Functional Overlap and Nonoverlap Between Lateral Line and Auditory Systems

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Keywords Differential water movement • Dipole source • Distant touch • Far field • Gas bladder • Hydrodynamic flow field • Mauthner neuron • Multisensory integration • Near field • Particle motion • Prey detection • Predator avoidance • Rheotaxis • Swim bladder • Wake tracking • Whole body acceleration

> "The mucous canals of the fishes are nothing else than an accessory hearing organ spread over the whole body surface. I am not wont to maintain that it elicits sensation of sound, but its function will be found to fall within the realm of this still imperfectly understood sense of hearing."
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> Mayser (1882, cited and translated by Lowenstein, 1967, p. 5)

> "… the lateral line organ responds to near-field displacements of sound sources; there is no longer any reason for considering the lateral line as a non-acoustic receptor system."
>
> van Bergeijk (1964, p. 291)

> "They [lateral-line organs] serve mainly to detect and locate moving animals (prey, enemies, social partners) at short range on the basis of current-like water disturbances… They are not engaged in the detection of propagated sonic or infrasonic sound waves…"
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> Dijkgraaf (1963, p. 95)

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1 Introduction

The problem of functional overlap between fish auditory and lateral line systems is, at its root, a problem of understanding other minds. Do fish “hear” with their lateral lines? If a source stimulates both the lateral line and the ear simultaneously, does that give rise to a perception that is something other than hearing? The very definitions of hearing and sound are so hopelessly intertwined that all definitions of auditory function are inherently tautological or anthropomorphic (e.g., reflected in concepts of infra- or ultrasonic with respect to the human hearing range). Nonetheless, animals other than humans have ears and respond to sounds in the audible band with remarkable commonalities in acuity and perceptual properties (Fay, 1988). In fishes, the ear also responds to sound (particle acceleration) of very low frequency, well into the infrasonic bandwidth (Sand & Karlsen, 1986, 2000).

For the terrestrial human species it is certainly a difficult task to envisage the sensory world of aquatic animals, and the sensations and perceptions provided by the lateral line and the related electroreceptive organs are impossible for humans to appreciate fully. Throughout the history of comparative physiology, the prevailing view has been to consider the lateral line as an accessory hearing organ. This idea culminated with Willem van Bergeijk’s (1964) erroneous arguments that the lateral line was the dominant hearing organ within the acoustic near field, and the only organ providing directional information about the sound source. Further, although he correctly stated that the inner ear also enables fish to detect sound in the acoustic far field, he also argued that this is possible only in species with a gas bladder that transforms sound pressure into particle motion. However, the extreme sensitivity of the inner ear to particle motion also enables fish lacking a gas bladder to detect far field sound (Chapman & Sand, 1974; Fay, 1984). The chapters by Coombs and Bleckmann in this volume provide a more thorough review of van Bergeijk’s influence.

In the same era, Sven Dijkgraaf (1963) argued for a contrasting view and described the sensory quality of the lateral line as “touch-at-a-distance.” He emphasized the very short detection range of the lateral line for both moving and stationary objects, arguing that the lateral line is able to detect vibratory sources only within a tiny fraction of the acoustic near field based on water movements relative to the surface of the fish. He also emphasized the role of the lateral line in detecting nearby objects by their distorting effects on the self-generated flow field around moving fish. This remarkable ability has now been studied extensively in the blind Mexican cavefish *Astyanax mexicanus* (e.g., von Campenhausen et al., 1981; Hassan, 1986; Windsor et al., 2008). Dijkgraaf’s way of thinking was strikingly different from the prevailing ideas of the lateral line as an accessory hearing organ, and touch-at-a-distance is clearly distinct from any sense of “hearing.” At a meeting in Bielefeldt, Germany, in 1987 on “The Mechanosensory Lateral Line,” Dijkgraaf’s vision of lateral line sensation representing a unique sensory modality separate from hearing was thoroughly addressed. To acknowledge and honor his scientific influence, the word “svenning” was suggested for this novel

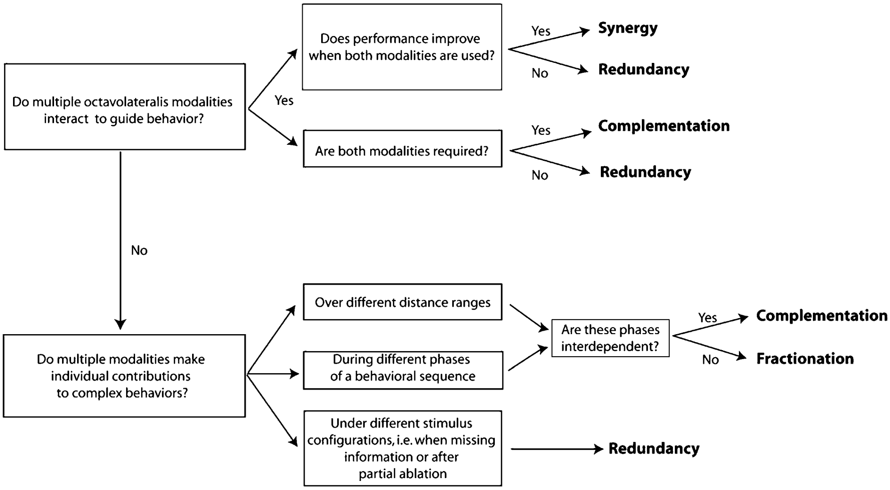

Fig. 1 A decision tree for evaluating multimodal interactions. The individual types of intermodal interactions are listed in boldface type

sensory modality (Platt et al., 1989). However, the deep commonalities in stimulus sources, physiological mechanisms, and ontogeny continue to require consideration of intersensory interactions between the inner ear and the lateral line.

The lateral line system has long been known to have both ontogenetic and phylogenetic ties to the inner ear. Like the ear, lateral line end organs also respond to water motions ranging from nearly DC up to 50–200 Hz (see Section 1.4.1), certainly overlapping with the inner ear bandwidth of fishes, if not humans. However, whereas the inner ear otolith organs are accelerometers responding to either linear acceleration of the fish in a sound field or local particle acceleration emanating from a pulsating gas bladder (for review, see Popper et al., 2003), the lateral line organs detect relative motions between the animal surface and the surrounding water. The historical persistence of the view that the lateral line is a subordinate hearing organ results from the fact that all vibrating and moving underwater objects produce both hydrodynamic flow fields in the form of water displacements caused by the moving source (near field particle motions), and sound pressure fields associated with far field particle motions (see Section 1.2). Thus, many sources that stimulate one sense contain energies that may stimulate the other as well, and it is a reasonable assumption that the two senses may often act in concert (Braun et al., 2002), in a number of possible modes of interaction (Fig. 1). However, the accumulation of neuroanatomical and behavioral evidence strongly supports a view of the lateral line as an independent sensory system with its own functions, distinct stimuli, neural pathways, and processing rules. The present chapter attempts to describe areas of functional overlap and nonoverlap between these two sensory systems related by common sources of proximal stimulation and a shared evolutionary history.

The question of functional overlap can be restated in a few specific ways, ranging from the highest levels of organization to the lowest. Are there specific behavioral tasks that require or are enhanced by the use of both channels? Are there functional connections between the neuronal pathways of each channel? Do bimodal neurons exist and how do they combine inputs from the two channels? Even more subtly, are there cross-modal interactions that might not relate to a single behavioral task, but rather a conflict between two or more? For example, when presented with female pheromones, male moths fail to take evasive action from bat echolocation calls (Skals et al., 2005). This is clearly an intersensory interaction, but one that arises from a conflict between motivational states. Thus, the animal behaves in a way that reflects contributions from two sensory systems, but not because their information is being combined in a meaningful way. This chapter surveys the literature on lateral line and inner ear function in an attempt to determine how information from these two systems might interact in natural behaviors.

1.1 Evolutionary and Developmental Relationships

Outside of any functional considerations, the lateral line system and the inner ear share intimate details of evolutionary history and development. The lateral line and inner ear capsule both develop from a series of ectodermal thickenings, the dorsolateral placodes (Northcutt, 1996), which are an important synapomorphy (a shared derived feature, generally used as diagnostic or definitive for a taxon) of the Craniata (see the chapter by Webb in this volume). The early conceptions of "hearing associated" functions for the lateral line system were tied to the acoustico-lateralis hypothesis (e.g., Ayers, 1892), the idea that the lateral line represents a primitive state from which the ear evolved (or vice versa). Studies of jawless fishes strongly suggest that the inner ear (including both linear and angular acceleration detectors) and the lateralis systems (including both mechanosensory and electrosensory systems) all arose at one moment in vertebrate history (Braun, 1996). Together, these are termed the octavolateralis systems because of their origin from the octaval and associated dorsolateral placodes. Instead of an "acoustico-lateralis theory," the common origin suggests that the two systems are (or were) intertwined, at least by developmental history, or perhaps by integrative functions (see also the chapter by Coombs & Bleckmann in this volume). The origin of this embryonic tissue was a key innovation in the origin of the vertebrates (Northcutt & Gans, 1983), and all living vertebrates today still possess some derivatives of dorsolateral placodes. These may include all end organs of the inner ear, the neuromasts of the mechanosensory lateral line, and the electrosensory lateral line system (Modrell et al., 2011).

The individual receptor mechanisms derived from octavolateralis systems are highly diverse and include both displacement-sensitive and voltage-sensitive sensory cells. A wide range of pre-receptor structures filter and channel environmental stimuli to increase the functional diversity of these systems. All octavolateralis systems share features of gross organization (Coombs & Montgomery, 2005; Braun, 2009) that may reflect either common developmental mechanisms (Baker et al., 2008), similar processing strategies, or both. In the case of the electrosensory and mechanosensory lateral lines, the organs share a similar distribution across the body surface, as well as many sources that are likely to stimulate both systems (e.g., emit a voltage field and create water motions). Thus, there is a great commonality in the central processing strategies that might be used by both systems (Montgomery et al., 1995). There is also recent evidence that object motion, as detected by the mechanosensory lateral line, enhances electrosensory responsiveness (Pluta & Kawasaki, 2008), but such cross-modal interactions have only been hinted at otherwise (Nelson et al., 2002; Schuster, 2006) and deserve future investigations.

1.2 The Multidimensional Hydrodynamic Source and Proximate Stimulation of the Lateral Line and Inner Ear

One reason to consider the functions of the lateral line and ear together is that the proximate stimuli are related, both in terms of their underlying physics and in that they often issue from a single source. Historically, there has been little distinction between hydrodynamics and acoustics (Richardson, 1954), and acoustic phenomena are really a particular type of fluid motion (Harris, 1964; Kalmijn, 1988). Objects that move through a fluid medium push the medium away at the advancing edge (increased pressure) and draw fluid in behind the trailing edge (decreased pressure), thus creating a hydrodynamic flow field around itself. Consequently, at a fixed point close to a moving object (e.g., a gliding fish), low-frequency fluctuations in both pressure and fluid motion will occur as the object passes. A stationary vibrating object (e.g., an oscillating fin) also generates local fluid motions, in addition to pressure fluctuations that propagate as a pressure wave away from the source. The amplitude of the pressure waves emitted from dipole sources, that is, objects vibrating with constant volume, is maximum along the axis of vibration and zero in directions perpendicular to this axis, whereas monopole sources, which pulsate in volume, emit pressure waves omnidirectionally. The propagating pressure waves are associated with oscillatory particle motion, which can be expressed as particle displacement, particle velocity, or particle acceleration. However, propagating sound causes no net flow of fluid, as is the case for the hydrodynamic flow close to a moving source. The oscillatory particle motion associated with the pressure wave depends on the elastic properties of the medium, and the ratio between particle motion and sound pressure defines the acoustic impedance of the fluid. In contrast, the hydrodynamic flow close to the source is ruled by the incompressible nature of fluids, and source motions cause net flow of the surrounding medium. These hydrodynamic motions attenuate steeply with distance, such as at a rate of

1/distance^3 for a dipole source and 1/distance^2 for a monopole source. In contrast, the propagating pressure wave and the associated particle motions attenuate at a rate of only 1/distance (Harris, 1964; Kalmijn, 1988). Very close to the source, the hydrodynamic fluid motions are much greater than the particle motions associated with the pressure wave. The difference in attenuation with distance means that at some distance from the source, the particle motions associated with the pressure wave are of equal amplitude to the more steeply attenuating hydrodynamic motions caused by incompressible flow. This distance is dependent on wavelength and is greatest at low frequencies. For a monopole source, the distance at which hydrodynamic flow and acoustic pressure fluctuations are equal can be estimated as the wavelength divided by 2π (for a 20-Hz dipole, this corresponds to about 12 m). For a dipole, the distance depends on the angle between the direction to the source and the axis of vibration, and is always larger than for a monopole source. Along the axis of source vibration, this distance can be estimated as 1.4 times the wavelength divided by 2π (i.e., about 17 m for a 20-Hz source).

This boundary heuristically defines two regions generally termed the acoustic near and far field, respectively. Particle motions associated with incompressible flow are commonly called near field flow, whereas those that are proportionate with sound pressure are called far field particle motions. However, these different types of particle motions, which are 90° out of phase, coexist in both the near and far field, but with very different magnitudes. Close to a moving source, incompressible motions of fluid predominate, and these near field components attenuate below relevant noise floors within a short distance from the source. Further from the source, particle motions associated with the propagating pressure wave attenuate less steeply and form a relatively spatially homogeneous acoustic far field. It should be noted that fish and other animals moving underwater mainly produce extremely low-frequency particle motions (Kalmijn, 1989; Bleckmann et al., 1991). The major components of the particle motions caused by swimming fish are even below 20 Hz. For biological sources generating such low frequencies, the near field may extend beyond the audible distance range, and far field detection is hardly biologically relevant. In addition, these ideal descriptions depend on an unbounded medium. In shallow water, sound propagation is severely impeded or prevented in a wavelength-dependent manner. The shallow water functions as a high-pass filter with a sharp cut-off frequency, which is dependent on both depth and substrate rigidity (Rogers & Cox, 1988; Forrest et al., 1993). For a perfectly rigid bottom, the wavelength of the cut-off frequency is four times the water depth. For a muddy bottom with high density of gas bubbles from decaying material, this figure is close to twice the depth. In nature, the wavelength of the cut-off frequency will usually be between these extremes, for example about three times the water depth for mixed bottom substrates. This implies that for a 20-Hz source, sound propagation requires a depth of more than about 25 m. Thus, in many natural circumstances, far field propagated pressure waves simply are not a relevant part of a fish's experience. For a more complete treatment of these hydroacoustic principles, the reader is referred to Harris (1964), van Bergeijk (1964), Kalmijn (1988, 1989), and the chapter by McHenry and Liao in this volume.

The lateral line and the inner ear both function to detect particle motions, but in different ways. The particle movements in the flow field close to the source (the near field component) are spatially complex (inhomogeneous) and independent of the elastic properties of the medium. Therefore, a fish will behave like a rigid body, with forced motions reflecting an integration of the particle motions in the surrounding flow field (Denton & Gray, 1982, 1983). This will cause relative movements between the fish surface and surrounding particle motions. The part of the fish closest to the source will move with smaller amplitude than the adjacent water particles, whereas the opposite is true for the part most distant from the source. The spatially dispersed neuromasts are stimulated by differential water movement across the body surface, and their positions at many points along the body surface make the lateral line system ideally suited to map local flow fields (Coombs et al., 1996).

The forced accelerations of the rigid fish caused by near field motions will also stimulate the inner ear. The otoliths have a mass density three times that of the surrounding liquid and soft tissue, and the otolith motions will thus lag behind, and have smaller amplitude than, the motions of the adjacent tissue (de Vries, 1950). The differential motion of the soft fish tissue and the denser otolith creates shearing forces on the macular hair cells, the first step in neuronal transduction of a sound field. In a conceptual sense, the inertial inner ear responds to whole body acceleration of the fish (a spatial integration of the hydrodynamic near field motions) and the lateral line responds to local, differential water motions along the body (the derivative of the hydrodynamic spatial pattern). Both the inner ear and individual lateral line organs also respond to temporal patterns of their respective stimuli, which is clearly important for signal analysis.

The soft tissues of fish are virtually acoustically transparent and behave as the surrounding water particles in the acoustic far field. Therefore, there will be no differential movements between the surface of the fish and the adjacent water. Dijkgraaf (1963) predicted that such homogeneous, vibrational movements of fish and surrounding water at the same phase and amplitude would fail to stimulate the lateral line, and this was later shown experimentally by Sand (1981, 1984). However, the inner ear is ideally suited to detect such movements. Whereas the incident sound makes the soft tissue vibrate with the same phase and amplitude as the adjacent water particles, the motions of the dense otoliths lag behind and display smaller amplitude owing to their inertia, thus stimulating the macular hair cells as described in the preceding text. The otolith organs function as accelerometers, with equal sensitivity to near field and far field motions (Chapman & Sand, 1974), but the presence of a gas bladder may still enhance the auditory sensitivity, particularly in the far field and at higher frequencies. In a sound field, the pressure oscillations will cause the gas bladder to pulsate in volume, and the radial motions of the bladder surface may exceed the particle motions of the incident sound. Thus, a gas bladder may enhance hearing sensitivity by acting as a pressure to motion transformer. It is still unclear if gas bladder enhancement requires some particular mechanical linkage or minimum distance between the bladder and the ear, and the relevant frequency range of such enhancement is uncertain. In Atlantic cod

(*Gadus morhua*), which has no direct bladder–ear connection, the gas bladder appears to enhance the auditory sensitivity mainly at higher frequencies, beginning around 50 Hz, with increasing enhancement at frequencies up to a few hundred Hertz (Sand & Enger, 1973). In other taxa, the degree of enhancement and relevant frequency range may differ based on bladder size and shape and the nature of linkage between the bladder and ear. In goldfish (*Carassius auratus*), gas bladder deflation decreased the sensitivity to a 40 Hz source by 17 dB (Fay & Popper, 1974; Dailey & Braun, 2009), so gas bladder enhancement may also be important for inner ear function in the near field and at low frequencies.

An obvious assumption would be that the two senses act together to interpret a single stimulus source. However, the more common situation seems to be that relevant sources at a given instant stimulate only one of these sensory systems. For example, a fairly large vibratory source may generate whole body accelerations of a nearby fish, thus stimulating the inner ear, and if the fish is sufficiently close to the source, lateral line organs may be simultaneously stimulated. However, the amplitude of the local water motions decline steeply with distance, such as 1/distance^3 for a dipole source, and the relative movements between the fish and surrounding water falls off even more steeply (Denton & Gray, 1982, 1983). Therefore, the lateral line will be completely insensitive to such a source at distances of less than the body length of even rather small fish (see Section 1.4.2). On the other hand, a tiny vibratory source, like for instance a small planktonic crustacean, may cause local water movements that are sufficient to stimulate the lateral line at very close range (Montgomery, 1989), although such small water motions may fail to cause sufficient whole body acceleration to stimulate the inner ear. Interestingly, the very short detection range of lateral organs protects this sensory system against being masked by ambient noise (Denton & Gray, 1983).

During the last two decades, it has become evident that wake tracking is a major function of the lateral line (see the chapter by Montgomery, Bleckmann, & Coombs in this volume). The stimuli used in these scenarios may have very weak pressure components and provide little or no stimulation to the inner ear (see the chapter by McHenry & Liao in this volume). A swimming fish leaves a trail of spinning vortices that persist for up to several minutes (Hanke et al., 2000; Hanke & Bleckmann, 2004). Such a wake can be detected by the lateral line of an intersecting fish and tracked, but is less likely to stimulate the inner ear. Obviously, wake tracking is very important in prey–predator interactions (Pohlmann et al., 2001, 2004). It is interesting to note that several groups of secondary aquatic vertebrates have developed “lateral line analogs” that may enable similar wake tracking, for example, sensitive vibrissae in seals and otters (Miersch et al., 2011), manatees (Reep et al., 2011), and mechanosensitive, cephalic appendices in water snakes (Catania et al., 2010). “Svenning” must be a very important sense for an aquatic animal.

Nevertheless, the two senses can in many cases act together to interpret a single stimulus source. It is this thought that led Braun et al. (2002) to ask “What is the nature of multisensory integration between octavolateralis systems?” It seems reasonable to assume that the nervous system should use all available information (meaning from multiple input channels) to form percepts of objects in the environment and that higher-order perception must result from various kinds of interactions between the relevant sensory pathways. Braun et al. (2002) suggested that because this assumption is not yet justified by evidence, one should assume the null hypothesis that animal nervous systems *do not* integrate multiple channels of inputs about a single source. Although it is quite clear that the lateral line system is independent of audition in many behavioral contexts, behavioral researchers are increasingly aware that a particular sense may or may not be important to a given task, depending on particular conditions or behavioral state. The examples that follow describe the relationships between the inner ear and the lateral line, but in many instances, it is clear that neither modality is truly independent. Vision, chemoreception, and touch are all important in many of the same behavioral contexts as audition and lateral line sensation and these senses will be mentioned where relevant data exist. Nonetheless, the interrelations of audition and lateral line systems specifically remain somewhat vague. These two systems are so closely related in many ways, yet it has been difficult to demonstrate that their behavioral uses overlap. There may be some cases where particular species use both senses in close concert (particularly during short-range communication and predation/predator avoidance), and these are given further scrutiny (see Section 2).

1.3 The Multichannel Octavolateralis System

A continually growing number of studies examining inner ear or lateral line responsiveness (or both) have been based on a common stimulus source: a vibratory dipole. This source is a reasonable approximation of biological sources (Kalmijn, 1989) for both the lateral line and multiple inner ear end organs and produces a simple sound field including well-defined patterns of hydrodynamic flow and acoustic pressure. In most experimental tanks and many natural environments, a propagating pressure wave is not produced because the water is too shallow or confined (Rogers & Cox, 1988), but this source is useful as a model of flapping fish tails, appendages, swimming animals, and other sound-producing natural objects. That this one source can provide stimulation to multiple octavolateralis systems is one of many reasons to expect some interaction between submodalities. However, the relative responsiveness of the different submodalities will depend on both source size and distance.

Experiments with dipole sources reveal several aspects of octavolateralis function. In Lake Michigan mottled sculpin (*Cottus bairdi*), the fairly large vibratory bead (5–8 mm diameter) used in many published studies is a potent stimulus to both the inner ear and the lateral line (Braun & Coombs, 2010). Behavioral and physiological studies of the lateral line in the sculpin (Coombs & Janssen, 1989, 1990), demonstrate that it is a sensor array detecting relative water velocity or acceleration (or a mixture of the two) at various points along the body, and provides the central nervous system with the information needed to analyze the three-dimensional flow pattern over the body surface (Coombs et al., 1996; Coombs & Patton 2009).

There have yet been no studies of inner ear physiology in mottled sculpin, but Braun and Coombs (2010) showed that these animals can use their inner ear to respond to a vibratory source of 40 Hz when the lateral line is pharmacologically ablated. Further, the performance of mottled sculpin in various behavioral tasks was generally either unaffected by the loss of specific sensory channels or completely eliminated, depending on the behavioral task. Distinct behavioral tasks (conditioned and unconditioned responses) seemed to rely on a single sense channel. Orienting responses, an innate component of feeding responses, were observed only when the lateral line was intact, and earlier studies have shown that partial ablations lead to partial orienting deficits (Hoekstra & Janssen 1985, 1986; Conley & Coombs 1998). Conditioned respiratory responses, on the other hand, were unaffected by lateral line ablation (Coombs, 1994). Sculpin could also be conditioned to respond to substrate vibration cues via their inner ear or ignore them, depending on the conditioning regime (Braun & Coombs, 2010). Similarly, Nauroth and Mogdans (2009) showed that both goldfish and oscars (*Astronotus ocellatus*) can be conditioned to respond to a 50-Hz vibrating bead without using their lateral line systems.

In goldfish, saccular units respond to a 50-Hz vibratory bead in proportion to the pressure encountered at the anterior chamber of the gas bladder. That is, saccular units responded proportionately to the change in pressure at the gas bladder as a vibratory source was moved in space relative to the gas bladder (Coombs et al., 2010). Conditioned behavioral response magnitudes also changed with bead position relative to the gas bladder, but these patterns were more variable than physiological responses. These authors also showed lagenar responses to the same source, but they did not show a clear pressure-detector location near the gas bladder, nor were these responses attenuated by gas bladder deflation (as saccular responses were). Together with data from Dailey and Braun (2009, 2011) and Coombs (1994), these results indicate that goldfish use their pressure sensitive inner ear (saccular end organ) to detect and analyze vibrating beads. For pure kinetic stimuli using a vibrating table, lagenar and utricular units show the same vibration sensitivity as saccular units, with thresholds of about 0.1 nm at 140 Hz (Fay, 1984). Thus, it is likely that the lagena and utricle are also involved in responses to vibrating sources, particularly regarding the directional characteristics of the stimuli (Sand & Bleckmann, 2008).

Casper and Mann (2006a) also used a dipole source to investigate hearing thresholds in two species of elasmobranchs. Elasmobranch audition is a subject of considerable debate, as field observations do not easily reconcile with laboratory data on hearing thresholds, and there is little agreement over which end organs are important for audition, and the mechanism of sound conduction through the head (see Myrberg, 2001 for review). Casper and Mann (2006a) showed high sensitivity to low-frequency dipoles, with particle acceleration thresholds lower than those previously published. This discrepancy may be due to differences in ambient noise levels, but Casper and Mann also suggested that stimulus type and orientation may affect which end organs are stimulated. By recording auditory evoked potentials, Casper and Mann (2006a) found that responses were greatest when the stimulus source was located close to the parietal fossa. This finding supports an old idea that elasmobranch hearing depends on stimulation of the macula neglecta, with a possible sound path through the parietal fossa (see also Fay et al., 1974; Bullock & Corwin, 1979; Casper & Mann, 2006b). Casper and Mann (2006a) speculate that earlier studies using more uniform sound fields produced by monopole speakers may be less effective at stimulating the macula neglecta, and that responses to such sounds may be mediated by the sacculus. This raises the possibility that elasmobranchs might use one end organ for far field sounds (or more spatially uniform fields) and another organ for local punctate sources such as dipoles, capable of local stimulation of the parietal fossa. Future investigations should focus on elasmobranch hearing using local sources and end-organ ablations to reveal more about the potential for multichannel inner ear function in these animals.

1.3.1 Multiple Modalities Within the Lateral Line System

In goldfish, extensive physiological studies also demonstrate that the lateral line responds as an array of differential water motion detectors capable of analyzing the three-dimensional flow pattern over the body surface (Bleckmann & Zelick, 2009). Both behavioral and physiological data suggest that the lateral line system contains two types of receptor systems, linked to canal organs and superficial neuromasts. Canal neuromasts (CNs) are sensitive mostly to acceleration of the surrounding water relative to the body surface and have high-pass frequency-response profiles. In contrast, superficial neuromasts (SNs) are sensitive to some combination of relative velocity and acceleration and show saturated responses to low-frequency stimulation (see the chapters by Bleckmann & Mogdans,Chagnaud & Coombs, and McHenry & van Netten in this volume).

Although there have been some studies of the differences in innervation of CNs and SNs (Münz, 1989; Bleckmann, 2007), very little is known of the organization of central projections or information processing streams within the central nervous system (cf. Plachta et al., 2003 and chapters by Bleckmann & Mogdans and Chagnaud & Coombs in this volume). Several studies suggest that CNs are used in localization tasks with point sources (e.g., dipoles), whereas SNs have been implicated in tasks involving more spatially diffuse and low-frequency currents, such as rheotaxis (orientation to currents) (Montgomery et al., 1997; Coombs et al., 2001). These studies used gentamicin treatment, which was thought to reversibly destroy CNs, but leave SNs unaffected (Song et al., 1995). Unfortunately, more recent studies (van Trump et al., 2010; Brown et al., 2012) have shown that gentamicin also inactivates SNs, probably through transduction channel inactivation, and thus cannot be used to dissect SN from CN function. These recent findings leave some confusion in the literature. Lake Michigan mottled sculpin deprived of their lateral line (full pharmacological ablation by Co^{2+} or by gentamicin) do not orient to dipole sources, but skin scraping (intended to damage only superficial neuromasts) does not affect orientation (Coombs et al., 2001). Thus, it seems reasonable to conclude that SNs play a limited role in dipole detection or may not be involved at all. It remains to be determined if other senses (i.e., inner ear senses) are also needed for dipole detection.

In a series of rheotaxis studies on different species, Montgomery and colleagues (1997) showed that gentamicin treatment had no effects on orientation to currents, but skin scraping generally reduced or eliminated this behavior. If indeed gentamicin eliminated both CNs and SNs but had no effect on rheotaxis, these results conflict with results showing that elimination of SNs alone eliminates orientation to currents. These studies will need to be repeated with careful controls and direct measurements (physiological or using vital dyes) of the effect of gentamicin and similar treatments. Nonetheless, there is still a developing body of evidence that the two submodalities are used in different behavioral contexts, and it is a reasonable hypothesis that CNs are responsible for the detection of objects and point sources and SNs are responsible for detection of larger-scale currents and stimuli that are spatially more uniform (see Section 2).

1.3.2 Special Cases

The lateral line and inner ear systems are both phylogenetically quite diverse (Braun & Grande 2008; see also the chapter by Webb in this volume). Some taxa have evolutionary novelties that alter the role of the lateral line or inner ear–associated structures in ways that conceivably link the functions of the two systems. For instance, in Clupeiformes (shad and herring), the recessus lateralis is a branch of the cephalic lateral line canal system that abuts a perilymphatic space (Denton & Blaxter, 1976). Pressure changes in the prootic, gas-filled bulla are translated to volume changes causing movements that are transmitted to the flexible wall of the recessus lateralis and inducing fluid motion within the lateral line canal. The function of this pressure sensitive portion of the lateral line has been the subject of some speculation, including use in source distance calculations (e.g., Schuijf & Budwalda, 1980). Denton and Gray (1983) suggested that neuronal comparisons of the distribution of the differential water motions sensed by the main lateral line system and the pressure sense provided by the end organs in the recessus lateralis could be used to obtain highly accurate source resolution, which might be essential for collision avoidance during the tight schooling seen in these fish. As it became known that some clupeiforms were able to detect the ultrasonic sonar clicks of their mammalian predators, most authors suggested that the complex arrangement of the utricle could be responsible for ultrasonic sensitivity (see Popper et al., 2004 for review). More recently, Wilson et al. (2009) showed that destruction of the lateral line neuromasts adjacent to the recessus lateralis eliminated ultrasonic sensitivity in Gulf menhaden (*Brevoortia patronus*). It is unknown if ultrasonic sensitivity also depends on the utricle or if cross-modal computations are required in some way. Future studies should examine the innervations of those specific neuromasts and follow their central projections to reveal differences with other neuromasts and possible points of convergence with auditory pathways.

A similar pressure-sensitive lateral line component is also present in butterfly fish (Chaetodontidae), and Webb (1998) termed this structure a laterophysic connection. The function of this specialization is still unknown, but many species of chaetodonitids exhibit elaborate communication displays that include tail slaps, low frequency sounds, and vocalizations within 100–500 Hz and above 3 kHz (Tricas et al., 2006). It is possible that specialized neuromasts adjacent to the laterophysic connection have a distinct function in pressure reception, particularly during communication displays. It is also possible that this specialization of the gas bladder imparts pressure sensitivity to the inner ear as well (Webb & Smith, 2000). Interestingly, inner ear anatomy suggests that the specialized gas bladder morphology in some species of chaetodontids is not associated with corresponding specializations of the otoliths or maculae, as is typical of pressure-sensitive fish (Popper, 1977; Webb et al., 2010). Hearing sensitivity tests before and after gas bladder deflation and anatomical and physiological studies of the neuromasts in question will resolve the auditory or lateral line functions of this gas bladder morphology and may uncover intermodal interactions.

Two other cases of potentially pressure-sensitive lateral line systems have also been reported: Mormyridae (Elephantnose fishes: Stipetić, 1939, cited by Bleckmann 1994), and loricariids (armored catfishes: Bleckmann et al., 1991; Aquino & Schaefer 2002). In these taxa, there is an association of some part of the lateral line system with a gas filled cavity, but the function of these linkages is not known. Even parts of the unspecialized trunk lateral line are in close proximity to a gas compartment in species possessing a gas bladder, being separated from the gas by only a relatively thin body wall. However, exceedingly high, unnatural sound pressures may be required to stimulate lateral line end organs through this route (Sand, 1981).

1.4 Specific Areas of Overlap and Nonoverlap in Sensitivity

Some summary of the specific sensitivities of octavolateralis channels can be made based on existing behavioral and physiological data (see Table 1).

1.4.1 Frequency

Functioning as accelerometers, it is likely that inner ear sensitivity extends down to DC, although responses have only been tested for frequencies down to 0.1 Hz (Sand & Karlsen, 1986; Karlsen, 1992a, b). Technical limitations, owing to the very large displacement amplitudes required to achieve a given acceleration at very low frequencies, makes it difficult to experimentally test responses to lower frequencies. However, no sign of a low frequency cut-off in acceleration sensitivity has been

Table 1 Overlap in frequency and distance ranges and functions between the lateral line and inertial audition

	Inertial audition	Lateral line sensing
Frequency band	<0.1 to $\times\ 10^2$ Hz	<0.1 to $\times\ 10^2$ Hz
Distance range	Near and far field	Stationary objects: Close range (~centimeters) Wake tracking: Variable, potentially wide, range (several meters)
Stimuli	Vibratory sources Currents Reafference?	Vibratory sources Currents Hydrodynamic structure Reafference Active sensing using reafferent carrier (damming flow)
Behavioral relevance	Orientation Navigation? Inertial guidance? Soundscape detection Communication Prey detection Predator avoidance Escape responses	Orientation Communication Prey detection Predator avoidance Escape response Swimming kinematics

noted in the few species that have been tested and indeed, audiograms of these species display a fairly flat sensitivity function below approximately 100 Hz with thresholds close to 10^{-5} ms^{-2} in the infrasonic range. This represents a sensitivity to linear acceleration several orders of magnitude higher than in humans (Todd et al., 2008). The lateral line is also exquisitely sensitive to low-frequency stimulation (Bleckmann, 1994; see also the chapter by Chagnaud & Coombs). The high-frequency cut-offs of both inertial audition and the lateral line have been the subjects of some debate (Kalmijn, 1988), in part because the same auditory or lateral line function can look quite different when plotted in terms of pressure, particle displacement, velocity, or acceleration. For the inertial inner ear, this question is sometimes further complicated by the presence of pressure-displacement transformers associated with gas-filled structures, which offer limited hearing enhancement (e.g., Chapman & Hawkins, 1973; Chapman & Sand, 1974) above a certain frequency that depends on gas volume and depth (Sand & Enger, 1973; Sand & Hawkins, 1973). This transition frequency may typically be 50–100 Hz. In all studies to date of species without any gas bladder–associated hearing enhancement, inner ear sensitivity declines rapidly above a few hundred Hertz, and most of these species do not respond to sounds above 1000 Hz (for review, see Popper et al., 2003). The upper frequency cut-off of the lateral line system is also difficult to estimate precisely. As discussed in Section 1.3.1 and in Chagnaud and Coombs (this volume), CN responses are proportional to acceleration of the fluid at the body surface, but SN responses are more directly related to velocity. In terms of velocity, SNs typically have low-pass response curves, with steep roll-offs in sensitivity somewhere in the tens of Hertz (Bleckmann, 1994; see also Chagnaud & Coombs, this volume). In terms of acceleration, CNs also have low-pass characteristics. The canal may act to filter very low frequency stimuli, but CN responsiveness is highest in the tens of Hertz, with sharp declines at 100 Hz or above (Kalmijn, 1988; see also the chapter by Chagnaud & Coombs, this volume).

Although there is some consensus that low-frequency hearing in the near field is mediated primarily via particle-motion detection by otolithic end organs, auxillary structures that enhance hearing (e.g., gas-filled structures such as the swim bladder) may also make important contributions at low frequency. As noted, such enhancements are most significant for pressure-sensitive high-frequency hearing (Braun & Grande, 2008). Thus, it seems logical that this derived, increased sensitivity is most behaviorally important at higher frequencies, where fish that lack such abilities become deaf. However, Dailey and Braun (2009) showed that behavioral detection of a 40-Hz vibrating bead, a relatively weak pressure source, relies primarily on the pressure sensitive hearing channel in goldfish, a finding that is consistent with evoked responses in goldfish saccular fibers to a 50-Hz dipole (Coombs et al., 2010). Moreover, both of these studies showed that behavioral as well as neural sensitivity was greatly decreased by deflation of the gas bladder. The function of pressure-sensitive hearing at low frequencies is relatively unexplored and deserves further study. Although the sensitivity at very low frequencies (below 40 Hz) may not be enhanced by derived pressure sensitivity (Sand & Hawkins, 1973), such sensitivity may still be behaviorally important at higher intensities, as Karlsen et al. (2004) have shown for the fast start escape responses induced by a 7-Hz stimulus in the cyprinid species roach (*Rutilus rutilus*).

In summary, the inner ear and the lateral line systems have nearly identical frequency bands, probably also overlapping with enhanced hearing systems. The lateral line may parcel frequency space between the two submodalities, but both inertial inner ear and the lateral line systems are low-frequency sensors, mostly sensitive to very low (approaching DC) frequencies, with drastically reduced sensitivity at greater than100 Hz. This overlap in frequency bandwidth is another factor favoring the assumption that the two systems could or should operate in concert, but evidence showing that they truly do is sparse.

1.4.2 Distance

One of the often-cited distinctions between lateral line and inner ear function has been distance range (e.g., Coombs & Montgomery, 1999). There are several reasons to conclude that the lateral line operates over a shorter distance range than inner ear senses. Most importantly, the different types of stimulus parameters discussed above (see Section 1.2) generated by a single source each differ in their attenuation with distance from the source. Within the acoustic near field, the particle motions important to the lateral line and inertial inner ear decline rapidly with source distance (1/distance^3 for a dipole), whereas acoustic pressure used by pressure-sensitive inner ear systems declines much less steeply with distance (1/distance). Even when detecting incident particle acceleration, that is, the pressure gradient, the inner ear can be expected to have a larger active space than the lateral line. For the inertial ear, the relevant pressure difference that provides whole-body acceleration in the local flow field is relative to the fish's body dimensions (e.g., head-to-tail, because the fish behaves like a rigid body in the local flow field), whereas for the lateral line (particularly CNs), a suprathreshold pressure gradient must be of a scale smaller than a body length to set up flow-field patterns that differentially stimulate adjacent neuromasts (Denton & Gray, 1983). Thus, it has been argued that both inertial audition and lateral line sensitivity should be dependent on body size, or neuromast spacing (which appears to scale with body size; many teleost taxa have inter-neuromast spacing of approximately 0.01 × body length: Coombs, personal communication of unpublished observations). These two considerations (sensitivity as a function of size and biophysical differences in proximate stimuli) have led numerous authors to claim that the lateral line is sensitive within one to two body lengths (e.g., Dijkgraaf, 1963;Denton & Gray, 1988; Coombs et al., 1992), whereas the inner ear sensitivity extends into the far field (e.g., Popper et al., 2003). Also in the true far field, where the particle motions are associated with sound pressure and the fish behaves acoustically as the surrounding water and not as a rigid body, the inner ear is stimulated by the incident particle acceleration in fish lacking a gas bladder (as described in Section 1.2). The detection of pressure mediated by a gas bladder is independent of fish length and has the greatest potential distance range, especially in the case of sources that produce propagating waves. Far field particle motions are inversely related to the first power of distance (1/distance) and thus attenuate much more gently with distance than the local flow fields generated by monopole (1/distance^2) or dipole (1/distance^3) sources, and should be detectable at much longer distances from the source. As noted, hearing in the true far field is not strictly dependent on the presence of a gas bladder, and such structures will increase the detection distance only as much as they enhance auditory sensitivity.

Although this range fractionation appears to be in effect in feeding behaviors (see Section 2.2), there are serious problems with this simple characterization of lateral line and inner ear functions. In a sense, asking which sense has a greater distance range is analogous to asking which human sense has a greater range, vision or olfaction? The answer obviously depends on the stimulus configuration and amplitude, the path and signal loss between source and receiver, and the ambient noise levels. Given favorable wind conditions, olfaction may identify a bakery long before one might read the business' sign, but a simple change in lighting or wind directions can reverse that hierarchy. The lateral line is stimulated by pressure gradients along the body surface, but such gradients might be part of the wake of a fish that passed minutes earlier (Hanke et al., 2000; Hanke & Bleckmann, 2004). How can the distance range of that detection be meaningfully expressed? Similarly, some water currents produced by animals (e.g., respiratory jets) can extend over very large distances. If an animal swims through such a hydrodynamic structure, a buried mollusk (for instance) might be detected at several fish lengths.

For such sources, time may be even more significant than distance, as these structures have a finite period before they decay into the ambient noise. Whereas the speed of sound determines the extremely short time lag between generation and detection of an auditory stimulus, the lateral line enables a fish to track vortices in a wake that is several minutes old and whose creator has long since swum away.

When used for hydrodynamic imaging (reviewed by Dijkgraaf, 1963), the extent of the self-generated local flow field around the body (and hence detection limits) may depend on swimming speed and body size and shape. There is some evidence that the swimming speed dictates the effective distance range of hydrodynamic imaging (Janssen, 1997, but see Windsor et al., 2010). Interestingly, object detection in burst-glide swimming (see the chapter by Montgomery et al. in this volume) is usually within a range of a few centimeters, much shorter than a body length (0.1 body lengths in Windsor et al., 2010 [wall detection], < 0.5 body lengths in Janssen, 1997 [prey orientation]). Using implanted electrodes and free swimming oyster toadfish (*Opsanus tau*), Palmer et al. (2005) also found that prey-induced neural activity in lateral line afferents occurred only when prey fish (minnows, *Fundulus heteroclitus*) were within a few centimeters, generally 0.4 body lengths. It should be noted that in the case of object detection using the distortion of the damming field, the stimulus energy is provided by the receiving fish. Hence, detection range is determined by the receiver's swimming speed and the resultant size of the damming field. In the case of detecting a swimming minnow, the stimulus energy is provided by the source's tail beats (vortices in the wake and the local flow field caused by movement of the fish's body through the water), and detection range thus depends on various factors, including the stimulus fish's size, swim speed, and tail beat frequency and amplitude.

Although the ultimate source of lateral line stimulation may be quite far away (as in the case of a buried mollusk, a jet produced by a fin flap, or the wake of fish), the proximate stimulation, the pressure gradient, must always be felt at the surface of the fish. In that respect, the distance range of the lateral line is literally millimeters, but the sources themselves dictate the space over which they establish suprathreshold pressure gradients. By analogy to olfaction—chemicals must reach the receptor cell membranes within the nose—but the effective distance range depends on the spread of the stimulus, which may spread and attenuate, become mixed by turbulence or convective processes, be projected in a directed manner (jets and currents), or even be deposited in a specific location with particular decay patterns (vortices and wake structures).

2 Integration and Nonintegration in Specific Behavioral Contexts

Auditory and lateral line senses are well known to be individually important in several contexts, particularly communication, feeding, and predator avoidance. Although the role of the behavioral significance of the lateral line is covered by many chapters in this volume (Coombs & Bleckmann; McHenry & Liao; Montgomery, Bleckmann, & Coombs), it is worthwhile to examine these specific cases and ask how these senses may or may not be used in together in each specific behavioral context.

2.1 Communication

It is widely appreciated that complex communication is often multimodal (Partan & Marler, 2005), but few studies have truly utilized this understanding experimentally (Coleman, 2009). Acoustic communication is well known in fishes (Bass & Ladich, 2008), but the role of lateral line in short range communication is less well studied. The best documented example is the vibrational spawning behavior of Himé salmon, *Oncorhynchus nerka* (Satou et al., 1994a,b). In this case, the lateral line system is necessary to detect the vibratory cues that pass between the sexes during spawning. Many other species include quivering, fin flaps, and close range swimming and fin movements in their courtship and agonistic displays (e.g., Tricas et al., 2006; see also Ladich & Myrberg, 2006), and these behaviors can be expected to generate strong lateral line signals. Experiments should be designed to test the idea that these signals are used as specific communication signals (e.g., in complementary or redundant interactions) or if they influence motivational states in an accessory way, increasing response probabilities or intensities. Himé salmon remains the only known example where the lateral line is essential in communication, but in this case, the role of audition is not known. Vision is important to salmon spawning (Satou et al., 1994b), and the integration between vision and lateral line should be investigated further in this and many other species (Coleman, 2009).

2.2 Feeding and Predator Avoidance

Feeding and predator avoidance are both essentially object localization and tracking tasks. The role of the lateral line in feeding has been well documented in many species (see the chapter by Montgomery, Bleckmann, & Coombs in this volume). Several experimental studies have investigated the interactions between vision and the lateral line system (e.g., Enger et al., 1989; New et al., 2001; Schwalbe et al., 2012). In most of these studies, lateral line ablation eliminated strikes or reduced accuracy particularly in the absence of vision. The lateral line appears to be essential for the final stages of prey capture, but initial stages of acquisition and tracking may be dependent on vision or audition (Liang et al., 1998; Montgomery et al., 2002). The role of inertial audition is difficult to study because it cannot be eliminated without major behavioral alterations. Given the role of inertial (and pressure-sensitive) hearing at short range and the low frequencies presented by predator and prey motions alike (generally below 25 Hz; Kalmijn, 1988), it is likely that the inner ear is also important in prey recognition and detection. In fact, such low frequencies may be particularly effective in inducing behavioral responses in fish (Knudsen et al., 1994, 1997; Sonny et al., 2006).

Predator avoidance, particularly escape behaviors, may be dependent on multiple octavolateralis systems. Mauthner neuron decision-making processes may include lateral line information (see Section 3.3 and Mirjany & Faber 2011), and the infrasonic sensitivity of the inner ear is also ideally suited for detecting approaching predators (Karlsen et al., 2004). As reviewed in Section 3.3, the Mauthner neuron escape network is a likely source of synergistic and complementary interactions between the inner ear and lateral line system. However, it is problematic that many studies investigating the role of audition and lateral line in prey–predator interactions, for example, the fast start escape responses discussed in Section 3.3, have employed frequencies far higher than those that are most biologically relevant.

2.3 Orientation to Currents, Including Rheotaxis and Object Entrainment

A number of recent studies have shown the involvement of the lateral line in orienting to currents (see the chapters by McHenry & Liao and Montgomery et al. in this volume), and these have already been discussed in Section 1.3.1. Initial studies suggested that only superficial neuromasts were responsible for rheotaxic behavior, but these conclusions may have been weakened by false assumptions about some of the blocking techniques (van Trump et al., 2010). Further, Montgomery et al., (2003) had already shown that both superficial and canal neuromasts were required for object entrainment in a stream, a typical use of rheotaxic abilities in fishes. It should be noted that orientation to a homogeneous current requires a fixed external reference frame, provided by visual or tactile stimuli, as Dijkgraaf (1963) thoroughly discussed in his influential review. Only when such an external reference frame is established, can the lateral line provide information about speed and direction of homogeneous currents.

Infrasonic or very low frequency detection by the inner ear may also be important for detecting relative current velocities. When a fish is swimming in a current with constant swimming activity, its velocity will change if the current velocity changes, either due to temporal current fluctuations or the fish entering a water body with a different current velocity. Such a change in the velocity of the fish may be sensed by the exceedingly sensitive linear acceleration detectors in the inner ear, thus providing information about the change in current velocity (Sand & Karlsen, 2000). For example, the relative speed and direction of layered ocean currents may be detected in this manner by a fish cruising at constant swimming speed through the boundary zone from one layer to the next. During the passage through the boundary zone, the fish may then experience a detectable acceleration, conveying information about the differences in current velocity between the layers.

This hypothesis may be prohibitively difficult to test, but it may be worthwhile to attempt to determine the response of the ear in a fish gently shifting its position relative to an object in a flow field. The presence of the object will cause local regions of different current velocities, which might be detected by the inner ear. The ability of a fish swimming in an experimental “tread-mill current” to detect subtle changes in current velocity should also be tested, for instance with behavioral conditioning techniques. In such experiments, a possible role of the inner ear could be established by blocking the mechanosensitivity of the lateral line, for instance using the cobalt method (Karlsen & Sand, 1987).

2.4 Schooling and Swimming

The importance of the lateral line in swimming and schooling has also been more clearly demonstrated by recent experimental studies (see Faucher et al., 2010; see also the chapter by McHenry & Liao in this volume). These new studies have confirmed the seminal finding of Pitcher et al. (1976) that blinded fish can school, although their responses to their neighbors’ motions were slower and less accurate. Animals deprived of both vision and the lateral line were unable to school (see also Partridge & Pitcher, 1980 for review). In the context of schooling, if the infrasonic sensitivity of the inner ear is used for inertial guidance or detection of local current inhomogeneities, inertial audition may also be important for detecting neighbor distances and changes in swimming direction (see also Denton & Gray, 1983). The relative roles of vision, lateral line and inertial audition in schooling await further investigations (Larsson, 2009).

3 Central Nervous System Processing

Another avenue of exploring the relationship between the lateral line and the auditory systems is found in electrophysiological and anatomical data on the central nervous pathways of the two systems (see the chapters by Wullimann & Grothe and Bleckmann & Mogdans in this volume). In general, the pathways of lateral line and auditory information processing within the brain are distinct. The organs are innervated by individually distinct cranial nerves and project to mostly nonoverlapping hindbrain centers. From there, the sensory information in these channels is passed up the neuraxis through essentially independent pathways. There are potential sites of cross-talk between processing centers at all levels of the nervous system, but the evidence for bimodal interactions or processing centers is scant. It is reasonable to assume that higher level perceptual interactions might be occurring only at the level of the forebrain, where the understanding of function remains primitive. As knowledge accumulates on forebrain processing in aquatic vertebrates, a more clear understanding of perceptual mixing between senses will emerge in the future.

3.1 Hindbrain Projection Zones

Early descriptions of octavolateralis central projections (e.g., Larsell, 1967) reported a large degree of overlap between inner ear and lateral line hindbrain representations, but this was clearly mistaken (McCormick, 1992), and more recent studies have documented a highly structured set of principal projection nuclei within the dorsal medulla, with little overlap between inner ear and lateral line projections (McCormick, 1999; McCormick & Wallace, 2012). Each octavolateralis end-organ has a unique pattern of projections to the hindbrain, with multiple overlapping targets for the otolithic end organs and the cupular end organs of the semicircular canals (Tomchick & Lu, 2005; McCormick & Wallace, 2012), with very little overlap between inner ear and lateral line organs in their primary projection nuclei. Some primary recipient hindbrain nuclei do receive inputs from multiple modalities, including the eminentia granularis and the magnocellular octavolateralis nucleus (Tomchick & Lu, 2005; Maruska & Tricas, 2009). Both of these structures have intimate connections with hindbrain reticular nuclei (McCormick, 1999) and may be involved in the multisensory regulation of startle responses (see Section 3.3). Although the other octaval nuclei do not appear to receive heavy projections from both inner ear and lateral line afferents, projection overlap may be more subtle, occurring at the transitional zones or via laterally extended dendrites of postsynaptic neurons. Eighth nerve afferents also sometimes terminate ventrally in the nucleus medialis, but this is taxonomically variable and not common in teleost fishes (McCormick, 1999). In the absence of overlapping projection zones, multimodal neurons may exist by virtue of dendritic connections between hindbrain nuclei. For instance, Weeg and Bass (2000) have shown that neurons within the dorsolateral division of the descending octaval nucleus (an inner ear recipient) receive inputs from both VIIIth nerve fibers and anterior lateral line nerve ganglion cells. These dual-modality neurons were identified after tracer injection in the auditory midbrain. On this basis, they suggested that already the dorsolateral descending octaval nucleus performs integrative functions. More intriguingly, these authors also showed a previously underappreciated interconnection between hindbrain primary recipient nuclei. Nucleus medialis (the lateral line recipient zone) is reciprocally and bilaterally connected to the magnocelluar octavolateralis nucleus and the dorsolateral division of the descending octaval nucleus. Medialis also receives projections from the intermediate divison of the descending octaval nucleus (also an inner ear recipient zone). Weeg and Bass (2000) suggested that some intermodality processing must occur within each "modality-specific" zone already in the hindbrain. The functional nature of this reticulation is still unclear, but low-level integration in supposedly "single-modality" brain areas may be a common feature of brain organization used to subtly process information based on descending influences from other modalities (Stoffregen & Bardy, 2001; Schroeder & Foxe, 2005). Descending influences, such as projections from the auditory torus to the medial pretoral nucleus and subsequently to the cerebellar crest (Yamamoto & Ito, 2005), also have potential to modify the responsiveness of one modality based on processing within another.

3.2 Midbrain and Higher Brain Centers

Central nervous processing of higher-order stimulus features for both modalities occurs at midbrain and forebrain levels. Any bimodal contribution to the control of complex behavior should rely most heavily on areas upstream from the hindbrain. But the crucial experiments to find these regions in the midbrain, the diencephalon or the forebrain have not yet been conducted. Anatomical and some physiological evidence points to possible locations of bimodal interactions, but careful physiological experiments using multiple stimulus types are still needed. Most existing studies used loudspeakers or vibrating dipoles only, rather than using both to uncover truly bimodal cells at higher levels of the neuraxis. As described elsewhere (Bass et al., 2001; see also the chapter by Bleckmann & Mogdans in this volume), lateral line information is conducted from nucleus medialis to the nucleus ventrolateralis (of the torus semicircularis), while inner ear lemniscal fibers ascend to the nucleus centralis (of the torus semicircularis). However, intrinisic connections between these two toral regions are not well documented, and each region could affect processing in the other via intermediary extrinsic connections. Some such interactions must exist, because multimodal physiological responses have been shown in nucleus ventrolateralis by Edds-Walton and Fay (2005). These authors also used anatomical tracers to show that bimodal cells in ventrolateralis receive inputs in some combination from nucleus medialis, the dorsal division of the descending octaval nucleus, the secondary octaval nucleus, and from perilemniscal neurons associated with the lateral lemniscus (Edds-Walton & Fay, 2005). Tracer injections within each toral region did not label the other, suggesting that intrinsic connections between ventrolateralis and centralis are minimal (see also Bass et al., 2000). The function of these bimodal ventrolateralis cells, recipients of both auditory and lateral line lemniscal inputs, is not yet known.

In contrast to these bimodal cells, Weeg and Bass (2000) described a series of intrinsic midbrain connections that could serve as points of functional integration with the midbrain nucleus preeminentialis, at least in the plainfin midshipman (*Porichthys notatus*). The organization of preeminentialis is poorly known, but the ventral portion typically receives inputs from both nucleus medialis and nucleus ventrolateralis of the torus, making this region a candidate center for mechanosensory processing (McCormick & Hernandez, 1996). Weeg and Bass (2000) showed that this region in midshipman also receives an extensive projection from nucleus centralis (an auditory region). The significance of this bimodal region within preeminentialis is unknown, as is the phylogenetic distribution of overlapping projections from both toral regions.

Ascending from toral regions, both auditory and lateral line information is carried by distinct pathways to the dorsal thalamus and the preglomerular complex, an important relay zone in teleost brains (Yamamoto & Ito, 2008). The preglomerular complex has only recently become a major target of tract-tracing studies (e.g., Northcutt, 2006), but it is the primary corticofugal center in the teleost diencephalon. The preglomerular nuclei appear to be unimodal, with discrete auditory (ventrally) and lateral line (dorsally) subdivisions within the lateral preglomerular nucleus. Both of these subdivisions project axons to the medial and lateral divisions of the pallium, but the specific target regions are distinct (von der Emde & Prechtl, 1999; Yamamoto & Ito, 2008). Similarly, field potentials recorded in pallium are largely unimodal (Prechtl et al., 1998). Thus, it appears that both the diencephalon and the forebrain process lateral line and auditory information largely independently. This suggests that higher-order control of behavior is unlikely to be based on multimodal integrations. Therefore, there may be no part of the higher nervous system that is a major integrator of both lateral line and auditory stimuli.

3.3 Mauthner Neuron Integration Between Lateral Line and Inner Ear Inputs

One place where lateral line and inner ear inputs are clearly integrated (at least in some species) is the Mauthner neurons. Mauthner neurons are large, characteristic neurons within the hindbrain reticular formation and are responsible for C-start type escape responses (Korn & Faber, 2005). The sensory input to Mauthner neurons probably varies between species, but auditory stimuli are rapid and ideally suited for threat detection. Accordingly, the main input to the Mauthner neuron is from the inner ear, but lateral line inputs are also known in both fish and amphibians (Will, 1986; Mirjany & Faber, 2011). Each inner ear end organ projects in a highly specific manner to portions of the Mauthner neuron lateral dendrite (Szabo et al., 2007). Sound pressure is a trigger of Mauthner neuron-initiated escapes in pressure sensitive fishes (Eaton & Popper, 1995). However, the kinetic sound component (acceleration) is of decisive importance at the low frequencies that are biologically most significant during predator strikes (Karlsen et al., 2004). Using a directionally well-defined stimulus at 7 Hz, Karlsen et al. (2004) showed that the fast start escape responses in the cyprinid species roach were in the general direction of the initial acceleration, and that the directional response persisted after blocking of the lateral line. However, Mirjany et al. (2011) have recently shown that the directionality of the response to a relatively high frequency (200 Hz) signal from a submerged loud speaker in a small container is dependent on lateral line inputs. Submerged loud speakers in small containers produce very complex acoustic fields, which may make it impossible for the fish to determine the direction to the source based on acceleration detection by the inner ear. On the other hand, detection of the local flow field by the lateral line might still give adequate directional information, and in the absence of lateral line function, goldfish escape directionality fell to chance levels. These authors also showed that lateral line information is used to provide context to the Mauthner neuron escape response and may influence the final stages of the escape sequence (coordinated by the rest of the hindbrain reticular formation). For example, if the goldfish was placed between the predator (a speaker) and a wall, the correct escape direction (away from the predator) would result in a collision. Intact fish rarely made such an ill-fated decision and generally modified their escape direction toward the predator or in an arc leading away from the wall; fewer than 10 % of subjects collided with the wall. After lateral line inactivation, however, collision rates significantly increased. Mirjany et al. (2011) also showed that this interaction is mediated by inhibitory connection of the anterior lateral line nerve with the Mauthner cell dendrite, proximal to the saccular inputs. Clearly, lateral line inputs to the Mauthner neuron may be taxonomically widespread and are worthy of future investigations.

The Mauthner neuron escape circuit is a site of functional integration between auditory and lateral line sensory inputs. Although the control of behavior dependent on this circuit is relatively simple, here, finally, is a part of the brain that is "listening" to multiple octavolateralis senses simultaneously. Mauthner neurons and the associated brain stem escape network may also be involved in more complex behaviors, particularly hunting and prey capture (Canfield & Rose, 1993; Saskia & Schuster, 2007). This raises the intriguing possibility that if sensory information from multiple octavolateralis channels is used together in a specific behavioral context, it may result from intersensory integration at very low levels in the neuraxis.

4 Summary and Outstanding Questions

Both physical considerations and experimental data suggest that there is amazingly little functional overlap between the inner ear and the lateral line, in spite of their common embryological origin and similar structure and physiology of the sensory cells. Evidence for interactions between these two sensory modalities in the central nervous system also seems to be scant. However, although higher level percepts informed by both lateral line and inner ear inputs may not be readily demonstrated, there are many situations in which both senses may guide behavior. Future studies of both senses should continue to question the importance of the other. Particularly in cases of object localization (including predator and prey detection, swimming in schools) and communication (particularly at short range), experiments should be designed to test the involvement of both senses.

The dichotomy between near- and far-field particle motions as stimuli for inertial hearing continues to erode (Popper & Fay, 2011), and it is clear that

Table 2 Potential neural correlates of the different modes of intermodal interactions

Type of intermodal interaction	Potential neural correlates
Synergy	Bimodal processing centers
Comparativelementation	Bimodal processing centers
	Integration at the level of the final common path
Accessory	Parallel processing pathways
	Integration at the level of motivation or behavioral state
Redundant	Parallel processing pathways
	Integration at the level of the final common path
Fractionation	Parallel processing pathways
	Integration at the level of the final common path
	Integration at higher levels of behavioral organization

sound pressure sensitivity in species with enhanced hearing lowers the auditory thresholds at higher frequencies and extends both the audible frequency range and the distance range for detection (Braun & Grande, 2008). However, the role of sound pressure sensitivity in close range detection of low-frequency sources has been little appreciated (Coombs 1994; Karlsen et al., 2004; Dailey & Braun, 2009) and should be further explored.

The distinction between canal and superficial neuromasts has been the subject of many recent studies, and the examples given above point to both unique roles and examples of complementation between the two subsystems. How is information from these two subtypes of end organs represented in the nervous system? Do separate projection paths exist or is information combined at low levels of the processing path? This same set of questions should be pursued in cases of specialized lateral line organs like those in butterflyfishes and Clupeiforms. Are there “special” neuromasts or groups of neuromasts whose information is processed separately?

As stated in the introduction, questions of overlap of sensory function can be posed in many ways, but ultimately these are questions about the umwelt of an animal. What information is used to guide behavior? Does information combine in ways that allow an animal to recognize a multidimensional source? These questions will ultimately be answered by a combination of psychophysical experiments and studies of the neurophysiology of central pathways (see Table 2), but always there remains the central question: Where in the processing stream does the percept of the multidimensional source arise?

References

Aquino, A. E., & Schaefer, S. A. (2002). The temporal region of the cranium of loricarioid catfishes (Teleostei: Siluriformes): Morphological diversity and phylogenetic significance. *Zoologische Anzeiger*, 241, 223–244.

Ayers, H. (1892). Vertebrate cephalogenesis. II. A contribution to the morphology of the vertebrate ear, with a reconsideration of its functions. *Journal of Morphology*, 6, 1–360.

Baker, C. V. H., O'Neill, P., & McCole, R.B. (2008). Lateral line, otic and epibranchial placodes: Developmental and evolutionary links? *Journal of Experimental Zoology*, 310B, 370–383.

Bass, A. H., & Ladich, F. (2008). Vocal-acoustic communication: From neurons to behavior. In J. F. Webb, A. N. Popper, & R. R. Fay (Eds.), *Fish bioacoustics* (pp. 253–278). New York: Springer.

Bass, A. H., Bodnar, D. A., & Marchaterre, M. A. (2000). Midbrain acoustic circuitry in a vocalizing fish. *Journal of Comparative Neurology*, 419, 505–531.

Bass, A. H., Bodnar, D. A., & Marchaterre, M. A. (2001). Acoustic nuclei in the medulla and midbrain of the vocalizing gulf toadfish (*Opsanus beta*). *Brain Behavior and Evolution*, 57, 63–79.

Bleckmann, H. (1994). *Reception of hydrodynamic stimuli in aquatic and semiaquatic animals*. Progress in Zoology, Vol. 41. Jena, Germany: Gustav Fischer Verlag.

Bleckmann H. (2007). The lateral line system of fish. In T. J. Hara & B. S. Zielinski (Eds.), *Sensory systems neuroscience* (Vol. 25, pp. 411–453), San Diego: Elsevier Academic Press.

Bleckmann, H., & Zelick, R. (2009). Lateral line system of fish. *International Journal of Zoology*, 4, 13–25.

Bleckmann, H., Niemann, U., & Fritzsch, B. (1991). Peripheral and central aspects of the acoustic and lateral line system of a bottom dwelling catfish, *Ancistrus* sp. *Journal of Comparative Neurology*, 314, 452– 466.

Braun, C. B. (1996). The sensory biology of the living jawless fishes: A phylogenetic assessment. *Brain Behavior and Evolution*, 48, 262–276.

Braun, C. B. (2009). Evolution of the mechanosensory and electrosensory lateral line systems. In M. Binder, N. Hirokawa, & U. Windhorst (Eds.), *Encyclopedia of neuroscience* (pp. 1367–1375). New York: Springer.

Braun, C. B., & Coombs, S. (2010). Vibratory sources as compound stimuli for the octavolateralis systems: Dissection of specific stimulation channels using multiple behavioral approaches. *Journal of Experimental Psychology-Animal Behavior Processes*, 36, 243–257.

Braun, C. B., & Grande, T. (2008). Evolution of peripheral mechanisms for the enhancement of sound reception. In J. F. Webb, A. N. Popper, & R. R. Fay (Eds.), *Fish bioacoustics* (pp. 99–144). New York: Springer.

Braun, C. B., Coombs, S. & Fay, R. R. (2002). What is the nature of multisensory interaction between octavolateralis sub-systems? *Brain*, *Behavior and Evolution*, 59, 162–176.

Brown, A. D., Mussen, T. D., Sisneros, J. A., & Coffin, A. B. (2012). Reevaluating the use of aminoglycoside antibiotics in behavioral studies of the lateral line. *Hearing Research*, 271, 1–4.

Bullock, T. H., & Corwin, J. T. (1979). Acoustic evoked activity in the brain in sharks. *Journal of Comparative Physiology A*, 129, 223–234.

Canfield, J., & Rose, G. (1993). Activation of Mauthner neurons during prey capture. *Journal of Comparative Physiology A*, 172, 611–618.

Casper, B. M., & Mann, D. A. (2006a). Dipole hearing measurements in elasmobranch fishes. *Journal of Experimental Biology*, 210, 75–81.

Casper, B. M., & Mann, D. A. (2006b). Evoked potential audiograms of the nurse shark (*Ginglymostoma cirratum*) and the yellow stingray (*Urobatis jamaicensis*). *Environmental Biology Fishes*, 76, 101–108.

Catania, K. C., Leitch, D. B., & Gauthier, D. (2010). Function of the appendages in tentacled snakes (*Erpeton tentaculatus*). *Journal of Experimental Biology*, 213, 359–367.

Chapman, C. J., & Hawkins, A. D. (1973). A field study of hearing in the cod, *Gadus morhua* L. *Journal of Comparative Physiology*, 85, 147–167.

Chapman, C. J., & Sand, O. (1974). Field studies of hearing in two species of flatfish *Pleuronectes platessa* (L.) and *Limanda limanda* (L.) (Family Pleuronectidae). *Comparative Biochemistry and Physiology A*, 47, 371–385.

Coleman, S. (2009). Taxonomic and sensory biases in the mate-choice literature: There are far too few studies of chemical and multimodal communication. *Acta Ethologica*, 12, 45–48.

Conley, R. A., & Coombs, S. (1998). Dipole source localization by mottled sculpin. III. Orientation after site-specific, unilateral denervation of the lateral line system. *Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology*, 183, 335–344. doi:10.1007/s003590050260

Coombs, S. (1994). Near field detection of dipole sources by the goldfish (*Carassius auratus*) and the mottled sculpin (*Cottus bairdi*). *Journal of Experimental Biology*, 190, 109–129.

Coombs, S., & Janssen, J. (1989). Peripheral processing by the lateral line system of the mottled sculpin (*Cottus bairdi*). In S. Coombs, P. Görner, & H. Münz (Eds.), *The mechanosensory lateral line: Neurobiology and behavior* (pp. 299–322). New York: Springer.

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

Coombs, S., & Montgomery, J. C. (1999). The enigmatic lateral line system. In R. R. Fay & A. N. Popper (Eds.), *Comparative hearing: Fish and amphibians* (pp. 319–262). New York: Springer.

Coombs, S., & Montgomery, J. (2005). Comparing octavolateralis sensory systems: What can we learn? In T. H. Bullock, C. D. Hopkins, A. N. Popper, & R. R. Fay (Eds.), *Electroreception* (pp. 318–359). New York: Springer.

Coombs, S., & Patton, P. (2009). Lateral line stimulation patterns and prey orienting behavior in the Lake Michigan mottled sculpin (*Cottus bairdi*). *Journal of Comparative Physiology A*, 195, 279–297.

Coombs, S., Janssen, J., & Montgomery, J. (1992). Functional and evolutionary implications of peripheral diversity in lateral line systems. In R. R. Fay & A. N. Popper (Eds.), *Evolutionary biology of hearing* (pp. 267–294). New York: Springer.

Coombs, S., Hastings, M., & Finneran, J. (1996). Modeling and measuring lateral line excitation patterns to changing dipole source locations. *Journal of Comparative Physiology A*, 178, 359–371.

Coombs, S., Braun, C. B., & Donovan B. (2001). Orienting response of Lake Michigan mottled sculpin is mediated by canal neuromasts. *Journal of Experimental Biology*, 204, 337–348.

Coombs, S., Fay, R. R., & Elepfandt, A. (2010). Dipole source encoding and tracking by the goldfish auditory system. *Journal of Experimental Biology*, 213, 3536–3547.

Dailey, D. D., & Braun, C. B. (2009). The detection of pressure fluctuations, sonic audition, is the dominant mode of dipole-source detection in goldfish (*Carassius auratus*). *Journal of Experimental Psychology: Animal Behavior Processes*, 35, 212–223.

Dailey, D. D., & Braun, C. B. (2011). Perception of frequency, amplitude, and azimuth of a vibratory dipole source by the octavolateralis system of goldfish (*Carasssius auratus*). *Journal of Comparative Psychology*, 125, 286–295.

Denton, E. J., & Blaxter, J. H. S. (1976). The mechanical relationships between the clupeid swimbladder, inner ear and lateral line. *Journal of the Marine Biology Association UK*, 56, 787–807.

Denton, E. J., & Gray, J. A. B. (1982). The rigidity of fish and patterns of lateral line stimulation. *Nature*, 297, 679–681.

Denton, E. J., & Gray, J. A. B. (1983). Mechanical factors in the excitation of clupeid lateral lines. *Proceedings of the Royal Society of London B*: *Biological Sciences*, 218, 1–26.

Denton, E. J., & Gray, J. A. B. (1988). Mechanical factors in the excitation of the lateral line of fishes. In J. Atema, R. R. Fay, A. N. Popper & W. N. Tavolga (Eds.), *Sensory biology of aquatic animals* (pp. 595–618). New York: Springer-Verlag.

de Vries, H. L. (1950). The mechanics of labyrinth otoliths. *Acta Oto-Laryngologica*, 38, 262–273.

Dijkgraaf, S. (1963). The Functioning and significance of the lateral-line organs. *Biological Review*, 38, 51–105.

Eaton, R., & Popper, A. N. (1995). The octavolateralis system and Mauthner cell: Interactions and questions. *Brain Behavior and Evolution*, 46, 124–130.

Edds-Walton, P. L., & Fay, R. R. (2005). Projections to bimodal sites in the torus semicircularis of the toadfish, *Opsanus tau*. *Brain Behavior and Evolution*, 66, 73–87.

Enger, P. S., Kalmijn, A. J., & Sand, O. (1989). Behavioral identification of lateral line and inner ear function. In S. Coombs, P. Görner, & H. Münz (Eds.), *The mechanosensory lateral line: Neurobiology and behavior* (pp. 575–587). New York: Springer-Verlag.

Faucher, K., Parmentier, E., Becco, C., Vandewalle, N., & Vandewalle, P. (2010). Fish lateral system is required for accurate control of shoaling behaviour. *Animal Behaviour*, 79, 679–687.

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

Fay, R. R. (1988). *Hearing in vertebrates: A psychophysics databook*. Winnetka, IL: Hill-Fay Associates.

Fay, R. R., & Popper, A. N. (1974). Acoustic stimulation of the ear of goldfish (*Carrassius auratus*). *Journal of Experimental Biology*, 61, 243–260.

Fay, R. R., Kendall, J. I., Popper, A. N., & Tester, A. L. (1974). Vibration detection by the macula neglecta of sharks. *Comparative Biochemistry and Physiology*, 47A, 1235–1240.

Forrest, T. G., Miller, G. L., & Zagar, J. R. (1993). Sound propagation in shallow water: Implications for acoustic communication by aquatic animals. *Bioacoustics*, 4, 259–270.

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. *Journal of Experimental Biology*, 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. *Journal of Experimental Biology*, 203, 1193–1200.

Harris, G. G. (1964). Considerations on the physics of sound production by fishes. In W. N. Tavolga (Ed.), *Marine bio-acoustics* (pp. 233–247). Oxford: Pergamon Press.

Hassan, E. S. (1986). On the discrimination of spatial intervals by the blind cave fish (*Anoptichthys jordani*). *Journal of Comparative Physiology A*, 159, 701–710.

Hoekstra, D., & Janssen, J. (1985). Non-visual feeding behavior of the mottled sculpin, *Cottus bairdi*, in Lake Michigan. *Environmental Biology of Fishes*, 12, 111–117.

Hoekstra, D., & Janssen, J. (1986). Lateral line receptivity in the mottled sculpin (*Cottus bairdi*). *Copeia*, 1986, 91–96.

Janssen, J. (1997). Comparison of response distance to prey via the lateral line in the ruffe and yellow perch. *Journal of Fish Biology*, 51, 921–930.

Kalmijn, A. J. (1988). Hydrodynamic and acoustic field detection. In J. Atema, R. R. Fay, A. N. Popper & W. N. Tavolga (Eds.), *Sensory biology of aquatic animals* (pp. 83–130). New York: Springer-Verlag.

Kalmijn, A. J. (1989). Functional evolution of lateral line and inner ear sensory systems. In S. Coombs, P. Görner, & H. Münz (Eds.), *The mechanosensory lateral line: Neurobiology and behavior* (pp.187–216). New York: Springer-Verlag.

Karlsen, H. E. (1992a). The inner ear is responsible for detection of infrasound in the perch (*Perca fluviatilis*). *Journal of Experimental Biology*, 171, 163–172.

Karlsen, H. E. (1992b). Infrasound sensitivity in the plaice (*Pleuronectes platessa*). *Journal of Experimental Biology*, 171, 173–187.

Karlsen, H. E., & Sand, O. (1987). Selective and reversible blocking of the lateral line in freshwater fish. *Journal of Experimental Biology*, 133, 249–267.

Karlsen, H. E., Piddington, R. W., Enger, P. S., & Sand, O. (2004). Infrasound initiates directional fast-start escape responses in juvenile roach *Rutilus rutilus*. *Journal of Experimental Biology*, 207, 4185–4193.

Knudsen, F. R., Enger, P. S., & Sand, O. (1994). Avoidance responses to low frequency sound in downstream migrating Atlantic salmon smolt, *Salmo salar* L. *Journal of Fish Biology*, 45, 227–233.

Knudsen, F. R., Schreck, C. B., Knapp, S. M., Enger, P. S., & Sand, O. (1997). Infrasound produces flight and avoidance responses in Pacific juvenile salmonids. *Journal of Fish Biology*, 51, 824–829.

Korn, H., & Faber, D. S. (2005). The Mauthner cell half a century later: A neurobiological model for decision-making? *Neuron*, 47, 13–28.

Ladich, F., & Myrberg, A. (2006). Agonistic behavior and acoustic communication. In F. Ladich, S. Collin, P. Moller, & B. Kapoor (Eds.), *Communication in fishes* (pp. 121–148). Enfield, NH: Science Publishers.

Larsell, O. (1967). *The comparative anatomy and histology of the cerebellum from Myxinoids through birds*. Minneapolis, MN: University of Minnesota Press.

Larsson, M. (2009). Possible functions of the octavolateralis system in fish schooling. *Fish and Fisheries*, 10, 344–353.

Liang, X. F., Liu, J. K., & Huang, B. Y. (1998). The role of sense organs in the feeding behavior of Chinese perch. *Journal of Fish Biology*, 52, 1058–1067.

Maruska, K. P., & Tricas, T. C. (2009). Central projections of octavolateralis nerves in the brain of a soniferous damselfish (*Abudefduf abdominalis*). *Journal of Comparative Neurology*, 512, 628–650.

McCormick, C. A. (1992). Evolution of central auditory pathways in anamniotes. In D.B. Webster, R. R. Fay, & A. N. Popper (Eds.), *The evolutionary biology of hearing* (pp. 323–350). New York: Springer-Verlag.

McCormick, C. A. (1999). Anatomy of the central auditory pathways of fish and amphibians. In R. R. Fay & A. N. Popper (Eds.), *Comparative hearing: Fish and amphibians* (pp. 155–217). New York: Springer-Verlag.

McCormick, C. A., & Hernandez, D. V. (1996). Connections of octaval and lateral line nuclei of the medulla in the goldfish, including the cytoarchitecture of the secondary octaval population in goldfish and catfish. *Brain Behavior and Evolution*, 47, 113–137.

McCormick, C. A., & Wallace, A. C. (2012). Otolith end organ projections to auditory neurons in the descending octaval nucleus of the goldfish, *Carassius auratus*: A confocal analysis. *Brain Behavior and Evolution*, 80, 41–63.

Miersch, L, Hanke, W., Wieskotton, S., Hanke, F. D., Oeffner, J., Leder, A., Brede, M., Witte, M., & Dehnhardt, G. (2011). Flow sensing by pinniped whiskers. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 366, 3077–3084.

Mirjany, M., & Faber, D. S. (2011). Characteristics of the anterior lateral line nerve input to the Mauthner cell. *Journal of Experimental Biology*, 214, 3368–3377.

Mirjany, M., Preuss, T., & Faber, D. S. (2011). Role of the lateral line mechanosensory system in directionality of goldfish auditory evoked escape response. *Journal of Experimental Biology*, 214, 3358–3367.

Modrell, M., Bemis, W. E., Northcutt, R. G., Davis, M., & Baker, C. (2011). Electrosensory ampullary organs are derived from lateral line placodes in bony fishes. *Nature Communications*, 2, 496.

Montgomery, J. (1989). Lateral line detection of planktonic prey. In S. Coombs, P. Görner, & H. Münz (Eds.), *The mechanosensory lateral line: Neurobiology and behavior* (pp. 561–574). New York: Springer-Verlag.

Montgomery, J. C., Coombs, S., Conley, R. A. & Bodznick, D. (1995). Hindbrain sensory processing in lateral line, electrosensory and auditory systems: A comparative overview of anatomical and functional similarities. *Auditory Neuroscience*, 1, 207–231.

Montgomery, J. C., Baker, C. F., & Carton, A. G. (1997). The lateral line can mediate rheotaxis in fish. *Nature*, 389, 960–963.

Montgomery, J., MacDonald, F., Baker, C. F., & Carton, A. G. (2002). Hydrodynamic contributions to multimodal guidance of prey capture behavior in fish. *Brain Behavior and Evolution*, 29, 190–198.

Montgomery, J. C., McDonald, F., Baker, C. F., Carton, A. G., & Ling, N. (2003). Sensory integration in the hydrodynamic world of rainbow trout. *Proceedings of the Royal Society of London B: Biological Sciences*, 270, S195–S197.

Münz H. (1989). Functional organization of the lateral line periphery. In S. Coombs, P. Görner, & H. Münz (Eds.), *The mechanosensory lateral line: Neurobiology and evolution* (pp. 285–298). New York: Springer-Verlag.

Myrberg, A. (2001). The acoustical biology of elasmobranchs. *Environmental Biology Fishes*, 60, 31–45.

Nauroth, I. E., & Mogdans, J. (2009). Goldfish and oscars have comparable responsiveness to dipole stimuli. *Naturwissenschaften*, 96, 1401–1409.

Nelson, M. E., MacIver, M. A., & Coombs, S. (2002). Modeling electrosensory and mechanosensory images during the predatory behavior of weakly electric fish. *Brain Behavior and Evolution*, 59, 199–210.

New, J. G., Fewkes, L. A., & Khan, A. N. (2001). Strike-feeding behavior in the muskellunge Esox masquinongy: Contributions of lateral line and visual sensory systems. *Journal of Experimental Biology*, 204, 1207–1221.

Northcutt, R. G. (1996). The origin of craniates: Neural crest, neurogenic placodes, and homeobox genes. *Israeli Journal of Zoology*, 42, S273–S313.

Northcutt, R. G. (2006). Connections of the lateral and medial divisions of the goldfish telencephalic pallium. *Journal of Comparative Neurology*, 494, 903–943.

Northcutt, R. G., & Gans, C. (1983). The genesis of neural crest and epidermal placodes: A reinterpretation of vertebrate origins. *Quarterly Review of Biology*, 58, 1–28.

Palmer, L. M., Deffenbaugh, M., & Mensinger, A. F. (2005). Sensitivity of the anterior lateral line to natural stimuli in the oyster toadfish, *Opsanus tau* (Linnaeus). *Journal of Experimental Biology*, 208, 3441–3450.

Partan, S. R., & Marler, P. (2005). Issues in the classification of multimodal communication signals. *American Naturalist*, 166, 231–245.

Partridge, B. L., & Pitcher, T. J. (1980). The sensory basis of fish schools: Relative roles of lateral line and vision. *Journal of Comparative Physiology A*, 135, 315–325.

Pitcher, T. J., Partridge, B. L., & Wardle, C. S/ (1976). A blind fish can school. *Science*, 194, 963–965.

Plachta, D. T. T., Hanke, W., & Bleckmann, H. (2003). A hydrodynamic topographic map in the midbrain of goldfish *Carassius auratus*. *Journal of Experimental Biology*, 206, 3479–3486.

Platt, C., Popper, A. N., & Fay, R. R. (1989). The ear as part of the octavolateralis system. In S. Coombs, P. Görner, & H. Münz (Eds.), *The mechanosensory lateral line: Neurobiology and behavior* (pp. 633–651). New York: Springer-Verlag.

Pluta, S. R., & Kawasaki, M. (2008). Multisensory enhancement of electromotor responses to a single moving object. *Journal of Experimental Biology*, 211, 2919–2930.

Pohlmann K., Grasso, F. W., & Breithaupt, T. (2001). Tracking wakes: The nocturnal predatory strategy of piscivorous catfish. *Proceedings of the National Academy of Sciences of the USA*, 98, 7371–7374.

Pohlmann, K., Atema, J., & Breithaupt, T. (2004). The importance of the lateral line in nocturnal predation of piscivorous catfish. *Journal of Experimental Biology*, 207, 2971–2978.

Popper, A. N. (1977). A scanning electron microscopic study of the sacculus and lagena in the ears of fifteen species of teleost fishes. *Journal of Morphology*, 153, 397–417.

Popper, A. N., & Fay, R. R.(2011). Rethinking sound detection by fishes. *Hearing Research*, 273, 25–36.

Popper, A. N., Fay, R. R., Platt, C., & Sand, O. (2003). Sound detection mechanisms and capabilities of teleost fishes. In S. P. Collin & J. N. Marshall (Eds.), *Sensory processing in aquatic environments* (pp. 3–38). New York: Springer.

Popper, A. N., Plachta, D. T., Mann, D. A., & Higgs, D. (2004). Response of clupeid fish to ultrasound: A review. *Ices Journal of Marine Science*, 61, 1057–1061.

Prechtl, J. C., von Der Emde, G., Wolfart, J., Karamürsel, S., Akoev, G. N., & Andrianov, Y. N. (1998). Sensory processing in the pallium of a mormyrid fish. *Journal of Neuroscience*, 18, 7381–7393.

Reep, R. L., Gaspard, J. C., Sarko, D., Rice, F. L., Mann, D. A., & Bauer, G. B. (2011). Manatee vibrissae: Evidence for a "lateral line" function. *Annals of the New York Academy of Sciences*, 1225, 101–109.

Richardson, E. G. (1954). The relations between acoustics and hydrodynamics. *Journal of the Acoustical Society of America*, 26, 615–617.

Rogers, P. H., & Cox, M. (1988). Underwater sound as a biological stimulus. In J. Atema, R. R. Fay, A. N. Popper, & W. N. Tavolga (Eds.), *Sensory biology of aquatic animals* (pp. 131–149). New York: Springer-Verlag.

Sand, O. (1981). The lateral-line and sound reception. In W. N. Tavolga, A. N. Popper, & R. R. Fay (Eds.), *Hearing and sound communication in fishes* (pp. 459–480). New York: Springer-Verlag.

Sand, O. (1984). Lateral line systems. In L. Bolis, R. D. Keynes, & S. H. P. Maddrell (Eds.), *Comparative physiology of sensory systems* (pp. 3–32). Cambridge, U.K.: Cambridge University Press.

Sand, O., & Enger, P. S. (1973). Evidence for an auditory function of the swim bladder in the cod. *Journal of Experimental Biology*, 59, 405–414.

Sand, O., & Hawkins, A. D. (1973). Acoustic properties of the cod swim bladder. *Journal of Experimental Biology*, 58, 797–820.

Sand, O., & Karlsen, H. E. (1986). Detection of infrasound by the Atlantic cod. *Journal of Experimental Biology*, 125, 197–204.

Sand, O., & Karlsen, H. E. (2000). Detection of infrasound and linear acceleration in fishes. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 355, 1295–1298.

Sand, O., & Bleckmann, H. (2008). Orientation to auditory and lateral line stimuli. In J. F. Webb, A. N. Popper, & R. R. Fay (Eds.), *Fish bioacoustics* (pp. 183–231). New York: Springer.

Saskia, W., & Schuster, S. (2007). The predictive start of a hunting archer fish: A flexible and precise motor pattern performed with the kinematics of an escape C-start. *Journal of Experimental Biology*, 210, 311–324.

Satou, M., Takeuchi, H. A., Nishii, J., Tanabe, M., Kitamura, S., & Okumoto, N. (1994a). Behavioral and electrophysiological evidences that the lateral line is involved in the intersexual vibrational communication of the himé salmon (landlocked red salmon, *Oncorhynchus nerka*). *Journal of Comparative Physiology*, 174, 539–549.

Satou, M., Takeuchi, H. A., Takei, K., Hasegawa, T., Matsushima, T., & Okumoto, N. (1994b). Characterization of vibrational and visual signals which elicit spawning behavior in the male himé salmon (landlocked red salmon, *Oncorhynchus nerka*). *Journal of Comparative Physiology*, 174, 527–537.

Schroeder, C., & Foxe, J. (2005). Multisensory contributions to low-level, 'unisensory' processing. *Current Opinion in Neurobiology*, 15, 454–458.

Schuijf, A., & Buwalda, R. J. A. (1980). Sound localization: A major problem in fish acoustics. In A. N. Popper & R. R. Fay (Eds.), *Comparative studies of hearing in vertebrates* (pp. 43–78). New York: Springer-Verlag.

Schuster, S. (2006). Integration of the electrosense with other senses: Implications for communication. In F. Ladich, S. P. Collin, P. Moller, & B. G. Kapoor (Eds.), *Communication in fishes* (pp. 781–804). Enfield, NH: Science Publishers.

Schwalbe, M. A. B., Bassett, D. K., & Webb, J. F. (2012). Feeding in the dark: Lateral-line-mediated prey detection in the peacock cichlid *Aulonocara stuartgranti*. *Journal of Experimental Biology*, 215, 2060–2071.

Skals, N., Anderson, P., Kanneworff, M., Lofstedt, C., & Surlykke, A. (2005). Her odours make him deaf: Crossmodal modulation of olfaction and hearing in a male moth. *Journal of Experimental Biology*, 208, 595–601.

Song, J., Yan, H. Y., & Popper, A. N. (1995). Damage and recovery of hair cells in fish canal (but not superficial) neuromasts after gentamicin exposure. *Hearing Research*, 91, 63–71.

Sonny, D., Knudsen, F. R., Enger, P. S., Kvernstuen, T., & Sand, O. (2006). Reactions of cyprinids to infrasound in a lake and at the cooling water inlet of a nuclear power plant. *Journal of Fish Biology*, 69, 735–748.

Stoffregen, T. A., & Bardy, B. G. (2001). On specification and the senses. *Behavioral Brain Sciences*, 24, 195–261.

Szabo, T. M., McCormick, C. A., & Faber, D. S. (2007). Otolith endorgan input to the Mauthner neuron in the goldfish. *Journal of Comparative Neurology*, 505, 511–525.

Todd, N. P. M., Rosengren, S. M., & Colebatch, J. G. (2008). Tuning and sensitivity of the human vestibular system to low-frequency vibration. *Neuroscience Letters*, 444, 36–41.

Tomchik, S. M., & Lu, Z. M. (2005). Octavolateral projections and organization in the medulla of a teleost fish, the sleeper goby (*Dormitator latifrons*). *Journal of Comparative Neurology*, 481, 96–117.

Tricas, T. C., Kajiura, S. M., & Kosaki, R. K. (2006). Acoustic communication in territorial butterflyfish: Test of the sound production hypothesis. *Journal of Experimental Biolog*y, 209, 4994–5004.

van Bergeijk, W. A. (1964). Directional and non-directional hearing in fish. In W. N. Tavolga (Ed.), *Marine bio-acoustics* (pp. 185–204). Oxford: Pergamon Press.

van Trump, W. J., Coombs, S., Duncan, K., & McHenry, M. J. (2010). Gentamicin is ototoxic to all hair cells in the fish lateral line system. *Hearing Research*, 261, 42–50.

von Campenhausen, C., Riess, I., & Weissert, R. (1981). Detection of stationary objects by the blind cavefish *Anoptichthys jordani* (Characidae). *Journal of Comparative Physiology A*, 143, 369–374.

von der Emde, G., & Prechtl, J. C. (1999). Anatomical connection of auditory and lateral line areas of the dorsal telencephalon (Dm) in the osteoglossomorph teleost, *Gnathonemus petersii*. *Brain Research*, 818, 355–367.

Webb, J. F. (1998). The laterophysic connection: A unique link between the swim bladder and the lateral-line system in *Chaetodon* (Perciformes: Chaetodontidae). *Copeia*, 1998, 1032–1036.

Webb, J. F., & Smith, W. L. (2000). The laterophysic connection in chaetodontid butterflyfish: Morphological variation and speculations on sensory function. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 355, 1125–1129.

Webb, J. F., Herman, J. L., Woods, C. F., & Ketten, D. R. (2010). The ears of butterflyfishes (Chaetodontidae): 'Hearing generalists' on noisy coral reefs? *Journal of Fish Biology*, 77, 1406–1423.

Weeg, M. S. & Bass, A. H. (2000). Central lateral line pathways in a vocalizing fish. *The Journal of Comparative Neurology*, 418, 41–64.

Will, U. (1986). Organization and projections of the area octavolateralis in amphibians. In B. Fritzsch, M. Ryan, W. Wilczynski, T. Hetherington, & W. Walkowiak (Eds.), *The evolution of the amphibian auditory system* (pp. 185–208). New York: John Wiley & Sons.

Wilson, M., Montie, E. W., Mann, K. A., & Mann, D. A. (2009). Ultrasound detection in the Gulf menhaden requires gas-filled bullae and an intact lateral line. *Journal of Experimental Biology*, 212, 3422–3427.

Windsor, S. P., Tan, D., & Montgomery, J. C. (2008). Swimming kinematics and hydrodynamic imaging in the blind Mexican cavefish (*Astyanax fasciatus*). *Journal of Experimental Biology*, 211, 2950–2959.

Windsor, S. P., Norris, S. E., Cameron, S. M., Mallinson, G. D., & Montgomery, J. C. (2010). The flow fields involved in hydrodynamic imaging by blind Mexican cave fish (*Astyanax fasciatus*). Part I: Open water and heading towards a wall. *Journal of Experimental Biology*, 213, 3819–3831.

Yamamoto, N., & Ito, H. (2005). Fiber connections of the anterior preglomerular nucleus in cyprinids with notes on telencephalic connections of the preglomerular complex. *Journal of Comparative Neurology*, 491, 212–233.

Yamamoto, N., & Ito, H. (2008). Visual, lateral line, and auditory ascending pathways to the dorsal telencephalic area through the rostrolateral region of the lateral preglomerular nucleus in cyprinids. *Journal of Comparative Neurology*, 508, 615–647.