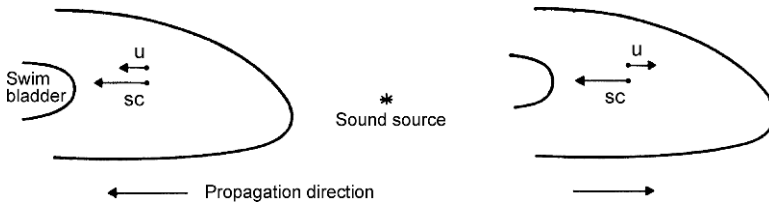
FIGURE 6.5. Principle of the phase model for solving the 180° auditory ambiguity in fish with a swimbladder. The left and right parts of the figure compare instants of maximum compression in the farfield at the same distance directly behind or in front of the source. The particle motions in the direct wave and the scattered wave emanating from the swimbladder are *u* and *sc*, respectively. If the sign of *sc* equals that of *u*, the source is in front of the fish. If the signs are different, the source is behind the fish. (From Scuijf 1975.)

section, a simple neural processing strategy for separation of acoustic pressure and particle motion was briefly described. Rogers et al. (1988) have elaborated on the phase model and proposed algorithms that the central nervous system might use to process acoustic information in order to localize the source.

The phase model was also adapted for sharks and other species lacking a swimbladder, and it was postulated that the 180° ambiguity was then resolved by comparing the phase between the direct sound and sound reaching the fish after reflection from the surface or the bottom (Schuijf 1975, 1976, 1981). Of course, this extension of the model has its limitations, and will fail if the fish is in midwater far from any reflecting surfaces. Rogers and Zeddies (Chapter 7) have suggested alternative, theoretical models that may resolve the 180° ambiguity for species both with and without a swimbladder. However, their speculations are not based on experimental data.

A prerequisite for the phase model in species possessing a swimbladder is separate encoding of sound pressure and incident particle motion, and phase comparison of these sound parameters. In the hearing specialists, such a task is clearly feasible, and the otophysan species ide (*Leuciscus idus*) is able to discriminate between opposing sound sources in the horizontal plane (Schuijf et al. 1977). Also in Atlantic cod, where an auditory function of the swimbladder has been demonstrated in both behavioral (Chapman and Hawkins 1973) and electrophysiological (Sand and Enger 1973) experiments, the phase relationship between incident particle motion and sound pressure is used to discriminate between opposing sound sources in both the horizontal (Schuijf and Buwalda 1975; Buwalda et al. 1983) and the median vertical plane (Buwalda et al. 1983).

Further, the Atlantic cod is capable of discriminating between much smaller phase differences than the 180° required for unambiguous detection of the propa-gation direction. The phase difference between particle motion and pressure is a function of distance to the source within the nearfield, and it was suggested that phase analysis could also enable the fish to detect the distance to a monopole

source (Buwalda et al. 1983). Later behavioral experiments did in fact demonstrate that the Atlantic cod can discriminate between sound form sources at different distances (Schuijf and Hawkins 1983). It is likely that this ability is based on phase comparison, although the ratio between the amplitudes of sound pressure and particle motion is also a function of distance within the nearfield. These behavioral experiments on Atlantic cod, which will be further discussed in Section 3, mark the culmination of the phase model for directional hearing in fish, and it was concluded that: "... it is quite likely that the cod is able to estimate the true distance of a sound source in its vicinity. Combined with its three-dimensional directional hearing capabilities, this would provide the cod, an animal living essentially in a three-dimensional habitat, with a real acoustical sense of space. In this respect the auditory capacities of cod would far exceed those of most terrestrial vertebrates..." (Schuijf and Hawkins 1983, p. 144).

This view on directional hearing in fish is certainly attractive, but should be treated with caution. At the time when the phase model was introduced and tested, the prevailing assumption was that most hearing nonspecialists possessing a swimbladder are sensitive to sound pressure close to threshold, at least within the upper part of the audible frequency range, but this view has recently been challenged (Yan et al. 2000). Further, the choices of sound sources (monopoles rather than dipoles) and frequencies (too high) in the behavioral tests of the model have been rather unphysiological, as discussed in Sections 2.3 and 3. It may turn out that the main physiological relevance of the phase model is related to the fast start escape responses, which are discussed in Section 4.

In the original phase model, neural common mode rejection by subtracting the outputs from binaurally symmetrical hair cell populations is suggested as a mechanism for resolving the incident particle movements. Conversely, adding such outputs emphasizes the pressure component. Therefore, the resolution of the 180° ambiguity according to the phase model depends on a binaural mechanism. However, an alternative processing strategy may utilize a basically monaural mechanism for resolving both the direction and the distance to the sound source. This variation of the phase model was suggested by Schellart and de Munck (1987), and is termed the orbit model.

The fact that particle movements associated with the incident sound wave and the scattered wave from the swimbladder are not in phase and have, in general, different directions, leads to elliptical particle motion orbits for pure tones (Schuijf 1981; de Munck and Schellart 1987; Scellart and de Munck 1987). The orbits are unique for each source position, and the orbit model predicts that the characteristics of the orbits themselves (shape, orientation of the length axis, direction of revolution) are analyzed, rather than extracting segregated information on the incident and scattered sound waves. For example, the 180° ambiguity is resolved by detection of the direction of revolution of the elliptical orbit. Although such a mechanism is inherently monaural, binaural comparison of motion orbits provides additional information that may improve source localization.

Behavioral determination of hearing thresholds as a function of source direction failed to provide unambiguous support of the orbit model (Schellart and Buwalda 1990). Further, recordings of directional responses of midbrain auditory neurons in rainbow trout gave results more in support of the original phase model than the orbit model (Wubbels and Schellart 1997, 1998). Hence, experimental support of the orbit model is scanty.

The focus on the 180° ambiguity problem in fish audition, and the efforts to develop a single, unifying model for its solution, may have been exaggerated. Terrestrial vertebrates, which determine sound direction by comparing sound parameters at the two ears, also encounter auditory ambiguity problems. Since no interaural differences will occur in timing, phase, and intensity of sound for all potential sound sources in the median plane, terrestrial animals must handle ambiguities in both elevation and front–back. Such ambiguities are solved by various measures, including movements of the head and pinnae, visual and olfactory cues, and estimation of the most likely source location based on experience. Considering the familiar solutions to the auditory ambiguity problems in terrestrial vertebrates, it is reasonable to suggest that also fish may employ a variety of mechanisms to resolve the 180° ambiguity.

2.3 The Guidance Model for Sound Source Localization

The emerging picture based on the phase model of directional hearing is that species with a swimbladder may have a vision-like, acoustical sense of space. However, the phase model is hampered with several uncertainties, and might not enable the fish to unambiguously locate the sound source at a distance. The model is based on two main assumptions:

- The particle motions are radial to the source.
- The phase information required to solve the 180° ambiguity is provided by a swimbladder or reflecting surfaces.

The first assumption is valid throughout the acoustic field for a monopole, but is valid only in the farfield for sources of higher order. For example, within the nearfield of a dipole, the direction of the particle movements at a certain point yields no information about the location of the sound source (van Bergeijk 1964), as illustrated in Figure 6.6. This limitation of the phase model would be of little significance if most natural underwater sound sources were monopoles, or if most acoustically evoked behaviors took place in the farfield. However, apart from fish that produce sound by swimbladder pulsations, most natural underwater sound sources do not change volume, and are thus not monopoles. Moving objects, like swimming fish, are best approximated by a dipole.

Further, fish and other animals moving underwater mainly produce extremely low-frequency sound (Kalmijn 1989; Bleckmann et al. 1991). The major components of the particle accelerations caused by swimming fish are even below 10 Hz. For biological sound sources generating such low frequencies the nearfield
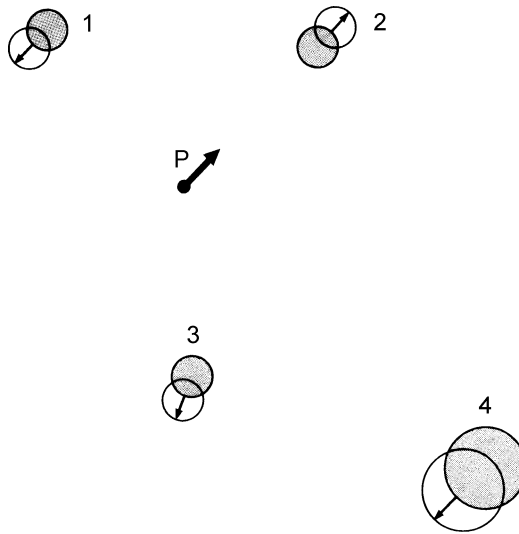
FIGURE 6.6. Ambiguity of the nearfield particle motions generated by a dipole sound source (vibrating sphere). An infinite number of potential dipoles might generate the indicated particle motions at point P, four of which are depicted. The magnitude of the vector at P is exaggerated for clarity. (From van Bergeijk 1964.)

extends beyond the audible range, and farfield detection is hardly biologically relevant. Fish are sensitive to extremely low-frequency sounds, even down to below 1 Hz, and infrasonic particle accelerations may be particularly effective in evoking behavioral responses in fish (see reviews by Sand and Karlsen 2000; Sand et al. 2001). It is also clear, in contrast to the view of van Bergeijk (1964), that the lateral line system is able to detect nearfield particle motions only up to at a distance of a few centimeters (Sand 1981, 1984; Enger et al. 1989). Within most of the nearfield, the acoustic detectors are the otolith organs, responding to whole-body acceleration of the fish. However, the lateral line can detect the vortices in a fish wake at considerable distance from the actual location of the wake generator (see Section 5.2.2).

The second assumption fails for a fish without a swimbladder in midwater, far from any reflecting surfaces. Moreover, the auditory gain provided by a swimbladder is frequency dependent, as the swimbladder pulsations exceed the free field particle motions only above a certain frequency, which will depend on both swimbladder volume and depth (Sand and Enger 1973; Sand and Hawkins 1973). Thus, the very low frequencies generated by moving objects are detected without the aid of the swimbladder at levels close to threshold (Sand and Karlsen 1986). However, pressure detection is essential for the startle responses evoked in otophysan species by low-frequency stimuli at high intensity (see Section 4).

The emerging picture from these considerations is that dipole sources producing extremely low-frequency sounds with extensive nearfields are among

the biologically most important sound sources. Such sources are detected within the nearfield without the aid of the swimbladder, and the direction of the particle motions at a single spot provides no information about the location of the source. The celebrated phase model is thus inadequate to explain directional hearing under such circumstances. The phase model is not necessarily wrong. Phase analysis of pressure and particle motion may tell the fish if it is detecting farfield sound or not, and thus if the direction of particle movements can be trusted to be radial to the source. The phase model may also explain the directed startle responses to high-level stimuli, as discussed in Section 4. However, an alternative model is needed to explain localization of dipole sources within the nearfield.

Kalmijn (1989, 1997) has suggested such an alternative model, based on a previous model for orientation of elasmobranches to bioelectric fields (Kalmijn 1982). The acceleration fields in the vicinity of moving objects are governed by the same mathematical equations as the bioelectric fields produced by aquatic animals. Hence, he has proposed that fish may reach the sound source by using their otolith organs in a similar fashion as elasmobranches use their electroreceptors in directed approaches toward concealed prey. The model predicts that the fish may locate a dipole source by merely sensing the direction of the acceleration field. While proceeding, the fish only has to turn in a manner that keeps a constant angle between the body axes and the incident particle acceleration detected by the inner ear. This simple strategy will guide the fish to the source (Fig. 6.7). The algorithm also works for monopoles and for combinations of monopoles, dipoles, and higher order sources. The hypothesis applies equally well for both sharks and teleosts and all types of sound sources at any distance. This unifying *guidance model for sound source localization* suggests that fish do not actually perceive the absolute location of sound sources at a distance, but are instead guided to the source. Of course, this strategy requires a more or less continuously emitting source during the approach.

It should be stressed that the guidance model has not yet been rigorously tested in behavioral experiments. However, the next section shows that most experiments on directional hearing in fish have revealed only that fish are able
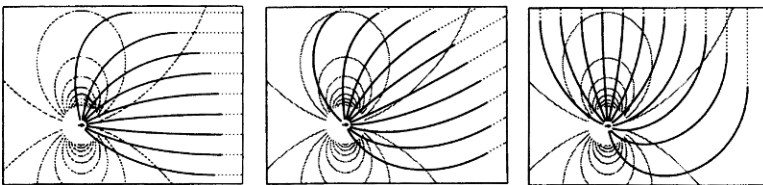

FIGURE 6.7. The guidance model for sound source localization. The shaded dipole field lines represent the acceleration field of a moving prey. The predator enters the field from three different directions along the paths indicated by dotted lines. When the local acceleration stimuli received by the otolith organs are sufficiently strong, the predator starts a guided approach. Along the approach paths indicated by heavy lines the predator maintains a constant angle between the local accelerations and its body axes. (From Kalmijn 1997.)

to discriminate between sounds from different directions. Very few, if any, experiments have demonstrated that fish are able to actually localize the sources from a distance.

3. Behavioral Studies of Directional Hearing

In the previous sections, various models for directional hearing in fish were described in considerable detail, but without confirmation by behavioral studies the validity of these models will remain uncertain. However, to design such studies is not a trivial task. The initial behavioral experiments in this field were simply aimed at demonstrating directional auditory responses in fish, but did still give conflicting results, probably due to the use of exceedingly complex stimulus fields in small tanks. Hence, the first indications of directional hearing in fish came from field observations of freely ranging sharks orienting toward sound sources, often from large distances (reviewed by Myrberg et al. 1976).

The first definite evidence of directional hearing in a teleost was provided by Schuijf et al. (1972), who trained the Ballan wrasse (*Labrus berggylta*) to discriminate between sounds emitted from either of two spatially separated sound sources. The experiments were carried out in a Norwegian fiord several meters from reflecting surfaces, and were based on conditioning with food as a reward. Within its netting cage the fish was trained to orient toward the active sound projector. Therefore, the fish was only required to detect the change in sound direction, rather than the actual *location* of the sound source. This serious limitation has also hampered most of the later behavioral studies of directional hearing in fish. The most noticeable exception is a study by Popper et al. (1973), who observed unconditioned directional orientations of Hawaiian squirrelfish (Holocentridae) toward a sound projector emitting a playback of squirrelfish alarm calls.

In the mid-1970s, the suggestion by van Bergeijk (1964) that any directional response to acoustic cues in fish must depend on the lateral line was still debated. However, Schuijf and Siemelink (1974) and Schuijf (1975) showed that Atlantic cod lost the ability to discriminate between different sound directions in the horizontal plane after severing the nerve roots innervating one of the labyrinths, although the lateral line system was still functioning. These experiments also indicated that information from both ears might be required for computation of azimuth, as originally proposed by Sand (1974).

In support of the phase model described in Section 2.2, Schuijf and Buwalda (1975) showed that Atlantic cod can discriminate traveling sound waves impinging on the head from those impinging on the tail. Furthermore, phase reversal of the acoustic pressure in the traveling wave, obtained by interference from a perpendicular standing wave generated by an opposing pair of sound projectors, caused 180° reversal of the directional response. Directional discrimination was also possible in the loop of a horizontal, standing wave, provided that appropriate pressure information in the correct phase was added.

Similar experiments were later performed by Schuijf et al. (1977) on the otophysan species ide (*Leuciscus idus*). In otophysan species, which possess Weberian ossicles that efficiently transmit sound pressure-induced pulsations of the unpaired swimbladder equally to both sacculi, it is reasonable to assume that the potential masking effects of the reradiated swimbladder motions on the particle motions in the incident wave is particularly severe. Nevertheless, even the ide displayed directional hearing and discriminated between sounds from sources 180° apart. However, except for this coarse discrimination, the ability of angular resolution was not studied further.

In all the studies by Schuif and collaborators mentioned so far, the fish was moving freely within a netting cage, and trained to approach or orient toward a particular source in a choice situation (Fig. 6.8A). During the training, the fish was rewarded at the food dispenser in line with the active sound projector. As noted, although the fish makes a correct choice during the test by displaying an oriented response toward the source, this experimental design cannot prove that the fish has in fact perceived the location of the source.

An alternative experimental strategy is to restrict the movements of the fish by a narrow confinement, and to monitor the response to a relevant stimulus (e.g., a change in the direction of a pulsed tone) by recording the heart rate. The fish is conditioned to display a reduced heart rate (bradycardia) in response to the stimulus, in anticipation of a mild electric shock applied just after the stimulus
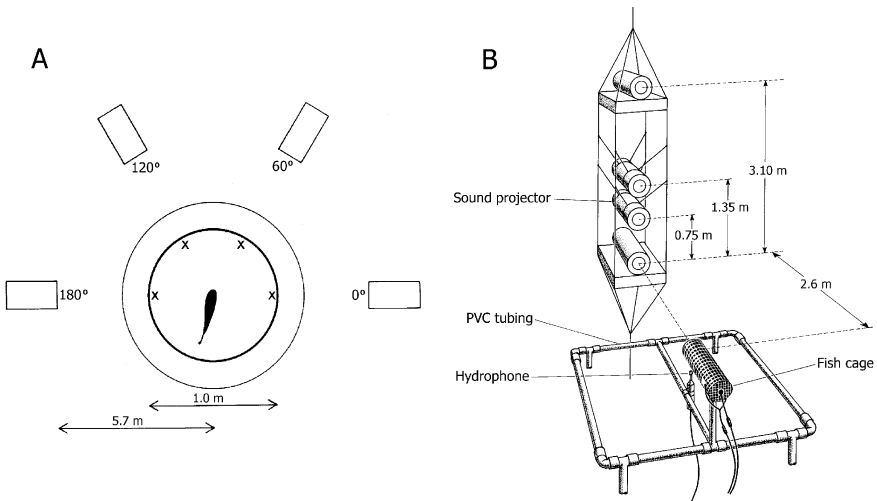

FIGURE 6.8. Examples of experimental designs for behavioral testing of directional discrimination. (**A**) The fish is free to move within a netting cage and is trained to orient toward the food dispenser (*x*) in line with the active sound transducer. (Redrawn from Schuijf 1975.) (**B**) The fish is confined in a small cage and gives a conditioned physiological response (i.e., reduced heart rate) to a change in sound direction. (From Hawkins and Sand 1977.) None of these experimental approaches can unambiguously determine if the fish can perceive the actual location of the sound source.

(Fig. 6.8B). Of course, also this method will only be able to reveal if the fish is able to discriminate between sound directions, whereas the ability to determine the position of the source is not tested.

By employing this technique, Chapman (1973) and Chapman and Johnstone (1974) studied auditory masking in Atlantic cod and haddock (*Melanogrammus aeglefinus*) to test if the fish nervous system is able to process differences in sound direction. The threshold of masked tones where recorded during emission of pure tones and noise from different projectors, and the auditory masking was reduced by about 7 dB when the angle between the sound projectors was 45° or greater (Fig. 6.9A). This result suggests that directional discrimination is well developed in these species. Chapman and Johnstone (1974) also showed that the Atlantic cod could readily be conditioned to a change in the direction of a pulsed tone switched between two equidistant sources. The limit for angular discrimination was close to 20° (Fig. 6.9B), which is in agreement with the angular threshold of about 22° estimated by Schuijf (1975), based on his choice experiments on the same species.

Further, Chapman and Johnstone (1974) reported that the threshold for discrimination between sound directions in Atlantic cod was considerably higher than the threshold for simply detecting the presence of a sound. This finding is in agreement with the notion that only the incident sound will give relevant directional information, in contrast to the amplified vibrations emanating from
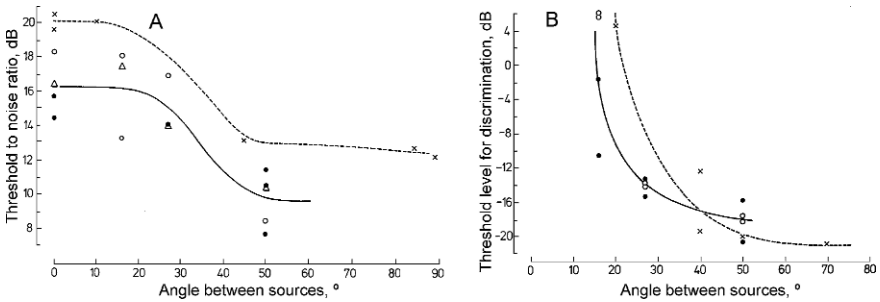

FIGURE 6.9. Angular discrimination by Atlantic cod in azimuth and elevation. A: threshold to noise ratio as a function of angle between two sound projectors transmitting a pure tone and masking noise, respectively. Symbols (o, •, Δ) represent data for 110 Hz from three fish with the projectors in the median vertical plane. Symbols (x) indicate comparable values with the projectors in the horizontal plane (data from Chapman and Johnstone 1974). The decrease in masking as the angular separation between tone and noise increases demonstrates that the nervous system is able to process differences in sound direction. (**B**) Sound pressure thresholds for detection of an angular change in the direction of a 110-Hz tone as a function of the angular change. Symbols (o, •) represent thresholds from two fish for changes in elevation. Symbols (x) indicate values for changes in azimuth (data from Chapman and Johnstone 1974). The steep increase in threshold toward the smaller angular separations indicates the limit of angular discrimination. (From Hawkins and Sand 1976.)

the swimbladder. At 200 Hz, the difference between detection threshold and the sound pressure required for directional discrimination was 23 dB, which corresponds to the reduction in microphonic sensitivity of about 20 dB at this frequency when the swimbladder in Atlantic cod is emptied (Sand and Enger 1973).

The behavioral studies on directional hearing performed during the first half of the 1970s were all designed to test discrimination ability in the horizontal plane. However, electrophysiological data (Sand 1974) indicated that the ability of fish to determine the elevation of a sound source should be at least as good as the resolution of azimuth, in contrast to humans, who are unable to discriminate between pure tones from sources at different elevations in the median vertical plane. Hawkins and Sand (1977) employed the cardiac conditioning technique to test this hypothesis, in experiments on Atlantic cod corresponding to those previously performed by Chapman and Johnstone (1974) in the horizontal plane. There was a significant decrease in auditory masking as the angular separation between tone and noise sources in the median vertical plane was increased (Fig. 6.9A), confirming the ability to perform an auditory discrimination based on directional cues. The power of angular resolution in the vertical plane, studied via directional change of a pulsed tone, was close to 16° (Fig. 6.9B), as compared to 20° previously reported for the horizontal plane. For fish living in a three-dimensional medium, in contrast to humans mainly confined to a surface, the ability to discriminate between source elevations is of course highly relevant.

The study by Hawkins and Sand (1977) prompted Buwalda et al. (1983) to test the validity of the phase model in Atlantic cod in three-dimensional space. They used the cardiac conditioning technique, combined with multiple, opposing pairs of sound projectors to generate both propagating waves and synthesized standing waves (Buwalda 1981). Switching a pulsed, pure tone from a reference source to an opposing source was detected under all conditions, whereas switching to a completely synthesized standing wave that simulated the phase relations of the reference source was not detected. However, switching to a standing wave simulating the phase relations of the opposite source was detected. It was concluded that the detection of sound propagation direction is based on the characteristic phase relationship between particle motion and sound pressure. Cues resulting from sound propagation itself are irrelevant, and apparently not perceived. The study demonstrated that Atlantic cod can resolve the 180° propagation ambiguity for all stimulus directions, which provides a basis for ambiguity-free directional detection in three-dimensional space. The authors acknowledged that the results did not provide irrefutable proof that fish are capable of determining the actual sound source position, and that there is a theoretical possibility that the observed phase discrimination was not related to directional detection and perception. However, the fact that the phase cue was so readily discriminated was accepted as evidence of its natural significance.

The study by Buwalda et al. (1983) also indicated a just noticeable phase difference between velocity and pressure of 20°–30°, which is much less the 180° associated with opposite source positions. This variable is a function of the

distance from a source, and ranges from 0° to –90° (or from 180° to 90°) for far and close sources, respectively. Consequently, the investigators suggested that fish might utilize phase discrimination also for determining the distance to a sound source. This hypothesis was strengthened in a subsequent study by Schuijf and Hawkins (1983), who demonstrated that Atlantic cod can discriminate between pure tones emitted alternately from two aligned sound projectors at different distances from the fish. This kind of distance discrimination is lacking in terrestrial vertebrates, and it was suggested that the Atlantic cod possesses a real acoustical sense of space.

Although the behavioral studies referred to above have shown that fish can discriminate between different sound directions, and between sound sources at different distances at the same azimuth and elevation, it is still not settled if they are able to perceive the actual location of sound sources. Further, all these studies have employed monopole sound sources, which generate radial particle motions in both the near- and farfield, and the prevailing models for directional hearing in fish assume that the axis of particle motion points to the source. However, apart from the pulsating swimbladder in vocalizing species, most sources of biological significance are best approximated as dipoles or more complex sources. The reactions to such sources commonly occur within the nearfield, where the axis of particle motion is not necessarily radial to the source. Thus, it is doubtful if resolving the axis of particle motion enables fish to perceive the actual location for most biologically significant sound sources in the nearfield. Nearly 70 years ago, von Frisch and Dijkgraaf (1935) performed the very first scientific study that specifically addressed the problem of directional hearing in fish. The title of their paper is "Können Fische die Schallrichtung wahrnehmen?" It is amazing that this question (Can fish sense the sound direction?) is as relevant today as it was in 1935. It certainly is difficult for the terrestrial mammal human to envisage how fish perceive their environment.

4. Directional Fast-Start Escape Responses

Fish display different types of fast-start escape responses to close range predatory strikes, defined by the pattern of the initial body bending (Domenici and Blake 1993; Hale 2002). The C-start response is the most common, and the best studied regarding sensory motor control (see reviews by Faber et al. 1989, 1991; Korn and Faber 1996; Zottoli and Faber 2000; Eaton et al. 2001). C-starts are typically triggered by high-intensity acousticolateral, somatic, and visual stimuli activating either of the paired Mauthner cells (M-cells) in the brainstem. Each M-cell receives massive input from the eighth nerve from the ear on the same side. The Mauthner axon crosses the midline and projects into the spinal cord, where it connects to motoneurons that innervate trunk muscle on the side opposite the M-cell soma. A typical C-start (Fig. 6.10) is triggered by one of the M-cells firing a single action potential, which elicits a virtually instant contraction of the muscles on the opposite side along the entire length of the fish.
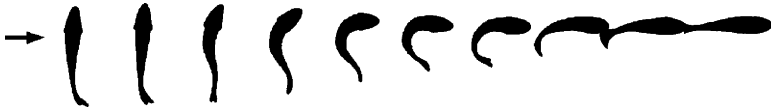
FIGURE 6.10. Movements during a C-start type of fast-start behavior. A startle stimulus (arrow) at the left side of a goldfish at rest triggers the startle response. The fish forms a C-shaped bend of its body before the first propulsive tail stroke, and accelerates away from the stimulus. Successive silhouettes viewed from above are displayed at 5-ms intervals and shifted a fixed distance to the right for clarity. (From Eaton et al. 2001.)

The M-cells belong to the reticulospinal system, which is a distributed network extending from the caudal midbrain to the spinal cord, and a C-start is probably initiated by parallel activity of the Mauthner neuron and commissural hind brain neurons (Kimmel et al. 1982; Metcalfe et al. 1986; Lee et al. 1993; Foreman and Eaton 1993). The propulsive phase of the C-response is probably controlled by more caudal medullar neurons with ipsilateral spinal projections (Forman and Eaton 1993; Eaton et al. 2001). An extensive and hierarchic brainstem escape network has recently been confirmed by using fluorescent calcium indicators to monitor the activity of reticulospinal neurons in the transparent larvae of zebrafish (Fetcho and O'Malley 1997; Liu and Fetcho 1999; Ritter et al. 2001; Gathan et al. 2002).

A striking feature of the C-starts in fish is the oriented response away from the aversive stimulus source. Directional responses to stimuli activating the touch, lateral line, and visual systems are easily explained by the topographic organization of the representation of cutaneous mechanoreceptors and the visual field in the central nervous system. The idea that the Mauthner system is directionally sensitive also to sound was originally suggested by Moulton and Dixon (1967), but remained controversial until directional C-starts away from controlled acoustic stimuli were convincingly demonstrated in Atlantic herring (*Clupea harrengus*) by Blaxter et al. (1981) and in goldfish by Eaton et al. (1981). Directional escape responses to acoustic stimuli have later been described in several other species (see reviews by Eaton 1995; Canfield and Rose 1996; Hale et al. 2002).

How is the fish able to utilize acoustic information to launch a directional escape away from an attacking predator? Eaton and Emberley (1991) addressed this problem by analyzing the relationship between the direction of the acoustic stimulus and the angular component of the initial escape movement. They suggested that the fish measures the angle to the sound source, which then determines the magnitude, or time span, of the initial, rotational phase of the C-response. At that time the phase model for directional hearing was well established, and Eaton (1995) and Guzik et al. (1999) adopted and developed this model to explain the directional escape responses in fish.

As noted in Section 2.2, the phase model is insufficient for the localization of dipoles and higher order sources within the acoustic nearfield, due to the directional ambiguity of the particle motions. The acoustics of a striking predator

may be best approximated by a dipole, and a potential prey will certainly respond within the nearfield of the attacker. At first glance, these conditions may seem incompatible with the phase model for directional discrimination. Further, the requirement for a separate pressure channel may not be fulfilled at threshold levels for the predominantly low-frequency signals generated by a striking predator, because the auditory gain provided by a swimbladder declines toward lower frequencies. However, in spite of these shortcomings of the phase model, it may still be applicable for the escape responses. The M-cell system is far from a low-level signal detector, and is activated by large particle motions and pressure changes generated by an accelerating predator at close range. Although the swimbladder is not involved in detection of infrasound at auditory threshold levels (Sand and Karlsen 1986), this input channel may still provide the required pressure information at the high pressure levels associated with fast-start escape responses. Further, Eaton et al. (2002) have pointed out that the primary axis of motion points directly at the prey during a predator attack, and the direction of particle acceleration detected by the prey is therefore most likely approximately in line with the approach path of the predator. Observed escape trajectories commonly display a wide scatter relative to the stimulus direction (Domenici and Blake 1993; Fig. 6.11A, B), and the model is only required to perform a coarse estimation of direction. In this game, speed is much more essential than accurate directional discrimination. In fact, a wide scatter of potential escape trajectories in the general direction away from the attacker may reflect an adaptive advantage, as it makes it difficult for the predator to predict the flight path and thus reduces the probability of a successful strike. This may be compared to the zigzag flight path of a rabbit chased by a fox.

The current neural model for the directional discrimination by the Mauthner system in hearing specialists suggests how a transient acoustic stimulus originating on either the left or the right side of a fish results in an initial orientation of an escape response away from the side of the stimulus (Eaton et al. 1995; Guzik et al. 1999). The model predicts that the M-cell system receives afferents that convey compression and rarefaction of the pressure component, and acceleration afferents conveying both left-to-right and right-to-left information. Intracellular recordings from M-cells and other relevant brainstem neurons in goldfish have shown that these neurons receive both pressure and acceleration inputs, as predicted by the model (Casagrand et al. 1999). An important feature of the current model is that both initial compression and rarefaction may contribute to the activation of the M-cell. Thus, an attack from the right will produce an initial right to left acceleration combined with a pressure increase, while a suction type of predator at this position will cause left to right acceleration and a rarefaction. According to the model, both these combinations of initial sound pressure and acceleration will elicit the appropriate escape to the left by inhibition of the left and activation of the right M-cell.

Although the current neural model for the C-start escape responses seems reasonable, the postulated efficiency of initial rarefaction to initiate the response lacks behavioral support. Most of the behavioral studies performed to date have
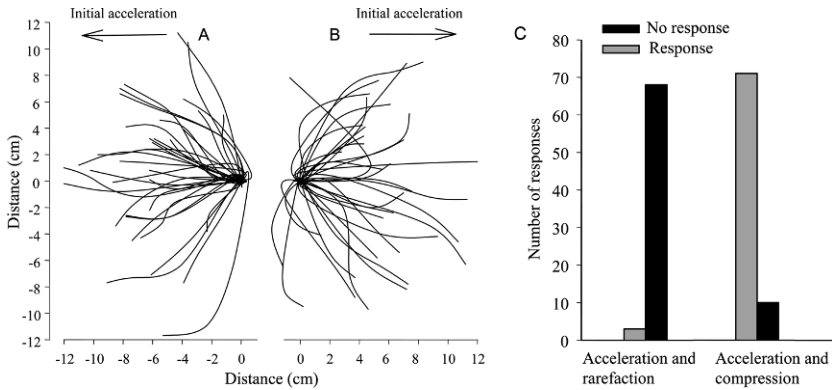
FIGURE 6.11. Startle trajectories in the horizontal plane displayed by juvenile roach in response to the initial half-cycle of an acceleration of 6.7 Hz. The fish were accelerated within a closed chamber at a stimulus level 15 dB above response threshold. The trajectories show movements of the head of the responding fish during 160 ms from the video frame before stimulus onset. (**A**) Trials with the initial acceleration to the left (push mode). (**B**) Tests with the initial acceleration to the right (pull mode). Startle responses in both stimulus situations were on average in the same direction as the initial acceleration. (**C**) Synergistic effects of acceleration and compression on triggering of the startle responses. The histograms present the number of responsive and nonresponsive fish in the leading (rarefaction) and trailing (compression) half of the test chamber, respectively. The fish mainly responded to the combination of linear acceleration and pressure increase. (From Karlsen et al. 2004.)

been hampered by insufficient control of the stimulus parameters. Generally, the frequency of the stimulus has been too high (100–2000 Hz) to reveal the relative effects of sound compression and rarefaction. Such frequencies may also be far above those associated with a real predator attack (Kalmijn 1989; Bleckmann et al. 1991). The otolith organs in fish are highly sensitive to the acceleration component of infrasound down to at least 0.1 Hz (Sand and Karlsen, 1986; Karlsen, 1992a,b), and typical behavioral threshold values are in the range of $10^{-5}\,\text{m/s}^2$. At higher intensities around $10^{-2}\,\text{m/s}^2$, infrasound may initiate strong avoidance responses in fish (see review by Sand et al., 2001).

For a prey fish, infrasonic acceleration may thus be a more realistic simulation of an approaching predator than the higher frequencies employed in previous studies, and Karlsen et al. (2004) have recently studied fast-start responses in the otophysan species roach (*Rutilus rutilus*) to infrasonic initial accelerations. The fish were accelerated in a controlled manner within a closed chamber suspended in a swing system (Karlsen 1992b). Typical C-start escape responses were indeed induced by accelerations within the infrasonic range, with a threshold of $0.023\,\text{m/s}^2$ for an initial acceleration at 6.7 Hz. The response trajectories displayed a wide scatter, but were on average in the same direction as the initial acceleration (Fig. 6.11A, B). Unexpectedly, startle responses occurred mainly in the trailing half of the test chamber, in which the fish were subjected to

linear acceleration and compression (Fig. 6.11C). This combination characterizes the stimuli produced by an approaching predator. Very few responses were observed in the leading half of the test chamber, where the fish were subjected to acceleration and rarefaction. This type of stimulus is expected from a retracting predator. The lack of response to initial acceleration and rarefaction may also be an adaptive behavior, since an unnoticed pray fish may be easily spotted by a predator if an unnecessary escape response is initiated. It was concluded that particle acceleration is essential for the directionality of the startle response to infrasound, and that synergistic effects of acceleration and compression trigger the response. Since the current neuronal model for fast-start escape responses predicts that compression and rarefaction are equally efficient in triggering the response in combination with acceleration, it may need revision.

   The sense of hearing in fish is an extremely sensitive sense that detects the faintest signals, including communication signals that are intended to be heard. The Mauthner system, on the other hand, may have evolved to do the opposite, namely to detect high intensity predatory signals that are intended to be concealed (Eaton and Popper 1995). A typical predator strike is characterized by a rapid acceleration of the head towards the prey, which generates low frequency compression and particle acceleration in the same direction as the strike, and Eaton and Popper (1995) have even suggested that aquatic predators might employ a "stealth strategy" to avoid acoustic detection. As predators accelerate towards the prey, various species open their oral cavities with a velocity equivalent to a 10–20 Hz signal. Rather than sucking the prey towards the mouth, this initial moth opening may reduce the acoustic and hydrodynamic noise associated with the acceleration of the predator. The final suction that pulls the prey into the oral cavity is not initiated before virtual contact with the prey.

5. The Lateral Line and Source Localization

The fish lateral line responds to midwater hydrodynamic events and to capillary surface waves (for reviews see Sand 1984; Bleckmann 1994; Coombs and Montgomery 1998). Since the physical properties of water surface waves and midwater hydrodynamic events are radically different, lateral line perception in midwater (and benthic) fish is treated separately from lateral line perception in surface feeding fish.

5.1 Surface Wave Perception

As first shown by Schwartz (1965, 1971), several teleost species of the families Cyprinodontidae, Hemirhamphidae, Gasteropelecidae and Pantodontidae can detect capillary surface waves with their cephalic lateral line (e.g., Fig. 6.12A). In their natural habitats such waves are usually caused by terrestrial (prey) insects fallen into the water. Capillary surface waves generated by a struggling insect often last for several seconds, are irregular in time course, have displacement amplitudes $< 100\,\mu m$, and contain frequencies in the range 10 to about 100 Hz (Lang 1980; Bleckmann 1985).
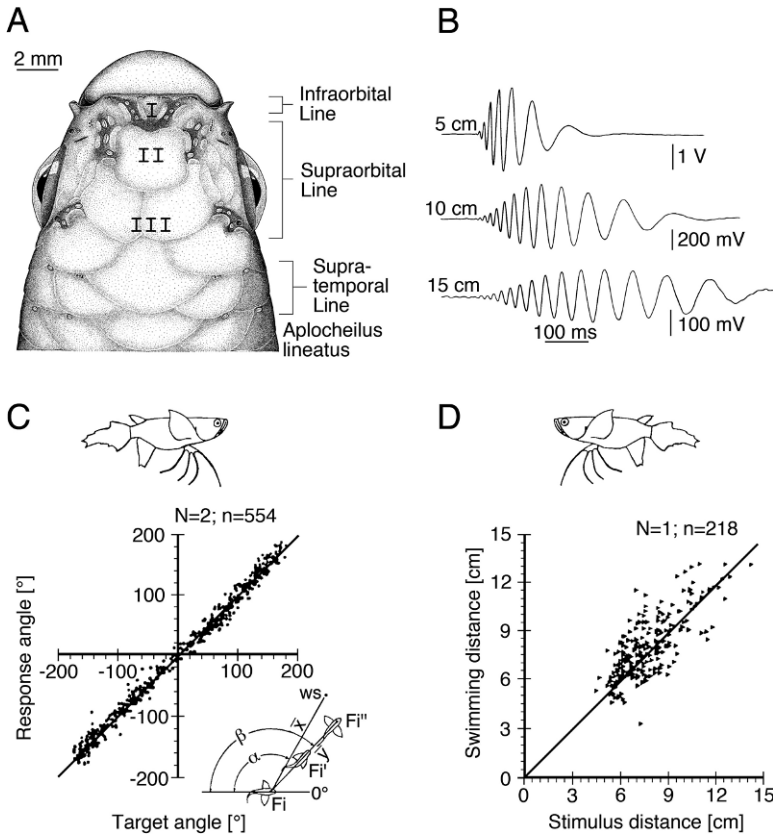
FIGURE 6.12. (**A**) Dorsal view of the head of the surface feeding fish *Aplocheilus lineatus*. The cephalic lateral line of *Aplocheilus* consists of three groups (labeled I, II, and III from rostral to caudal), each of which contains three single neuromasts. (The drawing was kindly provided by G. Tittel.) (**B**) A surface wave train (called a click) produced by dipping the tip of a small rod once into the water. The click stimulus was recorded at 5, 10, and 15 cm source distance. Note the differences in amplitude calibration. (Redrawn from Bleckmann and Schwartz 1982.) (**C, D**) Orientation behavior of mature, visually deprived *Pantodon buchholzi*. The accuracy of target angle determination (**C**) and distance determination (**D**) is shown. Each dot represents one response. Surface wave stimuli (clicks) were produced by dipping the tip of a small rod once into the water. Inset in **C**: Fi, animal at stimulus onset; Fi', animal during the phase of swimming; Fi", animal after stopping (identified by the spreading of pectoral fins); WS, wave source, X, source distance, Y:, swimming distance; α target angle, β, turning angle. (Redrawn from Bleckmann et al. 1989.)

5.1.1 Propagation of Surface Waves

Water surface waves radiate with dispersion, i.e., their propagation velocity is frequency dependent and has a minimum of 23 cm/s at a frequency f of 13 Hz (corresponding to a wave length λ of about 1.7 cm) (Lighthill 1980).

For frequencies higher than 13 Hz, this dispersion causes a frequency-downward modulation of the initial 7–9 wave cycles of any broadband wave stimulus (Bleckmann and Schwartz 1982). After traveling a certain distance, an initial dispersive wave group consists of a set of waves with different wavelengths and frequencies. Locally, λ can be defined by the crest-to-crest distance, but due to dispersion the distance between successive crests differs slightly (Fig. 6.12B). These differences reflect the distance-dependent frequency modulation of the wave group and the speed by which the wave packet spreads in space. The distance to a surface wave source can be determined unequivocally if the local frequency $\omega(=2\pi f)$ and the frequency modulation around ω are known (Käse and Bleckmann 1987). Besides being dispersed, water surface waves are attenuated during propagation. Due to geometrical spreading, this attenuation is strongest in the vicinity of a wave source. In addition, attenuation increases with frequency (decreasing λ), i.e., the water surface behaves like a low pass filter (see Bleckmann et al. [1989] for a thorough treatment of surface wave physics).

5.1.2 The Cephalic Lateral Line of Surface Feeding Fish

Surface feeding fish detect capillary surface waves with their cephalic lateral line, which consists of superficial neuromasts (e.g., *Aplocheilus lineatus*, Fig. 6.12A), canal neuromasts (*Fundulus notatus*), or large neuromasts contained in cavities (*Pantodon buchholzi*) (Schwartz 1970). The sensory epithelium of lateral line neuromasts consists of hair cells that are separated and surrounded by numerous supporting cells. The apical end of lateral line hair cells contains 30 to 150 stereovilli and a single true kinocilium that project into a cupula extending several hundred micrometers into the surrounding water. Displacement of the stereovilli toward the kinocilium causes a depolarization, while displacement in the opposite direction hyperpolarizes the hair cell. Consequently, the responses of a single hair cell vary with the stimulus angle in a cosine fashion, as also described in Section 2.1. Within a neuromast, hair cells are usually oriented with their kinocilia pointing in the direction of the long (most sensitive) axis of the neuromast. In both superficial and canal neuromasts, the hair cells are oriented in two opposing directions, i.e. any displacement of the cupula will cause responses of opposite polarities from the two sets of cells, which work 180° out of phase. Consequently, lateral line neuromasts, just like individual hair cells, are directionally sensitive. A single lateral line afferent may innervate more than one hair cell, but is coupled only to hair cells aligned in the same direction. An afferent fiber therefore responds best (with a decrease or increase in spontaneous discharge rate) if the cupula moves in one of the two possible directions with respect to the most sensitive axis of the neuromast. Like auditory fibers, primary lateral line afferents respond to a sinusoidal wave stimulus with phase coupling. Stimulus intensity is encoded both by the degree of phase coupling and by the firing rate. Single lateral line neuromasts therefore encode the intensity (via phase coupling and spike rate) and frequency (via phase coupling) of a sinusoidal wave stimulus. Since different cephalic neuromasts of surface feeding fish are

aligned in different directions (Schwartz 1970 and Fig. 6.12A), these fish are nearly equally sensitive to all wave directions.

5.1.3 Wave Source Localization

Even blinded surface feeding fish respond to a surface wave stimulus produced by dipping a rod once into the water with an orienting movement. At a distance up to about 15 cm, surface feeding fish can determine both the target angle and the distance to a wave source (Fig. 6.12C, D and Schwartz, 1971). They do so by exploiting the physical properties of the propagating wave stimulus.

5.1.3.1 Determination of Target Angle

According to the strong attenuation and low propagation velocity (23–50 cm/s in the relevant frequency range) of water surface waves, the direction to a surface wave source can be determined by:

- Measuring the intensity gradient of the stimulus
- Comparing the neuronal activity of primary lateral line afferents innervating cephalic neuromasts aligned in different directions
- Measuring arrival time differences between neuromasts

Localization via Intensity Gradients. Amplitude cues are well suited for target angle determination because amplitude gradients are steepest, and the distance to a wave source shortest, in the radial direction, i.e., perpendicular to the lines of equal stimulus intensity. Physiological experiments have shown that the steepness of amplitude curves obtained from the cephalic neuromasts of surface feeding fish increases with increasing stimulus frequency, i.e., high-frequency surface waves should be especially convenient for determining amplitude gradients (Mohr and Bleckmann 1998). Contrary to this consideration, the ability of surface feeding fish to determine the target angle does neither improve with increasing wave frequency nor with decreasing wave source distance (Bleckmann et al. 1989). It is therefore unlikely that amplitude cues are essential for target angle determination.

Localization via Angular Differences in Afferent Responses and Stimulus Arrival time. Up to about ±130° (0° is directly in front of the fish), target angle determination in an *Aplocheilus* with only one group of cephalic lateral line neuromasts left intact is not different from that of intact fish. In contrast, an *Aplocheilus* with only the supratemporal neuromasts and the neuromasts innervated by the dorsal branch of the trunk lateral line left intact, show a fairly accurate target angle determination only in the range 100°–160°. Regardless of target angle, unilaterally ablated fish always turn to the intact side (Schwartz 1965; Müller and Schwartz 1982).

An *Aplocheilus* with only one cephalic neuromast left intact remains sensitive to all wave directions, but it no longer determines the target angle (Fig. 6.13A). Instead, the degree of turning now correlates with the anterior–posterior position
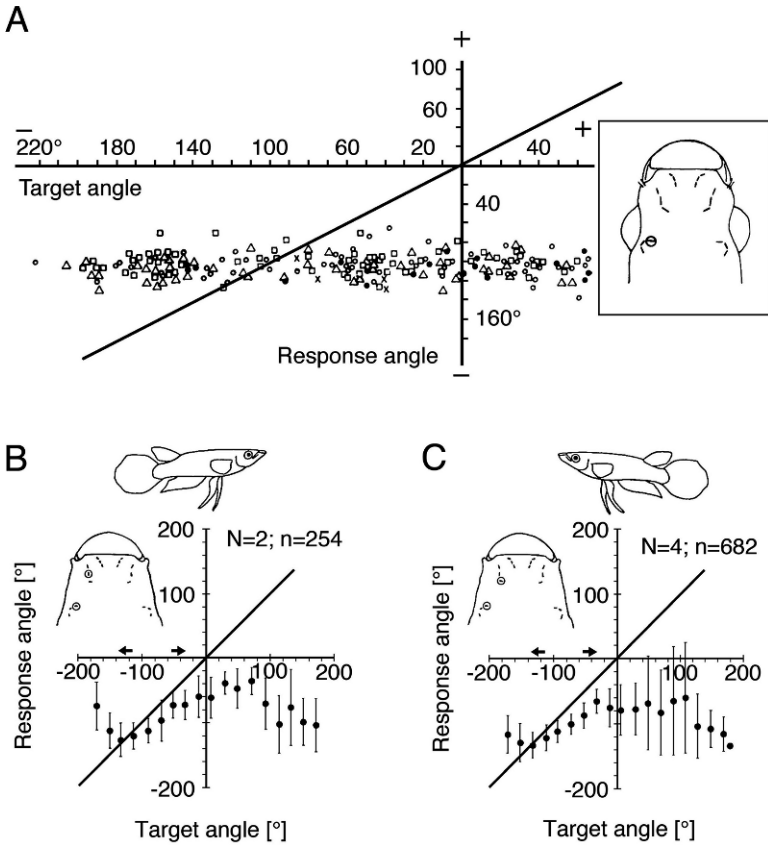
FIGURE 6.13. (**A**) Directional response of an *A. lineatus* with all but the encircled cephalic lateral line neuromasts destroyed (see inset; straight lines indicate the spatial arrangement of the neuromasts and neuromast orientations). Different symbols correspond to different test series performed with the same animal. 0° is in front, 180° is behind the fish. Positive angles are right, negative angles are left. (Redrawn from Müller and Schwartz 1982.) (**B, C**) Directional responses of an *A. lineatus* with all cephalic neuromasts destroyed except the two neuromasts encircled. Mean values and standard deviations are shown. The alignment of the long (most sensitive) axis of the two neuromasts differed by 83° in B and 19° in **C**. The distance of the two neuromasts from a fixed point at the fish's snout was 4.1 mm (**B**) and 2.8 mm (**C**). Arrowheads indicate the upper and lower limits of the dynamic range. (Redrawn from Bleckmann et al. 1989.)

of the particular neuromast in that a more caudal neuromast induces a larger response angle than a more rostral neuromast (Bleckmann et al. 1989). Thus, each neuromast appears to have a place value that determines the orienting response of the fish.

Within a certain dynamic range, an *Aplocheilus* with only two neuromasts left intact retains its ability to determine the target angle (Tittel et al. 1984).

Tittel (1991) performed carefully designed ablation experiments to test whether sensitivity differences due to neuromast directionality and/or arrival time differences between neuromast are used for target angle determination. The ablation combinations were chosen to give slight differences in neuromast position, but large differences in neuromast alignment (i.e., large differences in neuromast output), and vice versa (insets in Fig. 6.13B, C). The subsequent behavioral tests indicated that arrival time and/or phase differences between neuromasts – but not neuromast output differences - are the most important cues used for target angle determination. A second line of evidence also suggests that neuromast output differences based on neuromast directionality are less important: If single-frequency waves are presented, a 30-Hz stimulus leads to more accurate responses than a 80-Hz stimulus (Tittel 1985), despite the fact that input–output curves are steeper at higher wave frequencies (Mohr and Bleckmann 1998). It should be stressed that the correlation between arrival time differences at different neuromasts and the target angle is unequivocal only if the frequency-dependent wave propagation speed is taken into account (see preceding text). Obviously, surface-feeding fish do correct for this relationship.

5.1.3.2 Determination of Wave Source Distance

Close to the source, the distance to the center of a concentric surface wave stimulus can be determined by measuring the curvature of the stimulus. In addition, if the attenuation and distance-dependent frequency modulation of surface waves are known, the distance to a surface wave source can be determined by measuring:

- The relative amplitude decrease per unit of distance
- The mean frequency and the frequency modulation of the first 7–9 wave cycles
- The amplitude spectrum of a wave train

It should be stressed that in waves lacking higher frequencies the amplitude spectrum can give some information about the source distance only if compared with a commonly experienced standard.

Integration Time. The basic frequency of a wave train, its local frequency modulation, and its amplitude spectrum can be obtained only if the stimulus is integrated over at least a few wave cycles. The first stimulus-evoked muscle potentials can be recorded from a freely swimming *Aplocheilus* after the first 8.5 cycles of a wave train passing the head of the fish, independently of stimulus amplitude (Bleckmann and Schwartz 1981; Bleckmann 1982). Thus, the information sufficient for *Aplocheilus* to localize a wave source must be contained in these 8.5 wave cycles.

Responses to Artificial Wave Stimuli. Due to the low pass filter properties of the water surface (see Section 5.1.1), a rough estimation of source distance is possible by evaluating the amplitude and frequency content of a wave stimulus. For

instance, the determination of source distance could be based on the assumption that high-amplitude, broad-bandwidth stimuli on average have traveled a shorter distance than low-amplitude, low-frequency and narrow-bandwidth stimuli. Hoin-Radkovski et al. (1984) tested this assumption by stimulating the surface feeding fish *P. buchholzi* with clicks of different upper frequency limits. They found that the relative localization errors (for definition, see Hoin-Radkovski et al. 1984) of *Pantodon* are independent of stimulus frequency content and source distance. Therefore, in this fish the determination of source distance cannot be based on the evaluation of the wave spectrum alone.

Responses to Single-Frequency Wave Trains. Decoding of local frequency and frequency modulation of a wave stimulus is a possible strategy to determine the distance a surface wave stimulus has traveled. To test this prediction, Bleckmann (1980) and Hoin-Radkovski et al. (1984) presented single-frequency wave stimuli to *Aplocheilus* and *Pantodon.* As expected, this led to an impaired distance determination in both species, with a tendency to underestimate the source distance if it exceeded 6–8 cm. However, there was still a weak but significant correlation between source distance and swimming distance. For *A. lineatus* this was valid only for wave frequencies below 50 Hz (Bleckmann 1980). In general, the relative localization error at a given source distance grew with frequency, while it increased with source distance at a given frequency (Bleckmann 1988). Assuming that the curvature of the wave front is also used as a cue for wave source distance and that it is determined through arrival time differences, this is exactly what is to be expected (Hoin-Radkovski et al. 1984). At a given source distance, surface-feeding fish swam progressively shorter in response to single-frequency wave stimuli of higher frequencies. This indicates that the amplitude spectrum is also evaluated, because, if no other cues are available, a high-frequency stimulus can be "expected" to have traveled a shorter distance than a low frequency stimulus. Considering the low pass filter properties of the water surface, this reflects a likely localization strategy. Application of frequency-upward modulated stimuli that contained high-frequency wave components also caused an underestimation of source distance, which supports the notion that surface-feeding fish do follow the strategy outlined in the preceding text.

Responses to Altered Wave Trains. When confronted with a computer controlled wave stimulus that was generated at a distance of 7 cm, but simulated the frequency modulation of a click that had traveled a distance of 15 cm, the fish swam on average 4–6 cm beyond the wave source (Bleckmann and Schwartz 1982; Hoin-Radkovski et al. 1984). This result was the final proof that local frequency modulation of a wave train is one of the cues used by surface feeding fish to determine the source distance. The use of frequency modulation for distance determination was further supported in experiments with *Aplocheilus*, in which all but one cephalic neuromast were destroyed. Although such a fish had no way to determine the curvature of the wave front or the amplitude decrease per unit of distance, it still showed an increase of

swimming distance with wave source distance if clicks were presented (Müller and Schwartz 1982). Distance determination in ablated fish was, however, somewhat impaired. This indicates again that surface feeding fish use also other parameters than frequency modulation for distance determination.

Sound Waves. Any object that causes water motions also generates sound pressure waves. Since sound pressure propagates with a speed of about 1500 m/s in water and the propagation velocity of surface waves is in the cm per second range (see Section 5.1.1), fish could calculate the wave source distance by comparing the arrival times of pressure (acoustic) and surface waves. However, up to now the use of pressure waves for localization of surface wave sources has not been demonstrated in surface-feeding fish (for a detailed discussion of distance determination in surface feeding fish see Bleckmann 1988).

5.2 Perception of Subsurface Water Motions

Midwater and bottom dwelling fish also use the lateral line to detect and localize sound sources, provided the sound of these sources causes relative movements between the fish and the water surrounding the fish. At relevant stimulus frequencies, this is only the case if the fish is within the innermost part of the acoustic nearfield. At larger distances, the whole body motions of the fish deprive the lateral line of its stimulus (Sand 1981). If the light conditions are adequate, most fish primarily use visual cues for detection of a sound source (e.g., a prey or a predator). During daytime, piscivorous fish may initiate their pursuits from distances of several body lengths. However, in darkness a strike usually only occurs if the prey distance is less than 5–10 cm (Enger et al. 1989). In complete darkness, a fish in hunting mood typically glides slowly through the water, driven only by occasional tail flips. In the dark, an intact lateral line is essential for the initiation of a strike from some distance. If the lateral line is blocked with cobalt ions (Karlsen and Sand 1987), bluegills (*Lepomis macrochirus*) never make a successful attack at a preyfish, nor do they bite a simulated prey object, unless the simulated prey accidentally is touched (Enger et al. 1989).

5.2.1 Prey Detection in the Mottled Sculpin

The mottled sculpin (*Cottus bairdi*) is a benthic fish that exhibits a natural and unconditioned orienting response to both live prey and vibrating spheres (Coombs and Janssen 1990). In the absence of nonmechanosensory cues (such as vision), the initial orientation and approach behavior of mottled sculpins relies heavily, if not exclusively, on lateral line input (Coombs 1994). The peripheral lateral line of the mottled sculpin consists of superficial and canal neuromasts (Janssen et al. 1987). In blinded sculpin, the approach behavior to a dipole source depends largely on the initial orientation of the fish relative to the source (and the axis of source vibration). Indirect approaches in which the fish either keeps the source continuously to one side of the body (Fig. 6.14A), or alternates
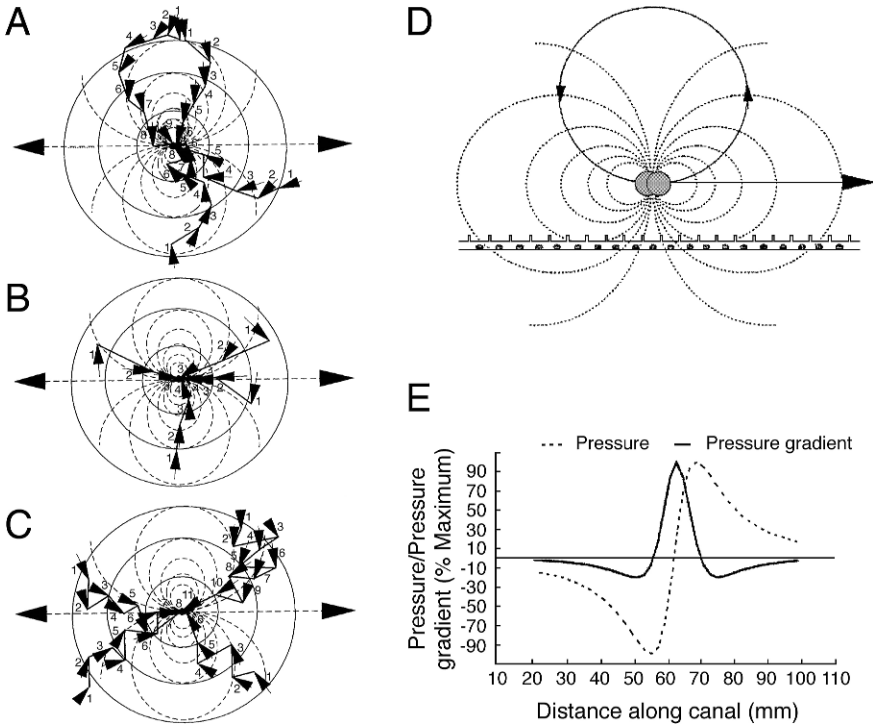
FIGURE 6.14. (**A–C**) Step-by-step approaches of a mottled sculpin to a dipole source. (**A**) Smoothly arching approaches in which the fish keeps its head to one side of the source. (**B**) Direct approach paths in which the vibrating sphere is kept mainly in front of the fish's head. (**C**) Zig-zag approaches in which the fish alternates between being to the left and to the right of the source. Dashed lines indicate flow lines about the source (center of graph), whereas thin-lined circles represent fixed radial distances of 3, 6, and 9 cm from the source center. (Redrawn from Coombs et al. 2000.) (**D**) Schematic representation of iso-pressure contours (dashed lines) and flow lines (solid lines with arrows) around a dipole source. Iso-pressure contours are depicted for a single plane that bisects the source along its axis of oscillation indicated by the large arrowhead to the right. A lateral line canal is modeled as a single tube with an array of pressure sampling points (canal pores) at 2-mm intervals (not to scale). In the example shown, the canal is confined to a single horizontal plane through the source center and its long axis is parallel to the axis of source oscillation. (**E**) Corresponding plots of pressure (dashed line) and pressure gradient (solid line) distribution across the modeled trunk lateral line canal. Note that the maximal pressure gradient is centered at the source, arbitrarily located at X distance = 61 mm along the modeled canal. (Redrawn from Coombs and Conley 1995.)

between keeping the source to the left and right side of the body, tend to occur when the fish is pointing toward the source at signal onset (Fig. 6.14C). When the source is to the side of the fish at the time of stimulus onset, mottled sculpin approach the source in a more direct path (Fig. 6.14B) (Coombs et al. 2000). Blinded sculpin not only determine the direction, but also the distance to a dipole

source as long as the lateral line is intact on the side of the fish facing the dipole (Janssen and Corcoran 1993). The ability to estimate source distance is, however, restricted to short ranges (about one fish body length), as are most, but not all (e.g., hydrodynamic trail following, see later), lateral line sensing abilities.

As described by Webb, Montgomery, and Mogdans (Chapter 5), the fish lateral line encodes water movements and pressure gradients in spatially nonuniform flow fields. Figure 6.14D illustrates the isopressure contours and flow lines about a dipole source, and Figure 6.14E depicts the calculated pressure and pressure gradients across a hypothetical trunk lateral line canal. The pressure gradient pattern along this canal (solid line in Fig. 6.14E) was derived by computing the pressure difference across consecutive pairs of pores. The calculated pressure gradient distribution reveals a complex but predictable pattern consisting of a large, central, and positive peak surrounded by two smaller negative peaks on either side. At certain points the pressure gradient function passes through zero, i.e., at these points the sign of the pressure gradient passes from negative to positive, or vice versa. Theoretical calculations and pressure measurements with a miniature hydrophone show that the points of phase reversals are invariant as a function of source amplitude but change as a function of source distance. As source distance increases, the spatial separation between side peaks and phase reversal points increases. At the same time the peak amplitude decreases at a fall-off-rate of $1/distance^3$, i.e., at a rate predicted for dipole sources (Kalmijn 1988).

Recordings from primary lateral line afferents or of neuromast receptor potentials reveal that information about the position of a vibrating sphere relative to the fish is linearly coded in excitation patterns that reflects the spatial characteristics of the pressure gradients distributed along the lateral line canal (Sand 1981; Coombs et al. 1996; Curcic-Blake and van Netten 2006). This means that the excitation patterns of lateral line canal neuromasts can be predicted if one knows the course of lateral line canals on the animal's body, the interpore spacing, and the pressure distribution around the source (Coombs et al. 1996). An algorithm developed by Curcic-Blake and van Netten (2006) and Goulet et al. (2008) even shows that lateral line excitation patterns not only provide the information about source location but also about the direction of sphere vibration.

Calculations of lateral line excitation patterns for a linear array of canal neuromasts at different distances from the source indicate that the information about source azimuth is contained in the location of the maximum pressure-difference amplitude, whereas information about source distance is contained in the spread of excitation. This distance cue is robust and unambiguous; that is, if source vibration amplitude or size is increased at a given distance, the level, but not the spread, of lateral line excitation increases. Thus, although peak excitation levels may be identical for a distant, high-amplitude (or large) source and a near-by, low-amplitude (or small) source, there is sufficient information in the spread of excitation to distinguish between the two. Therefore, the spatial representation of source distance along a two-dimensional array of sensors may provide the mottled sculpin with a mechanism of depth perception like that

already suggested for the lateral line of the blind cavefish *Anoptichthys jordani* (Hassan 1989). Unlike visual images, which get smaller as the source moves further away, hydrodynamic images get larger, as do electrosensory images (Emde et al. 1998).

The approach behavior (Fig. 6.14A–C), and the hypothesis that spatial excitation patterns along the lateral line system of mottled sculpin (Fig. 6.14D) play a major role in encoding both source direction and source distance, suggest the following strategies used by the mottled sculpin in finding a dipole source:

- Moving in a direction that increases the pressure difference along the head while keeping it consistently low across the head
- Narrowing the fish-to-source gap with each successive movement
- Keeping the source lateralized
- Avoiding approach positions that are perpendicular to the flow line or that place the fish in the pressure zero area of a dipole field

5.2.2 Source Localization by Wake Tracking

Whenever a fish moves, it involuntarily becomes a sound source. The low-frequency nearfields caused by a moving fish are, to a first approximation, dipolar. However, besides a dipolar flow field a swimming fish involuntarily generates a wake that may persist for up to several minutes (Fig. 6.15). Fishborne wakes consist of vortices and contain frequencies from below 10 Hz up to about 100 Hz and water velocities that reach several mm/s (Hanke et al. 2004). The sensitivity of the fish lateral line covers the amplitude and frequency range of the water motions found in the wakes of even a small fish (Bleckmann et al. 1991). In addition, the widespread spatial distribution of lateral line neuromasts on the head and body of fish should ease the analysis of complex three-dimensional water motions like those found in the wakes of fish.

Wake height and the lateral distance between the vortices in a fish wake correspond to the size of the tail fin of the fish that generated the wake. The specific structure of fish wakes also provides information about swimming style. Detection of rotation and traveling direction of the vortices and the direction of the dragged water give information on swimming direction. The mean velocity and maximum vorticity contain information about the time that has passed since the wake generator swam by (Hanke et al. 2000, Hanke and Bleckmann 2004). All these facts and the observation that many piscivorous fish hunt at night, or at depths where low light levels limit vision, led to the question whether the wakes left by swimming fish are used by some predators to track their piscine prey, analogous to the way by which dogs (Steen and Wilsson 1990) and snakes (Chiszar et al. 1990) follow the tracks left by their terrestrial prey. Recent behavioral experiments have shown that the nocturnal piscivorous European catfish (*Siluris glanis*) can track the wakes and thus the swim path of a prey fish (guppy, *Poecilia reticulata*) even in complete darkness (Fig. 6.16). Wakes up to 10 s old were followed over distances that covered up to 55 times the body length of the prey (Pohlmann et al. 2001). Blocking the lateral line with Co^{2+}
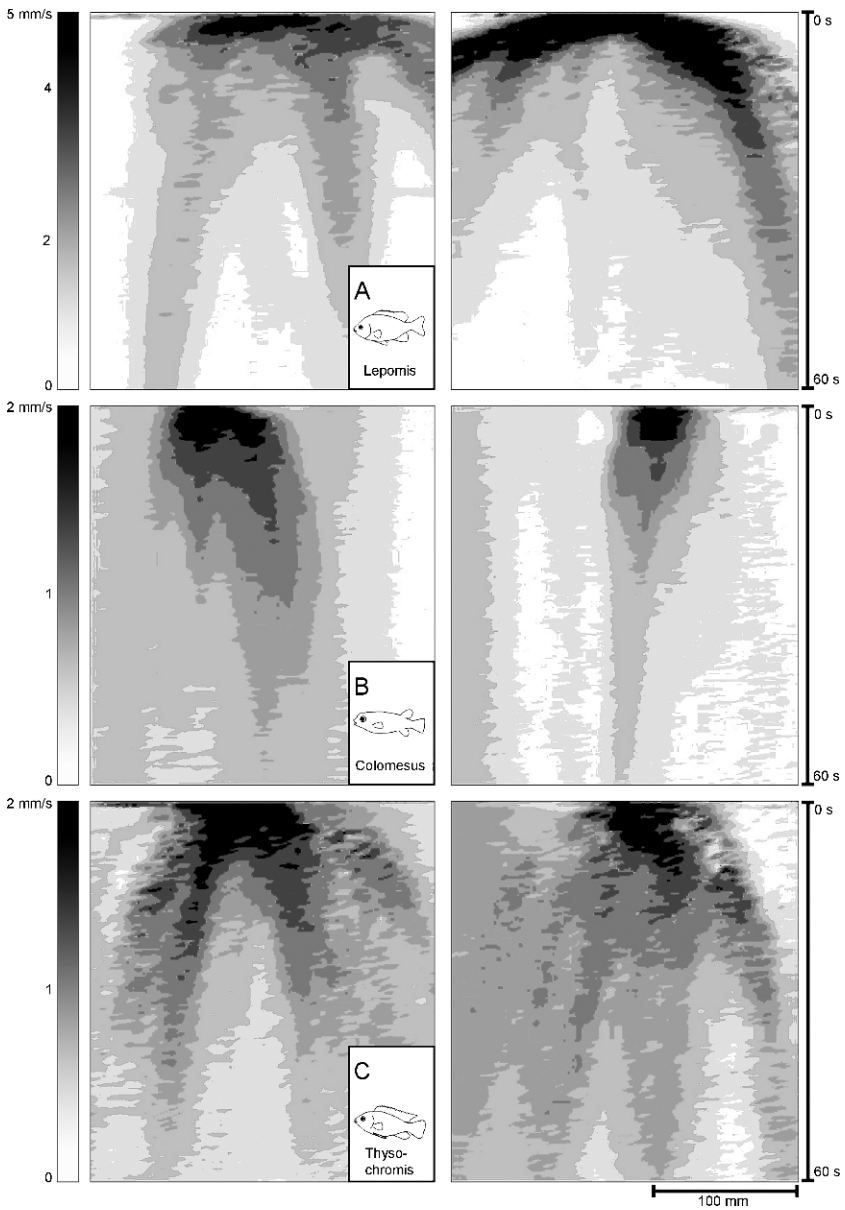
FIGURE 6.15. Spatial extent of wakes (*x*-axis) caused by swimming *Lepomis gibbosus* (**A**), *Colomesus psittacus* (**B**), and *Thysochromis ansorgii* (**C**) as function of time (*y*-axis). To resolve the low water velocities in aged trails, all velocities larger than 5 mm/s (**A**) or 2 mm/s (**B, C**) were coded in dark black. (Redrawn from Hanke and Bleckmann 2004.) (A color version of this figure can be found online at http://www.springer.com/978-0-387-73028-8.)
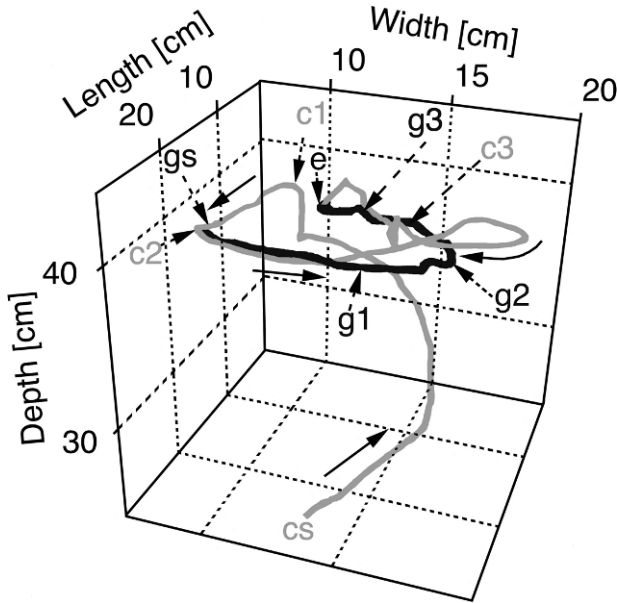
FIGURE 6.16. Three-dimensional plot with temporal information of an attack categorized as wake following. Gray, predator; black, prey. The numbers depict cm and correspond to calibrated positions in the test tank. Solid arrows indicate swimming direction. Three points in time (1 = 11.3 s, 2 = 8.6 s, 3 = 3.4 s before the attack) were chosen to indicate the locations of both fish. The positions of the catfish and the prey fish are indicated by c and g, respectively. The path-following appears to begin when the prey is at g2 and the predator is at c2. (Redrawn from Pohlmann et al. 2001.)

showed that lateral line input was indispensable for wake tracking (Pohlmann et al. 2004). It should be stressed that a predator tracking a wake usually does not perceive the instantaneous location of its prey. Therefore, it cannot approach the prey directly or in an arc, intercepting the prey's path. Nevertheless, wake tracking considerably extends the area in which prey is detectable and thus enhances the encounter probability (Hanke and Bleckmann 2004).

5.2.3 The Lateral Line and Spatial Orientation

Surgically blinded fish avoid aquarium walls without actual touch (Hofer 1908; Dijkgraaf and Kalmijn 1962). Ablation experiments have shown that blind fish use lateral line input for the avoidance of walls or other objects. The cavefish *Astyanax mexicanus* (formerly *Anoptichthys jordani*) is a champion in lateral line perception. Although this species lacks functioning eyes, it can pass through a barrier of rods without touching them (Hahn 1960). Hence, *Astyanax* can determine the position and shape of an object by using nonvisual cues. Studies by von Campenhausen and coworkers (von Campenhausen et al. 1981; Weissert and von Campenhausen 1981; Teyke 1985; Abdel-Latif et al. 1990;

Hassan 1992a, 1992b; Hassan et al. 1992; Hassan 1993) have shown that a gliding fish produces a flow field that is altered by nearby objects. Blind cavefish obviously use lateral line input to evaluate these alterations while gliding past an object. The ability of blind cavefish to detect, localize and discriminate between objects is remarkable. For instance, under favorable conditions *Astyanax* distinguishes between two "fences," each of which has six bars differing only slightly with respect to their relative positions.

Blind cavefish increase their swimming speed in a new environment (Teyke 1985). The increased water velocity across their body surface decreases the boundary layer thickness, which enhances lateral line perception (Teyke 1988, 1989). This behavior provides an excellent method for measuring the ability of cavefish to discriminate between objects and environments in space. By allowing the fish to learn a landmark array before changing the landmark positions within the configuration and recording swimming velocity, De Perera (2004) showed that blind cavefish use hydrodynamic information to develop an inner map of their environment. After learning the position of four landmarks, spaced equally apart, blind cavefish showed a significant increase in swimming velocity when exposed to landmark transformations. Therefore, the fish compare the environment they perceive with an internal representation of the environment they have learnt. The data also indicate that blind cavefish use lateral line input to encode the absolute distance between landmarks and possibly also shape within their spatial maps (De Perera 2004).

5.3 Central Processing of Lateral Line Input

5.3.1 Directional Coding

In surface feeding fish and aquatic amphibians (*Xenopus laevis*), individual lateral line neuromasts can be stimulated by water surface waves from many directions (Zittlau et al. 1986; Elepfandt and Wiedemer 1987). However, because the response of a single primary lateral line afferent depends on both stimulus amplitude and direction, it cannot signal the direction of surface wave propagation unequivocally. In contrast, some lateral line units recorded from the torus or tectum of aquatic amphibians (*Ambystoma*, *Xenopus*) show strong preference for a certain stimulus direction (e.g., Behrend et al. 2006). In the few cases tested, directional tuning was independent of stimulus intensity and/or stimulus frequency (Zittlau et al. 1986; Bartels et al. 1990). Hence, some tectal (midbrain) lateral line units unequivocally encode for stimulus direction. If the tectal recording sites were shifted from a caudomedial to a rostrolateral position in *Xenopus* and *Ambystoma*, the receptive fields shifted from caudal to rostral on the contralateral water surface (Zittlau et al. 1986; Bartels et al. 1990). Therefore, stimulus direction is a lateral line parameter mapped in the tectum of aquatic amphibians. Unfortunately, comparable studies in fish are lacking.

The physiologically identified tectal maps of wave direction in amphibians suggest involvement of the tectum in wave source localization, and small tectal lesions are sufficient to alter the turning responses of *Xenopus* (Claas et al. 1989).

For stimulus directions corresponding to the receptive fields of the destroyed neuronal populations, the response frequency was reduced and a precise localization of stimulus direction no longer occurred. Consequently, frogs with an ablated tectum completely failed to orient to a water surface wave source (Claas et al. 1989). Most likely, the tectum of *Xenopus* is part of the sensorimotor interface for orienting reactions.

5.3.2 Coding of Object Distance

Surface feeding fish determine the wave source distance up to about 15 cm. Hence, the question arises whether there are central lateral line units that encode wave source distance, but this has not been investigated in surface feeding fish. In *Xenopus*, however, some tectal units respond only at specific distances between the frog and a surface wave source (test range 6–16 cm) (Claas et al. 1989).

   Little is known about the coding of wave source direction and wave source distance in midwater and bottom-dwelling fish. None of the medullary and midbrain lateral line units tested so far have shown signs of directional coding or distance coding. What has been found, however, are central units that encode the motion direction of an object passing the fish laterally (Bleckmann and Zelick 1993; Müller et al. 1993; Wojtenek et al. 1998; Engelmann and Bleckmann 2004) or the motion direction of a vibrating sphere (Meyer and Bleckmann, unpublished). Evidently, more data are needed to learn whether and how central lateral line neurons encode the position of an object in space.

6. Summary and Suggestions for Future Work

Although numerous studies have shown that fish can discriminate between different sound directions in three-dimensional space, it is still not settled if fish are able to perceive the actual location of a sound source at a distance. Current models for directional hearing in fish are based on neural calculation of the direction of particle movements of the incident sound by vectorial weighing of input from different regions of the sensory maculae. However, a simple particle motion detector is unable to discriminate between opposing sound sources (180° ambiguity). The directions of farfield particle motion and wave propagation coincide during acoustic compression. The phase model for directional hearing predicts that species with a swimbladder detect both the direction of the incident particle movements and the sound pressure, and the 180° ambiguity is resolved by decoding the phase difference between these components. Such phase analysis might also enable fish to detect the distance to a monopole source within the nearfield.

   Most behavioral studies have focused on detection of changes in sound direction, rather than detection of the actual location of a sound source. In the acoustic farfield, the radial particle motions simplify possible computation of source location, whereas the situation is more complex in the nearfield of a

dipole or higher order source. The unifying guidance model, which works for all types of sound sources, suggests that fish do not perceive the source location at a distance, but are instead guided to the source by turning in a manner that keeps a constant angle between the body axes and the incident particle acceleration detected by the inner ear.

Behavioral evidence supporting auditory source localization has mainly been obtained in studies of the fast C-start escape response to short-range acoustic stimuli of high intensity. Such stimuli activate either of the paired Mauthner cells in the brain stem, which then elicits instant contraction of muscles on the opposite side, followed by directed acceleration away from the source. Recent experiments indicate that simultaneous infrasonic acceleration and compression, i.e., characteristics of stimuli produced by an approaching predator, is more efficient in triggering the response than combined acceleration and rarefaction.

Surface feeding fish use their cephalic lateral line to detect the capillary surface waves caused by terrestrial insects fallen into the water. Target angle determination is based on arrival time and/or phase differences between neuromasts. This is feasible due to the low propagation speed of surface waves. The distance to the wave source (determined up to about 15 cm) is determined by evaluating the distance-dependent frequency modulation of the signal.

Midwater (and benthic) species may use their lateral line to localize moving objects at close range (within about one body length). Information about source azimuth is contained in the location of the maximum pressure-difference amplitude, whereas information about source distance is contained in the spread of excitation along linear arrays of neuromasts.

The lateral line may also detect the vortices in a fish wake, which provide information about fish size, swimming direction, and the time since the wake generator passed by.

Finally, a gliding fish produces a flow field that is sensed by the lateral line. This flow field is altered by nearby objects, and fish may thus use lateral line input to evaluate these alterations while gliding past an object. This ability is particularly well developed in blind cavefish, which perceive their physical environment, and construct an internal representation of it, based on lateral line input.

The field of directional hearing and sound source localization in fish is stilled riddled by numerous unsolved problems, although it has been an active research field for 70 years. Also regarding the reception of hydrodynamic stimuli by the lateral line, many basic questions remain unanswered. Among the most important questions that should be addressed in future experiments, are the following:

1. To which extent are fish able to perceive the actual location of a sound source at a distance? This problem relates to determination of both direction and distance, and must be addressed for farfield and nearfield detection of both monopole and dipole sources.
2. Does the brain use information from all otolith organs in its computation of sound direction? Although afferents from all otolith organs are sufficiently

sensitive to respond to particle motions associated with sounds of normal intensity, this question is still not settled.

3. Is the elevation of a sound source determined by a monaural mechanism? Some studies of the optimal axes of primary afferents indicate that computation of azimuth requires information from both ears, whereas one ear might suffice for computation of sound source elevation. The first assumption is supported by behavioral studies (ablation experiments), whereas the second assumption still needs experimental clarification.

4. How, and to which degree, is the directional information in the incident particle acceleration protected against masking by the amplified secondary particle motions radiating from the swimbladder? Both peripheral (appropriate alignment of hair cell populations) and central mechanisms (common mode rejection) may be involved, but the possible existence of such mechanisms lacks experimental verification.

5. Are only fish utilizing the swimbladder as an accessory hearing organ able to resolve the 180° ambiguity, or to discriminate between sources at different distances? So far, these questions, which relate to discrimination rather than to absolute localization, have only been addressed for species in which the swimbladder has an auditory function.

6. Is the advantage of a swimbladder in lowering auditory thresholds at the expense of acute directional hearing? As opposed to hearing nonspecialists, single units in the torus semicircularis in goldfish lack the diversity in the axes of optimal vibration direction observed among primary afferents. Does this finding reflect poor directional hearing in goldfish (and other hearing specialists), or is it due to inadequate sampling of higher order auditory neurons? So far, no behavioral studies have determined the limits for angular discrimination in otophysans.

7. How are directional information processed in the central nervous system? Some studies have addressed this question, but central processing of directional information is still incompletely understood. This also applies to possible multimodal processing that may integrate directional information from otolith organs and the lateral line.

8. If fish are unable to localize a sound source at a distance, are they still able to approach a source by the mechanism postulated by the guidance model? This question may be addressed by tracking of the approach paths toward concealed monopole and dipole sources.

9. Do predators striking prey at close range employ a "stealth strategy" to boost their success rate? It has been suggested that the predator may delay triggering of fast start escape responses by gradually opening the mouth during the strike prior to the final suction, thereby reducing its own bow wave that alerts the prey. This interesting hypothesis lacks experimental verification.

10. What is the relationship between acceleration and pressure in stimuli that triggers fast start escape responses in different species? Recent observations indicate that synergistic effects of initial acceleration and compression trigger

such responses in otophysans, while the current model for computation of the escape direction does not discriminate between compression and rarefaction. Comparison of species with different swimbladder anatomy, combined with experiments allowing independent control of acceleration and pressure at low frequencies, may clarify this issue.

11. What potential information about the sender (e.g., size, species, direction and velocity of movement) do hydrodynamic stimuli sensed by the lateral line contain? Studies of the physical properties (time course, frequency, and amplitude content), three-dimensional extension, and aging of biologically relevant hydrodynamic stimuli (like the wakes left by swimming fish) are only in their beginning.

12. What kinds of hydrodynamic noise do fish encounter in their natural habitats, and how does the lateral line cope with different noise levels? Discrimination between signal and noise is a general problem in sensory systems. In addition, at the behavioral level little is known about the kind of information fish can extract with their lateral line from the ambient subsurface and surface water motions. This question is especially intriguing in view of the many peripheral specializations seen in the lateral line, i.e., what kind of ethoecological adaptations are there?

13. How is lateral line input processed in the central nervous system? Some of the specific questions are: How are simple and complex hydrodynamic stimuli coded in single channels, and across channels? Are there both parallel and distributed processing of hydrodynamic input at successive levels of the brain? Are there differences between species in central wave source localization algorithms, e.g., in midwater and surface feeding fish? What kinds of simple or multiple mappings—computed as well as topographic—are there in the central lateral line pathway? Are there subsystems for wave source recognition and wave source localization? How are lateral line and auditory information integrated in the CNS?

References

Abdel-Latif H, Hassan ES, von Campenhausen C (1990) Sensory performance of blind Mexican cavefish after destruction of the canal neuromasts. Naturwissenschaften 77:237–239.

Bartels M, Münz H, Claas B (1990) Representation of lateral line and electrosensory systems in the midbrain of the axolotl, *Ambystoma mexicanum*. J Comp Physiol A 167:347–356.

Behrend O, Branoner F, Zhivkov Z, Ziem U (2006) Neural responses to water surface waves in the midbrain of the aquatic predator *Xenopus laevis*. Eur J Neurosci 23: 729–744

Blaxter JHS, Gray JAB, Denton EJ (1981) Sound and startle responses in herring shoals. J Mar Biol Assoc UK 61:851–869.

Bleckmann H (1980) Reaction time and stimulus frequency in prey localization in the surface-feeding fish *Aplocheilus lineatus*. J Comp Physiol A 140:163–172.

Bleckmann H (1982) Reaction time, threshold values and localization of prey in stationary and swimming surface feeding fish *Aplocheilus lineatus* (Cyprinodontidae). Zool Jahrb Abt Physiol 86:71–81.

Bleckmann H (1985) Discrimination between prey and non-prey wave signals in the fishing spider *Dolomedes triton* (Pisauridae). In: Kalmring K, Elsner N (eds) Acoustic and Vibrational Communication in Insects. Berlin: Paul Parey, pp. 215–222.

Bleckmann H (1988) Prey identification and prey localization in surface-feeding fish and fishing spiders. In: Atema J, Fay RR, Popper AN, Tavolga WN (eds) Sensory Biology of Aquatic Animals. New York: Springer-Verlag, pp. 619–641.

Bleckmann H (1994) Reception of hydrodynamic stimuli in aquatic and semiaquatic animals. In: Rathmayer W (ed) Progress in Zoology, Vol 41. Stuttgart: Gustav Fischer, pp. 1–115.

Bleckmann H, Schwartz E (1981) Reaction time of the topminnow *Aplocheilus lineatus* to surface waves determined by video- and electromyogram recordings. Experientia 37:362–363.

Bleckmann H, Schwartz E (1982) The functional significance of frequency modulation within a wave train for prey localization in the surface-feeding fish *Aplocheilus lineatus*. J Comp Physiol A 145:331–339.

Bleckmann H, Zelick R (1993) The responses of peripheral and central mechanosensory lateral line units of weakly electric fish to moving objects. J Comp Physiol A 172:115–128.

Bleckmann H, Tittel G, Blübaum-Gronau E (1989) The lateral line system of surface-feeding fish: anatomy, physiology, and behavior. In: Coombs S, Görner P, Münz H (eds) The Mechanosensory Lateral Line. Neurobiology and Evolution. New York: Springer-Verlag, pp. 501–526.

Bleckmann H, Breihaupt T, Blickman R, Tautz J (1991) The time course and frequency content of local flow fields caused by moving fish, frog and crayfish. J Comp Physiol A 168:749–757.

Buwalda RJA (1981) Segregation of directional and nondirectional acoustic information in the cod. In: Tavolga WN, Popper AN, Fay RR (eds) Hearing and Sound Communication in Fishes. New York: Springer-Verlag, pp. 139–172.

Buwalda RJA, van der Steen J (1979) The sensitivity of the cod sacculus to directional and non-directional stimuli. Comp Biochem Physiol A 64:467–471.

Buwalda RJA, Schuijf A, Hawkins AD (1983) Discrimination by the cod of sound from opposing directions. J Comp Physiol A 150:175–184.

Canfield JG, Rose GJ (1996) Hierarchical sensory guidance of Mauthner-mediated escape responses in goldfish (*Carassuis auratus*) and cichlids (*Haplochromis burtoni*). Brain Behav Evol 48:137–156.

Casagrand JL, Guzik AL, Eaton RC (1999) Mauthner and reticulospinal responses to onset of acoustic pressure and acceleration stimuli. J Neurophysiol 82:1422–1437.

Chapman CJ (1973) Field studies of hearing in teleost fish. Helgoländer wiss Meeresunters 24:371–390.

Chapman CJ, Hawkins AD (1973) A field study of hearing in the cod, *Gadus morhua* L. J Comp Physiol 85:147–167.

Chapman CJ, Johnstone ADF (1974) Some auditory discrimination experiments on marine fish. J Exp Biol 61:521–528.

Chapman CJ, Sand O (1974) Field studies of hearing in two species of flatfish *Pleuronectes platessa* (L.) and *Limanda limanda* (L.) (Family Pleuronectidae). Comp Biochem Physiol A 47:371–385.

Chiszar, David, Ted Melcer, Robert Lee and David Duvall (1990) Chemical cues used by prairie rattlesnakes (*Crotalus viridis*) to follow trails of rodent prey. J Chem Ecol 16: 79–86.

Claas B, Münz H, Zittlau KE (1989) Direction coding in central parts of the lateral line system. In: Coombs S, Görner P, Münz H (eds) The Mechanosensory Lateral Line. Neurobiology and Evolution. New York: Springer-Verlag, pp. 409–419.

Coombs S (1994) Nearfield detection of dipole sources by the goldfish (*Carassius auratus*) and the mottled sculpin (*Cottus bairdi*). J Exp Biol 190:109–129.

Coombs S, Conley RA (1995) Source distance determination by the mottled sculpin lateral line. In: Burrows M, Mattheson T, Newland PL, Schuppe H (eds) Nervous Systems and Behaviour. Stuttgart: Thieme Verlag, pp. 349.

Coombs S, Janssen J (1990) Behavioral and neurophysiological assessment of lateral line sensitivity in the mottled sculpin, *Cottus bairdi*. J Comp Physiol A 167:557–567.

Coombs S, Montgomery JC (1998) The enigmatic lateral line system. In: Fay RR, Popper AN (eds) Comparative Hearing: Fish and Amphibians. New York: Springer-Verlag, pp. 319–362.

Coombs S, Hastings M, Finneran J (1996) Modeling and measuring lateral line excitation patterns to changing dipole source locations. J Comp Physiol A 178:359–371.

Coombs S, Finneran JJ, Conley RA (2000) Hydrodynamic imaging formation by the lateral line system of the Lake Michigan mottled sculpin, *Cottus bairdi*. Philos Trans Roy Soc B 355:1111–1114.

Curcic-Blake B, van Netten SM (2006) Source location encoding in the fish lateral line canal. J Exp Biol 209: 1548–1559.

de Munck JC, Schellart NAM (1987) A model for the nearfield acoustics of the fish swimbladder and its relevance for directional hearing. J Acoust Soc Am 81:556–560.

De Perera T (2004) Spatial parameters encoded in the spatial map of the blind Mexican cavefish, *Astyanax fasciatus*. Anim Behav 68:291–295.

de Vries H (1950) The mechanics of the labyrinth otoliths. Acta Oto-Laryngol 38:262–273.

Dijkgraaf S, Kalmijn AJ (1962) Verhaltensversuche zur Funktion der Lorenzinischen Ampullen. Naturwissenschaften 49:400.

Domenici P, Blake RW (1993) The kinematics and performance of fish fast-start swimming. J Exp Biol 200:1165–1178.

Eaton RC, Emberley DS (1991) How stimulus direction determines the trajectory of the Mauthner-initiated escape response in a teleost fish. J Exp Biol 161:469–487.

Eaton RC, Popper AN (1995) The octavolateralis system and Mauthner cell: interactions and questions. Brain Behav Evol 46:124–130.

Eaton RC, Lavender WA, Wieland CM (1981) Identification of Mauthner initiated response patterns in goldfish: evidence from simultaneous cinematography and electrophysiology. J Comp Physiol A 144:521–531.

Eaton RC, Canfield JG, Guzik AL (1995) Left-right discrimination of sound onset by the Mauthner system. Brain Behav Evol 46:165–179.

Eaton RC, Lee RKK, Foreman MB (2001) The Mauthner cell and other identified neurons of the brainstem escape network of fish. Prog Neurobiol 63:467–485.

Eaton RC, Casagrand JL, Cummins GI (2002) Neural implementation of the phase model for localizing impulse sounds by the Mathner system. Bioacoustics 12:209–212.

Edds-Walton PL (1998) Anatomical evidence for binaural processing in the descending octaval nucleus of the toadfish (*Opsanus tau*). Hear Res 123:41–54.

Edds-Walton PL, Fay RR (2003) Directional selectivity and frequency tuning of midbrain cells in the oyster toadfish, *Opsanus tau*. J Comp Physiol A 189:527–543.

Edds-Walton PL, Fay RR (2005a) Sharpening of directional responses along the auditory pathway of the oyster toadfish, *Opsanus tau*. J Comp Physiol A 191:1079–1086.

Edds-Walton PL, Fay RR (2005b) Projections to bimodal sites in the torus semicircularis of the toadfish, *Opsanus tau*. Brain Behav Evol 66:73–87.

Edds-Walton PL, Fay RR, Highstein S (1999) Dendritic arbors and central projections of physiologically characterized auditory fibers from the saccule of the toadfish, *Opsanus tau*. J Comp Neurol 411:212–238.

Elepfandt A, Wiedemer L (1987) Lateral-line responses to water surface waves in the clawed frog, *Xenopus laevis*. J Comp Physiol A 160:667–682.

Emde G von der, Schwarz S, Gomez L, Budelli R, Grant K (1998) Electric fish measure distance in the dark. Nature 395:890–894.

Engelmann J, Bleckmann H (2004) Coding of lateral line stimuli in the goldfish midbrain in still and running water. Zoology 107: 135–151.

Enger PS (1976) On the orientation of hair cells in the labyrinth of perch (*Perca fluviatilis*). In: Schuijf A, Hawkins AD (eds) Sound Reception in Fish. Amsterdam: Elsevier, pp. 49–62.

Enger PS, Hawkins AD, Sand O, Chapman C J (1973) Directional sensitivity of saccular microphonic potentials in the haddock. J Exp Biol 59:425–434.

Enger PS, Kalmijn AJ, Sand O (1989) Behavioral investigations on the functions of the lateral line and inner ear in predation. In: Coombs S, Görner P, Münz H (eds) The Mechanosensory Lateral lLine—Neurobiology and Evolution. New York: Springer-Verlag, pp. 575–587.

Faber DS, Fetcho JR, Korn H (1989) Neural networks underlying the escape response in goldfish. Ann NY Acad Sci 563:11–33.

Faber DS, Korn H, Lin JW (1991) Role of medullary networks and postsynaptic membrane properties in regulating Mauthner cell responsiveness to sensory excitation. Brain Behav Evol 37:286–297.

Fay, RR (1984) The goldfish ear codes the axis of acoustic particle motion in three dimensions. Science 225:951–954.

Fay RR, Edds-Walton PL (1997) Directional response properties of saccular afferents of the toadfish, *Opsanus tau*. Hear Res 111:1–21.

Fay RR, Edds-Walton, PL (2000) Directional encoding by fish auditory systems. Philos Trans Roy Soc Lond B 355:1281–1284.

Fay RR, Olsho LW (1979) Discharge patterns of lagenar and saccular neurons of the goldfish eighth nerve: displacement sensitivity and directional characteristics. Comp Biochem Physiol A 62:377–386.

Fetcho JR., O'Malley DM (1997) Imaging neuronal networks in behaving animals. Curr Opin Neurosci 7:832–838.

Flock Å (1965) Electromicroscopical and electrophysiological studies on the lateral line canal organ. Acta Otolaryngol Suppl 199:1–90.

Forman MB, Eaton RC (1993) The direction change concept for reticulospinal control of goldfish escape. J Neurosci 13:4101–4113.

Gathan E, Sankrithi N, Campos, JB, O'Malley DM (2002) Evidence for a widespread brain stem escape network in larval zebrafish. J Neurophysiol 87:608–614.

Goulet J, Engelmann J, Chagnaud B, Franosch J-MP, Suttner MD, van Hemmen JL (2008) Object localization through the lateral line system of fish: theory and experiment. J Comp physical A 194:1–17.

Guzik AL, Eaton RC, Mathis DW (1999). A connectionist model of left-right sound discrimination by the Mauthner system. J Comput Neurosci 6:121–144.

Hahn G (1960) Ferntastsinn und Strömungssinn beim augenlosen Höhlenfisch *Anoptichthys jordani* Hubbs und Innes im Vergleich zu anderen Teleosteern. Naturwissenschaften 47:611.

Hale M E (2002) S- and C-start escape responses of the muskellunge (*Esox masquinongy*) require alternative neuromotor mechanisms. J Exp Biol 205:2005–2016.

Hale ME, Long Jr JH, McHenry M J, Westneat MW (2002) Evolution of behaviour and neural control of the fast-start escape response. Evolution 56:993–1007.

Hanke W, Bleckmann H (2004) The hydrodynamic trails of *Lepomis gibbosus* (Centrarchidae), *Colomesus psittacus* (Tetraodontidae) and *Thysochromis ansorgii* (Cichlidae) investigated with scanning particle image velocimetry. J Exp Biol 207:1585–1596.

Hanke W, Brücker C, Bleckmann H (2000) The ageing of the low frequency water disturbances caused by swimming goldfish and its possible relevance to prey detection. J Exp Biol 203:1193–1200.

Harris GG (1964) Considerations on the physics of sound produced by fishes. In: Tavolga WN (ed) Marine Bio-acoustics. Oxford: Pergamon Press, pp. 233–247.

Hassan ES (1989) Hydrodynamic imaging of the surroundings by the lateral line of the blind cavefish *Anoptichthys jordani*. In: Coombs S, Görner P, Münz H (eds) The Mechanosensory Lateral Line. Neurobiology and Evolution. New York: Springer-Verlag, pp. 217–228.

Hassan ES (1992a) Mathematical description of the stimuli to the lateral line system of fish, derived from a three-dimensional flow field analysis. I. The case of moving in open water and of gliding towards a plane surface. Biol Cyber 66:443–452.

Hassan ES (1992b) Mathematical description of the stimuli to the lateral line system of fish, derived from a three-dimensional flow field analysis. II. The case of gliding alongside or above a plane surface. Biol Cyber 66:453–461.

Hassan E-S (1993) Mathematical description of the stimuli to the lateral line system of fish, derived from a three-dimensional flow field analysis. III. The case of an oscillating sphere near the fish. Biol Cyber 69:535–538.

Hassan ES, Abdel-Latif H, Biebricher R (1992) Studies on the effects of Ca^{++} and Co^{++} on the swimming behavior of the blind Mexican cavefish. J Comp Physiol A 171:413–419.

Hawkins AD, Horner K (1981) Directional characteristics of primary auditory neurons from the cod ear. In: Tavolga WN, Popper AN, Fay RR (eds) Hearing and Sound Communication in Fishes. New York: Springer-Verlag, pp. 311–328.

Hawkins AD, Sand O (1977) Directional hearing in the median vertical plane by the cod. J Comp Physiol A 122:1–8.

Hofer B (1908) Studien über die Hautsinnesorgane der Fische I. Die Funktion der Seitenorgane bei den Fischen. Ber königl Bayer biol Versuchsstation München 1:115–168.

Hoin-Radkovski I, Bleckmann H, Schwartz E (1984) Determination of source distance in the surface-feeding fish *Pantodon buchholzi* (Pantodontidae). Anim Behav 32:840–851.

Horner K, Sand O, Enger PS (1980) Binaural interaction in the cod. J Exp Biol 85:323–331.

Hudspeth AJ, Corey DP (1977) Sensitivity, polarity and conductance change in the response of vertebrate hair cells to controlled mechanical stimuli. Proc Natl Acad Sci USA 74:2407–2411.

Janssen J, Corcoran J (1993) Lateral line stimuli can override vision to determine sunfish strike trajectory. J Exp Biol 176:299–305.

Janssen J, Coombs S, Hoekstra D, Platt C (1987) Anatomy and differential growth of the lateral line system of the mottled sculpin, *Cottus bairdi* (Scorpaeniformes: Cottidae). Brain Behav Evol 30:210–229.

Kalmijn AJ (1982) Electric and magnetic field detection in elasmobranch fishes. Science 218:916–918.

Kalmijn AJ (1988) Hydrodynamic and acoustic field detection. In: Atema J, Fay RR, Popper AN, Tavolga WN (eds) Sensory Biology of Aquatic Animals. New York: Springer-Verlag, pp. 83–130.

Kalmijn AJ (1989) Functional evolution of lateral line and inner ear sensory systems. In: Coombs S, Görner P, Münz H (eds) The Mechanosensory Lateral Line—Neurobiology and Evolution. New York: Springer-Verlag, pp. 187–215.

Kalmijn AJ (1997) Electric and near-field acoustic detection, a comparative study. Acta Physiol Scand 161(Suppl) 638: 25–38.

Karlsen HE (1992a) The inner ear is responsible for detection of infrasound in the perch (*Perca fluviatili*s). J Exp Biol 171:163–172.

Karlsen HE (1992b) Infrasound sensitivity in the plaice (*Pleuronectes platess*a). J Exp Biol 171:173–187.

Karlsen HE, Sand O (1987) Selective and reversible blocking of the lateral line in freshwater fish. J Exp Biol. 133:249–267.

Karlsen HE, Piddington RW, Enger PS, Sand O (2004) Infrasound initiates directional fast-start escape responses in juvenile roach (*Rutilus rutilus*). J Exp Biol. 207:4185–4193.

Käse R, Bleckmann H (1987) Prey localization by surface wave-ray tracing—fish track bugs like oceanographers track storm. Experientia 43:290–293.

Kimmel CB, Powell SL, Metcalfe, WK (1982) Brain neurons which project to the spinal cord in young larvae of the zebrafish. J Comp Neurol 205:112–127.

Kleerekoper H, Chagnon EC (1954) Hearing in fish with special reference to *Semotilus atromaculatus*. J Fish Res Bd Can 11:130–152.

Korn H, Faber DS (1996) Escape behaviour—brainstem and spinal cord circuitry and function. Curr Opin Neurobiol 6:826–832.

Lang HH (1980) Surface wave discrimination between prey and nonprey by the back swimmer *Notonecta glauca* L. (Hemiptera, Heteroptera). Behav Ecol Sociobiol 6:233–246.

Lee RKK, Eaton RC, Zottoli SJ (1993) Segmental arrangement of reticulospinal neurons in the goldfish hindbrain. J Comp Neurol 327:1–18.

Lighthill J (1980) Waves in Fluids. Cambridge, UK: Cambridge University Press.

Liu KS, Fetcho JR (1999) Laser ablations reveal functional relationships of segmental hindbrain neurons in zebrafish. Neuron 23:325–335.

Lu Z, Popper AN (1998) Morphological polarizations of sensory hair cells in the three otolithic organs of a teleost fish: fluorescent imaging of ciliary bundles. Hear Res 126:47–57.

Lu Z, Popper AN (2001) Neural response directionality correlates of hair cell orientation in a teleost fish. J Comp Physiol A 187:453–465.

Lu Z, Song J, Popper AN (1998) Encoding of acoustic directional information by saccular afferents of the sleeper goby, *Dormitator latifrons*. J Comp Physiol A 182:805–815.

Lu Z, Xu Z, Buchser WJ (2003) Acoustic response properties of lagenar nerve fibers in the sleeper goby, *Dormitator latifrons*. J Comp Physiol A 189:889–905.

Lu Z, Xu Z, Buchser WJ (2004) Coding of acoustic particle motion by utricular fibers in the sleeper goby, *Dormitator latifrons*. J Comp Physiol A 190:923–938.

Ma WLD, Fay RR (2002) Neural representations of the axis of acoustic particle motion in nucleus centralis of the torus semicircularis of the goldfish, *Carassius auratus*. J Comp Physiol A 188:301–313.

McCormick CA, Hernandez DV (1996) Organization of inner ear endorgan projections in the goldfish, *Carassius auratus*. Brain Behav Evol 43:189–205.

Metcalfe WK, Mendelson B, Kimmel CB (1986) Segmental homologies among reticu-lospinal neurons in the hindbrain of the zebrafish larva. J Comp Neurol 251:147–159.

Mohr C, Bleckmann H (1998) Electrophysiology of the cephalic lateral line of the surface-feeding fish *Aplocheilus lineatus*. Comp Biochem Physiol A 119:807–815.

Moulton JM, Dixon RH (1967) Directional hearing in fishes. In: Tacvolga WN (ed) Marine Bioacoustics, Vol 2. Oxford: Pergamon Press, pp. 187–232.

Müller U, Schwartz E (1982) Influence of single neuromasts on prey-localizing behavior of surface-feeding fish *Aplocheilus lineatus*. J Comp Physiol A 149:399–408.

Müller HM, Fleck A, Bleckmann H (1993) The responses of central octavolateralis cells to moving sources. J Comp Physiol A 179: 455–471.

Myrberg AA Jr, Banner A, Richaard JD (1969) Shark attraction using a video-acoustic system. Mar Biol 2:264–276.

Myrberg AA Jr, Gordon CR, Klimley AP (1976) Attraction of free ranging sharks by low frequency sound, with comments on its biological significance. In: Schuijf A, Hawkins AD (eds) Sound Reception in Fish. Amsterdam: Elsevier, pp. 205–228.

Nelson DR, Gruber SH (1963) Sharks: attraction by low-frequency sounds. Science 142:975–977.

Parvulescu A (1967) The acoustics of small tanks. In: Tavolga WN (ed) Marine Bio-acoustics II. Oxford: Pergamon Press, pp. 7–14.

Piddington RW (1972) Auditory discrimination between compressions and rarefactions by goldfish. J Exp Biol 56:403–419.

Pohlmann K, Grasso FW, Breithaupt T (2001) Tracking wakes: the nocturnal predatory strategy of piscivorous catfish. Proc Natl Acad Sci USA 98:7371–7374.

Pohlmann K, Atema J, Breithaupt T (2004) The importance of the lateral line in nocturnal predation of piscivorous catfish. J Exp Biol 207: 2971–2978.

Popper AN, Coombs S (1982) The morphology and evolution of the ear in Actinopterygian fishes. Am Zool 22:311–328.

Popper AN, Salmon M, Parvulescu A (1973) Sound localization by two species of Hawaiian squirrelfish, *Myripristis berndti* and *M. argyromus.* Anim Behav 21:86–97.

Reinhardt F (1935) Über Richtungswahrnehmung bei Fischen, besonders bei der Elritze (*Phoxinus laevis* L.) und beim Zwergwels (*Amiurus nebulosus* Raf.). Z Vergl Physiol 22:570–603.

Ritter DA, Bhatt DH, Fetcho JR (2001) In vivo imaging of zebrafish reveals differences in the spinal networks for escape and swimming movements. J Neurosci 21:8956–8965.

Rogers PH, Popper AN, Cox M, Saidel WM (1988) Prosessing of acoustic signals in the auditory system of bony fish. J Acoust Soc Am 83:338–349.

Sand O (1974) Directional sensitivity of microphonic potentials from the perch ear. J Exp Biol 60:881–899.

Sand O (1981) The lateral-line and sound reception. In: Tavolga WN, Popper AN, Fay RR (eds) Hearing and Sound Communication in Fishes. New York: Springer-Verlag, pp. 459–480.

Sand O (1984) Lateral line systems. In: Bolis L, Keynes RD, Maddrell SHP (eds) Comparative Physiology of Sensory Systems. Cambridge, UK: Cambridge University Press, pp. 3–32.

Sand O, Enger PS (1973) Evidence for an auditory function of the swim bladder in the cod. J Exp Biol 59:405–414.

Sand O, Hawkins AD (1973) Acoustic properties of the cod swim bladder. J Exp Biol 58:797–820.

Sand O, Karlsen HE (1986) Detection of infrasound by the Atlantic cod. J Exp Biol 125:197–204.

Sand O, Karlsen HE (2000) Detection of infrasound and linear acceleration in fish. Philos Trans Roy Soc Lond B 355:1295–1298.

Sand O, Enger PS, Karlsen HE, Knudsen FR (2001) Detection of infrasound in fish and behavioural responses to intense infrasound in juvenile salmonids and European silver eels: a minireview. Am Fish Soc Symp 26:183–193.

Schellart NAM, Buwalda RJA (1990) Directional variant and invariant hearing thresholds in the rainbow trout (*Salmo gairdneri*). J Exp Biol 149:113–131.

Schellart NAM, de Munck JC (1987) A model for directional and distance hearing in swim bladder-bearing fish based on the displacement orbits of the hair cells. J Acoust Soc Am 82:822–829.

Schuijf A (1975) Directional hearing of cod (*Gadus morhua*) under approximate free field conditions. J Comp Physiol 98:307–332.

Schuijf A (1976) The phase model of directional hearing in fish. In: Schuijf A, Hawkins AD (eds) Sound Reception in Fish. Amsterdam: Elsevier, pp. 63–86.

Schuijf A (1981) Models of acoustic localization. In: Tavolga WN, Popper AN, Fay RR (eds) Hearing and Sound Communication in Fishes. New York: Springer-Verlag, pp. 267–310.

Schuijf A, Buwalda RJA (1975) On the mechanism of directional hearing in cod (*Gadus morhua*). J Comp Physiol 98:333–344.

Schuijf A, Hawkins AD (1983) Acoustic distance discrimination by the cod. Nature 302:143–144.

Schuijf A, Siemelink M (1974) The ability of cod (*Gadus morhua*) to orient towards a sound source. Experientia 30:773–774.

Schuijf A, Baretta JW, Wildschut JT (1972). A field investigation on the discrimination of sound direction in *Labrus berggylta* (Pisces: Perci-formes). Netherlands J Zool 22:81–104.

Schuijf A, Visser C, Willers AFM, Buwalda RJA (1977) Acoustic localization in an ostariophysian fish. Experientia 33:1062–1063.

Schwartz E (1965) Bau und Funktion der Seitenlinie des Streifenhechtlings (*Aplocheilus lineatus* Cuv. u. Val.). Z vergl Physiol 50:55–87.

Schwartz E (1970) Ferntastsinnesorgane von Oberflächenfischen. Z Morphol Tiere 67:40–57.

Schwartz E (1971) Die Ortung von Wasserwellen durch Oberflächenfische. Z vergl Physiol 74:64–80.

Steen JB, Wilsson E (1990) How do dogs determine the direction of tracks? Acta Physiol Scand 139:531–534.

Teyke T (1985) Collision with and avoidance of obstacles by blind cavefish *Anoptichthys jordani* (Characidae). J Comp Physiol A 157:837–843

Teyke T (1988) Flow field, swimming velocity and boundery layer: parameters which affect the stimulus for the lateral line organ in blind fish. J Comp Physiol A 163:53–61.

Teyke T (1989) Learning and remembering the environment in the blind cavefish *Anoptichthys jordani*. J Comp Physiol A 164:655–662.

Tittel G (1985) Determination of stimulus direction by the topminnow, *Aplocheilus lineatus*. A model of two dimensional orientation with the lateral line system. In: Barth FG (ed) Verhandlungen der Deutschen Zoologischen Gesellschaft 78. Stuttgart: Gustav Fischer, p. 242.

Tittel G (1991) Verhaltensphysiologische, ultrastrukturelle und ontogenetische Studien am Seitenliniensystem von *Aplocheilus lineatus*. Ein vorläufiges Modell zur Richtungsdetermination von Beuteobjekten. PhD Thesis, University of Giessen, 445 pp.

Tittel G, Müller U, Schwartz E (1984) Determination of stimulus direction by the topminnow *Aplocheilus lineatus*. In: Varju D, Schnitzler HU (eds) Localization and Orientation in Biology and Engineering. New York: Springer-Verlag, pp. 69–72.

van Bergeijk WA (1964) Directional and nondirctional hearing in fish. In: Tavolga WN (ed) Marine Bio-acoustics. Oxford: Pergamon Press, pp. 281–299.

van Bergeijk WA (1967) The evolution of vertebrate hearing. In: Neff WD (ed) Contributions to Sensory Physiology, Vol. 2. New York: Academic Press, pp. 1–49.

von Campenhausen C, Riess I, Weissert R (1981) Detection of stationary objects in the blind cavefish *Anoptichthys jordani* (Characidae). J Comp Physiol A 143:369–374.

von Frisch K, Dijkgraaf S (1935) Können Fische die Schallrichtung Wahrnehmen? Z Vergl Physiol 2:641–655.

Weeg MS, Fay RR, Bass AH (2002) Directionality and frequency tuning of primary saccular afferents of a vocal fish, the plainfin midshipman (*Porichthys notatus*). J Comp Physiol A 188:631–641.

Weissert R, von Campenhausen C (1981) Discrimination between stationary objects by the blind cavefish *Anoptichthys jordani*. J Comp Physiol A 143:375–382.

Wojtenek W, Mogdans J, Bleckmann H (1998) The responses of midbrain lateral line units of the goldfish *Carassius auratus* to moving objects. Zoology 101:69–82.

Wubbels RJ, Schellart NAM (1997) Neuronal encoding of sound direction in the auditory midbrain of the rainbow trout. J Neurophysiol 77:3060–3074.

Wubbels RJ, Schellart NAM (1998) An analysis of the relationship between the response characteristics and topography of directional- and non-directional auditory neurons in the torus semicircularis of the rainbow trout. J Exp Biol 201:1947–1958.

Wubbels RJ, Schellart NAM, Goossens JHHLM (1995) Mapping of sound direction in the trout lower midbrain. Neurosci Lett 199:179–182.

Yan H, Fine ML, Horn NS, Colón WE (2000) Variability in the role of the gasbladder in fish audition. J Comp Physiol A 186:435–445.

Zittlau KE, Claas B, Münz H (1986) Directional sensitivity of lateral line units in the clawed toad *Xenopus laevis* Daudin. J Comp Physiol A 158:469–477.

Zottoli SJ, Faber DS (2000) The Mauthner cell: what has it taught us? Neuroscientist 6:26–38.