The Gems of the Past: A Brief History of Lateral Line Research in the Context of the Hearing Sciences

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1 Introduction

In this day and age of Internet search engines, information overload, online journals, and pressures to publish at record-breaking paces, it is somewhat dismaying, but perhaps understandable, that the contributions of our academic forefathers are too often lost and forgotten. Yet, as any true scholar knows, the older literature contains many "gems" that young investigators coming into their fields would do well to read and understand. In reading some of these classics, they will be surprised as well as inspired by the many insights and research ideas that the older literature contains and that are ripe for the plucking. One such example in lateral line research is the classic 50-page review paper by Dijkgraaf (1962), a veritable gold mine of information for anyone interested in the lateral line. The goal of this chapter is to inspire an interest in the classics by identifying and highlighting some of the key players, discoveries, and debates that have shaped our understanding of lateral line function, especially in the context of the hearing sciences. More details on the

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history of the field can be found in several early reviews (Parker, 1904; Johnson, 1917; Wright, 1951; Dijkgraaf, 1962) and two lateral line conference proceedings (Cahn, 1967; Coombs et al., 1989).

2 Early Notions on the Sensory Nature and Function of the Lateral Line

The earliest description of the lateral line was published in the 17th century by Stenonis (aka Stensen, Steno; 1664), who, according to Leydig (1868), described lateral line structures (canal pores) in elasmobranchs (sharks, skates, and rays). A few years later, Lorenzini (1678) reported additional pored structures that would later be called the ampullae of Lorenzini. The notion that these and other superficially located ampullary and tuberous organs on freshwater bony fishes might have an entirely different function from that of the "ordinary" lateral line did not become clearly evident until the discovery of electroreceptors nearly three centuries later (Lissmann & Machin, 1958; Murray, 1960; Bullock et al., 1961). Thus, throughout most of scientific history, mechanosensory and electrosensory organs have been lumped together under the lateral line umbrella as if they were one and the same system. Even though there is now ample evidence that each system is unique in its own right, responding to fundamentally different types of stimuli and with separate pathways and processing regions in the brain (McCormick, 1982), the term "lateral line" is still used in connection with both systems (e.g., lateral line nerves that innervate electroreceptors). This is, in no small part, due to the close developmental and evolutionary ties between the two systems (see the chapter by Wullimann & Grothe). Nevertheless, the term lateral line is becoming increasingly reserved for the mechanosensory component alone, and this is the convention adopted here and in most of the other chapters in this volume.

Likely biased by his own research interests in glands and lymph nodes, Stenonis (1664) proposed slime (mucus) production as the main function of the lateral line. This view of lateral line function remained essentially unchanged for the next 200 years until the German anatomist Franz Leydig published his influential paper on the "sixth sense" (Leydig, 1868) (Fig. 1). Leydig's paper reviewed the anatomical evidence for the sensory nature of the lateral line, beginning with his discovery of large, easily identified sense organs in the wide head canals of the ruffe (*Gymnocephalus cernua*), which Leydig called "Nervenknöpfe" (nerve buttons; Fig. 2) (Leydig, 1850, 1851), and culminating with the discovery by Schulze (1861) (Fig. 1) of a second type of sense organ ("Seitenorgane") on the skin surface of fish and aquatic amphibians (Fig. 3). These two types of sense organs are now recognized as belonging to two distinct submodalities of the lateral line: canal (CN) and superficial (SN) neuromasts. Each submodality can be distinguished in terms of not only developmental and morphological characteristics (chapter by

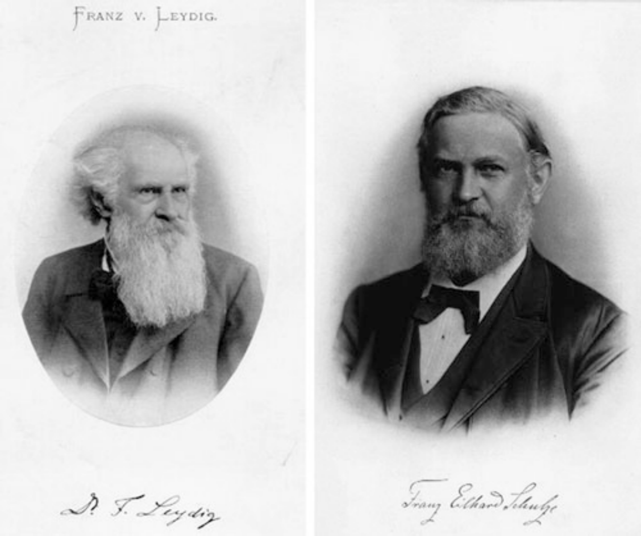

Fig. 1 Two 19th-century pioneers—Franz Leydig and Franz Schulze—who provided some of the first anatomical evidence for the sensory nature of lateral line sense organs, as illustrated in Figs. 2 and 3

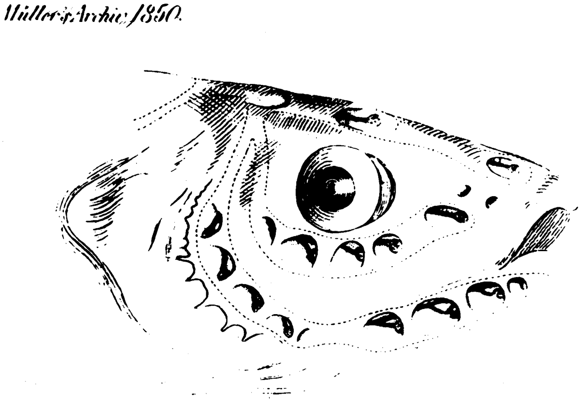

Fig. 2 Large canal neuromasts (Nervenknöpfe) on the head of the ruffe (*Gymnocephalus cernua*). The canal roof has been removed to reveal the underlying neuromasts in the supraorbital, infraorbital, and preopercular-mandibular canals. [From Leydig (1850) as reprinted in Dijkgraaf (1989)]

Webb), but also function, as evidenced from hydrodynamic (chapter by McHenry & Liao), biomechanical (chapter by van Netten & McHenry), physiological (chapter by Chagnaud & Coombs), and behavioral (chapter by Montgomery, Bleckmann, & Coombs) studies.

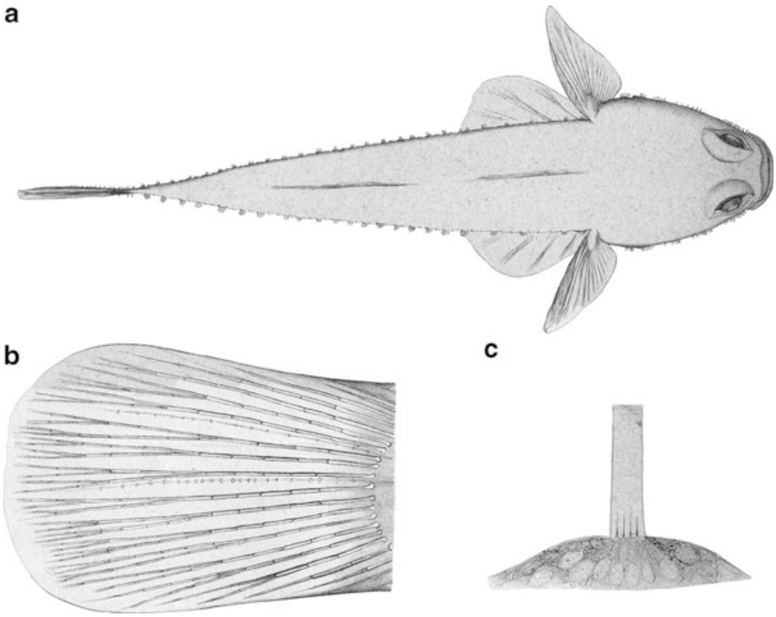

Fig. 3 Superficial neuromasts (Seitenorganröhren) along the lateral surface of the trunk (as seen from a dorsal view, **a**) and along the caudal fin rays (**b**) of the sand goby (*Pomatoschistus minutus*). In (**c**), a cephalic neuromast from a 16-mm larval *Triton taeniatus* (current genus species unknown) illustrating the pear-shaped sensory cells (hair cells) with their apical hairs projecting into an overlying cupula. [From Schulze (1850)]

3 The Big Debate: Is the Lateral Line a Sense of Hearing, Touch, or Something in Between?

When Schulze (1861) identified the features (pear-shaped sensory cells innervated by nerve fibers) that revealed the sensory nature of his Seitenorgane (Fig. 3b), he also described for the first time the fragile and nearly translucent structure (cupula) that covered them (Fig. 3b). Many years later, Schulze made the important discovery that the cupulae of these SNs could be displaced by weak water currents, leading him to suggest that water motions, but perhaps also low-frequency sound waves, were the relevant stimuli (Schulze, 1870). Following up on this idea, Dercum (1879) proposed that even CNs could be stimulated by water motions over the skin surface (and canal pores) by virtue of induced fluid motions inside the canals. It is now known from the classic work of Sir Eric Denton and Sir John Gray (reviewed in Denton and Gray, 1988, 1989) that accelerating flows (or, in other words, pressure differences) along canal pores cause fluid movements inside the canal (see also the chapters by McHenry & Liao and Chagnaud & Coombs).

The first experimental evidence that the lateral line responds to flowing water, what Sven Dijkgraaf (1989) would later call the "true" function of the lateral line, was provided by the German ichthyologist Bruno Hofer (1908). Hofer observed the ability of blinded northern pike (*Esox lucius*) to orient to water currents and to avoid collisions with the walls of the aquarium. Both of these behaviors were abolished when the lateral line nerves were cut. From these experiments, Hofer concluded that fish use their lateral line to “feel at a distance,” and further that rheotaxis (orientation to water currents) must be the principal behavioral function of the lateral line. Dijkgraaf (1934) challenged the rheotaxis idea after repeating the experiments of Lyon (1904) to confirm that rheotaxis relied mainly on visual and, to a lesser extent, tactile senses, but not the lateral line. Ironically, some 60 years later, Montgomery et al. (1997) discovered a subtle role for lateral line SNs, but not CNs, in the ability of fish to orient to slow but not fast currents.

Unfortunately, Hofer’s little-known finding (having been published in an obscure fisheries journal) was overlooked (Dijkgraaf, 1989), and the prevailing view during most of the 19th and well into the 20th century was that the lateral line was an accessory organ of hearing specialized for the detection of low-frequency sound. Lowenstein (1967) credits the pivotal review paper of Mayser (1882) for the popularity of this view, which persisted for many decades, despite evidence that the inner ear and not the lateral line mediated behavioral responses of fish to low-frequency sound (von Frisch, 1923; von Frisch & Stetter, 1932). According to Lowenstein (1967), Mayser was a physician at the County Psychiatric Hospital in Munich, who, after an extensive review of the literature, proclaimed that “the mucous canals of fishes are nothing else than an accessory hearing organ spread over the whole body surface” (p. 5).

It is worth noting that the primary support for a hearing function of the lateral line was the shared anatomical characteristics of the two systems, including receptor cell structure (e.g., Schulze, 1861), close proximity during development (Wilson & Mattocks, 1897), and nerve fibers that appeared to originate from the same area of the hindbrain, the so-called acoustic tubercle (Mayser, 1882; see also the chapter by Braun & Sand). The evidence for a common termination site for both lateral line (including electrosensory component) and auditory nerve fibers was later augmented by the classic neuroanatomical studies of Pearson (1936a, b), Larsell (1967), and others on the “acousticolateralis area” of the hindbrain (reviewed in the chapter by Wullimann & Grothe).

Direct physiological evidence for lateral line responses to “sound” was not provided until the classic study of Harris and van Bergeijk (1962) on the responses of lateral line nerve fibers to the low-frequency vibrations of a nearby sound source. Their paper was very instructive, not only because it provided direct physiological evidence of responsiveness, but also because it provided additional insight as to the physical nature of the stimulus likely to excite the lateral line. Harris and van Bergeijk (1962) emphasized for biologists what was already known by physicists: that in the near field of a sound source, water behaves as if it is both compressible and incompressible, and thus both water motions (bulk flow) and propagated sound pressure waves are generated. Given that the near-field duality extends over distances significantly greater than a typical fish body length, especially at low frequencies (e.g., ~2 m at 100 Hz and 20 m at 10 Hz), the near field takes on additional biological significance for fish. Knowing that the lateral line is actually responding to the local incompressible flow rather than the pressure wave, as Dijkgraaf (1934) and also Harris and van Berjeijk (1962) correctly assumed, the argument about the function of the lateral line and what fish "perceive" through the lateral line now becomes one of semantics and how sound and hearing are defined. If sound is defined strictly as propagated pressure waves, then it would be difficult to conclude that the "typical"[1] lateral line is an accessory organ of hearing. If, however, sound close to the source is defined as a combination of both flow and propagated pressure waves, then the idea of the lateral line as an accessory organ of hearing is quite plausible.[1]

van Bergeijk (1967) was careful to point out that although he and Harris could not "say very much about *what* the fish perceives" (p. 73) from their physiological studies, they could at the very least, say something about "the class of stimuli that fish *could* perceive" (p. 73). Although it is nearly impossible to know *what* fish actually perceive through their lateral line, the seminal studies of Catherine McCormick tell us that information from the lateral line in most fishes is processed by areas and pathways in the brain that are separate from those that process either auditory or electrosensory information (McCormick, 1982, 1989; reviewed in the chapter by Wullimann & Grothe). Thus, if the concept of labeled lines (separate pathways for different sensory modalities) applies to sensory perceptions, it follows that lateral line perceptions, called "svenning" by Platt et al. (1989) in honor of Sven Dijkgraaf, are distinct from the auditory perceptions of hearing.

In the foreword to Phyllis Cahn's 1967 book *Lateral Line Detectors*, George von Békésy (who won the Nobel Prize in Medicine or Physiology for his research on the function of the mammalian cochlea) wrote "When thinking about the lateral line system in fish, I always found myself starting with the physical stimulus, then going over to physiology, from there to gross anatomy and histology, and then back to physics again, and finally trying to make both ends of this ring fit"(p. ix). This fundamental approach to understanding sensory function was typical of many sensory psychologists and physiologists at the time (especially in America) and was certainly consistent with the approach that Harris and van Bergeijk (1962) took to understand sensory function at the level of isolated lateral line sense organs. In contrast, Dijkgraaf's seminal behavioral work in the Netherlands, likely inspired by the European ethologists Konrad Lorenz and Niko Tinbergen, paved the way for a fuller appreciation for the behavioral relevance of the lateral line at the level of the whole animal (as reviewed in the chapter by Montgomery, Bleckmann, & Coombs). Among other things, Dijkgraaf (1934, 1947) was instrumental in following up on Hofer's (1908) original studies to

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[1] There are rare cases in which parts of the lateral line system may be adapted for pressure detection via a close association with compressible gas cavities, e.g., clupeids (Denton & Blaxter, 1976; Gray, 1984), chaetodontids (Webb & Blum, 1990), and some silurids (Bleckmann et al., 1991). There is also evidence that the lateral line/gas cavity association may be involved in ultrasound detection in some clupeids (Wilson et al., 2009).

show that blinded fish could detect nearby stationary obstacles by virtue of the distortions they created in the fish's self-generated flow field. Dijkgraaf called this ability *Ferntastsinn* or "touch-at-a-distance." Remarkably, Knox (1825) had similar ideas a century earlier when he proposed that this was a system of "touch, so modified, however, as to hold an intermediate place between the sensations of touch and hearing" (as quoted by Parker, 1904, p.186). In any event, touch-at-a-distance is now generally accepted as a more apt description of lateral line function than hearing, and there is now considerable hydrodynamic and behavioral evidence for this ability in blind cavefish (*Astyanax mexicanus*; reviewed in Windsor et al., 2008, 2010).

Semantics aside, it is becoming abundantly clear that low-frequency vibrations of a nearby body are capable of evoking neural responses from both lateral line and auditory nerve fibers, as well as both conditioned and unconditioned behaviors (reviewed in the chapter by Braun & Sand). This should be of particular interest to researchers interested in fish bioacoustics because many, if not all, biologically relevant sound sources produce complex hydroacoustic near fields that are capable of stimulating both the ear and lateral line of fish. Although in most fishes the ability of the lateral line to respond to the hydrodynamic (incompressible flow) component of a sound source is limited to the near field, many fish behaviors are as well. Thus, the different bits and pieces of information that each sense encodes are likely to be combined in the nervous system in as yet unknown ways to affect behavior. As Braun and Sand suggest in their chapter, many questions remain about the functional overlap between the two mechanosensory modalities—perhaps most importantly, how and where in the brain is information from the two senses integrated and to what behavioral effect?

4 Historical Contributions of Lateral Line Research to the Hearing Sciences

Although the auditory and lateral line systems of fish and amphibians are now regarded as separate sensory systems, the striking similarities and functional overlap between them continue to inform us about shared principles of operation. The sections that follow provide examples of how lateral line research has contributed to the hearing sciences in particular, but also to a broader understanding of hair cell systems in general.

4.1 A Unifying Concept of Hair Cell Function

Åke Flock's anatomical and physiological studies on the lateral line canal system of the freshwater burbot (*Lota lota*) in the 1960s and early 1970s (Flock & Wersäll, 1962; Flock, 1965a, b; Harris et al., 1970) were instrumental in providing a conceptual framework of hair cell function that could explain the variability of observed physiological responses in different systems, including those in the cochlea, semicircular canals, and otolithic end organs of vertebrates. As was well known at the time, hair cells in all of these end organs share basic features, including most especially the anatomical asymmetry of the hair bundle, which gives rise to the directional sensitivity of the hair cell (reviewed in the chapter by Chagnaud & Coombs). Flock's hypothesis of how hair cells respond to opposite directions of displacement (now known to be correct) helped to resolve the apparent discrepancies between extracellular responses recorded from different hair cell end organs. That is, the summed extracellular responses from cochlear and semicircular canal hair cells faithfully followed the frequency of the stimulus, whereas those in the lateral line exhibited a doubling of the frequency – the so-called *double microphonic* response (Jielof et al., 1952) (Fig. 4).

Flock was astute enough to realize that the differences were based on the grouping of hair cells into two, oppositely oriented, populations in the lateral line, but into a single population of similar orientations in the cochlea and crista ampullaris of the semicircular canals. He reasoned that it would be impossible to get any microphonic responses at all from the lateral line if the receptor potentials of oppositely oriented hair cells were equal in amplitude because they would effectively cancel each other out. Based on this reasoning, he and his colleague Jan Wersäll proposed a theory of hair cell function that included a nonlinear component; that is, that displacement of the stereovilli in the best excitatory direction causes a depolarizing response, whereas an equal displacement in the opposite direction causes a hyperpolarizing response of much smaller magnitude (Flock & Wersäll, 1962) (Fig. 4). Flock then went on to demonstrate via several clever experiments that he could turn a double microphonic response into a single microphonic response by simultaneously biasing the responses of opposing populations of hair cells with a static displacement of the cupula, effectively eliminating the contribution of one population (Flock 1965b). It goes without saying that Flock's contributions to hair cell function scarcely ended there; his initial work on the lateral line launched a long and distinguished career in the hearing sciences.

4.2 The Octavolateralis Efferent System

There is no question that both the lateral line and the auditory system of fish share a common efferent supply from the octavolateralis efferent nucleus in the hindbrain and that with rare exceptions, efferent innervation is a fundamental feature of all vertebrate hair cell systems (Roberts & Meredith, 1989). For reasons still not well understood, efferent innervation does not extend to the closely allied electrosensory system (Bodznick, 1989). Early lateral line studies played a substantial role in determining the pharmacology of the efferent synapse (Russell, 1971b; Flock & Russell, 1973; Flock & Lam, 1974), as well as the inhibitory

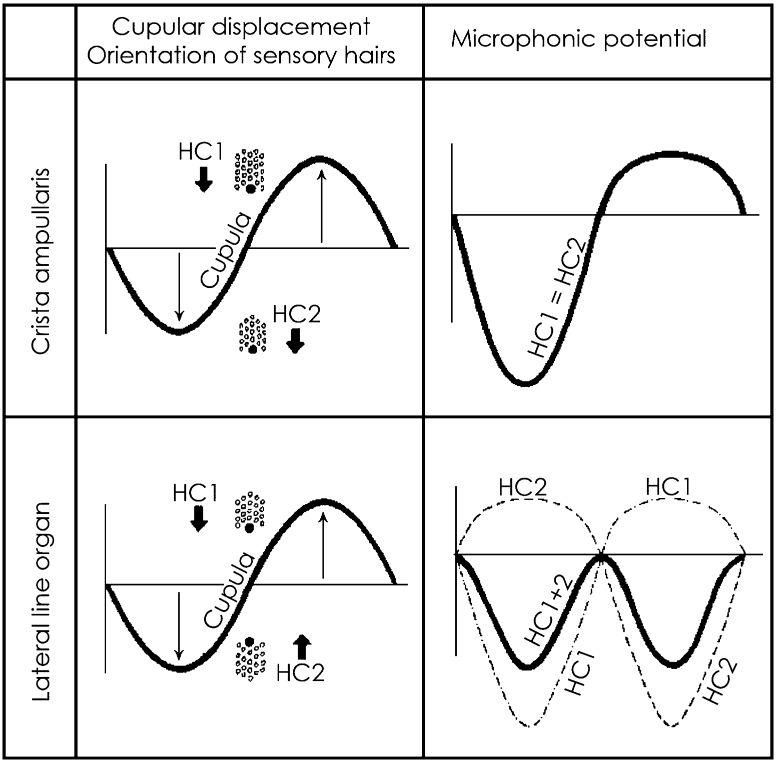

Fig. 4 Illustration from Flock and Wersäll (1962) to explain how the summed extracellular (microphonic) potentials of two hair cell organs can differ when their overlying cupula is sinusoidally displaced in two opposing directions (thin arrows). The microphonic potential of lateral line neuromasts (bottom panel) is twice the frequency of the sinusoidal stimulus, whereas that of the crista ampullaris (vestibular sense organ in the semicircular canals, top panel) is the same. The difference arises because all hair cells (HCs) in the crista ampullaris have the same orientation, whereas those in the lateral line are divided into two, oppositely oriented populations. HC orientation is determined by the arrangement of stereovilli (open circles) relative to a single, eccentrically placed kinocilium (filled circle). Because depolarizing responses of individual HCs to stimulus directions in the best excitatory direction (in the direction of the kinocilium, as indicated by the thick arrows) are larger in magnitude than hyperpolarizing responses to the opposite direction, oppositely oriented populations of hair cells in the lateral line system give rise to a summed potential that is double the frequency of the applied stimulus

effects of the efferent system on spontaneous and evoked activity (Russell, 1971a; Flock & Russell, 1973). It is now known that the efferent system has both excitatory and inhibitory effects that mediate complex, context-dependent modulation of hair cell gain through both feed-forward and feedback loops (reviewed by Köppl, 2011 and in the chapter by Chagnaud & Coombs). Toward that end, lateral line studies have contributed to our understanding of how the efferent system operates in animal behavior (Roberts, 1972; Roberts & Russell, 1972; Tricas & Highstein, 1990, 1991). From these studies, it has been shown that the

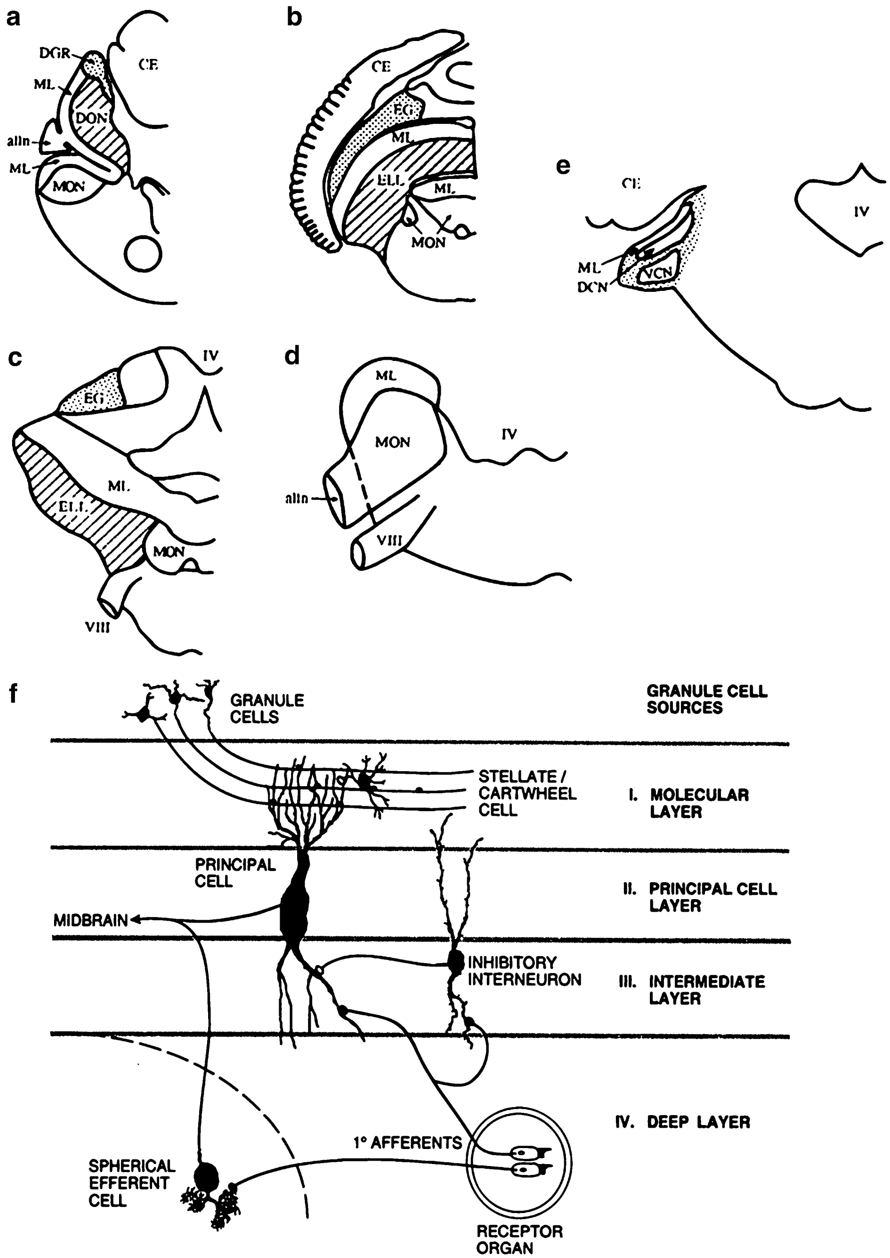

Fig. 5 Example of how comparisons across different octavolateralis systems can reveal basic principles of organization and operation. First-order, brain stem nuclei (hatched areas in **a**–**e**) all share common associations with an overlying molecular layer (ML) of parallel fibers from granule cell masses (stippled regions), which provide descending inputs to the principal (output) cells in the nucleus (**f**). Different octavolateralis nuclei include (1) the mechanosensory lateral line

efferent system can be activated by stimulation of different sensory modalities, such as touch and vision (Roberts & Russell, 1972; Tricas & Highstein, 1990), but also by motor acts (e.g., vocalization, swimming motions) that cause self-stimulation of octavolateralis sense organs (sensory reafference) (Tricas & Highstein, 1991; Weeg et al., 2005).

4.3 *Adaptive Filters in First-Order Octavolateralis Brain Stem Nuclei*

The octavolateralis efferent system is but one strategy that animals can employ for improving signal-to-noise ratios—especially in the presence of self-generated noise. Mechanisms such as this are extremely important, because the exquisite mechanical sensitivity of hair cells to displacements in the nanometer range render them useless in noisy environments capable of interfering with the detection of biologically relevant signals. Although biomechanical and neural filters for separating signals and noise along different stimulus dimensions (e.g., frequency, intensity, location, or time) are powerful strategies for dealing with this problem, there is yet another strategy that animals use. This strategy relies on prior knowledge of often-repeated and thus “expected” noises that can be adaptively filtered out to improve signal-to-noise ratios. As first discovered by Bell (1981, 1982), the electrosensory lateral line lobe in the medulla of weakly electric mormyrid fish contains an adaptive filter or modifiable efference copy mechanism that constructs a negative image of the expected temporal pattern of reafferent input. Evidence for similar adaptive filter mechanisms in the brain stem regions of other groups of other electric fish, as well as in lateral line (mechanosensory) brain stem regions of both electroreceptive and nonelectroreceptive species, suggests that common features (i.e., cerebellar-like circuitries) are responsible (Fig. 5) (reviewed in Montgomery et al., 1995, Bell et al., 1997, 2008). Interestingly, the shared features extend to the dorsal cochlear nucleus of mammals (reviewed in Montgomery et al., 1995; Bell et al., 1997), and comparisons among different

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Fig. 5 (continued) nucleus, the medial octavolateralis nucleus (MON), of all fishes (**a**–**d**), (2) electrosensory nuclei, the dorsal octavolateralis nucleus (DON) in cartilaginous fishes (**a**) and the electrosensory lateral line lobe (ELL) in bony fishes (**b** and **c**), and (3) the dorsal cochlear nucleus (DCN) of the mammalian auditory system (E). Granule cell masses in cartilaginous and bony fishes are called the dorsal granular ridge (DGR, **a**) and the eminentia granularis (EG, **b**,**c**), respectively. In addition, octavolateralis nuclei have similar cell types and circuitries (**f**), including cerebellar-like Purkinje cells, which function as the principal (output) cells of the nuclei and receive primary afferent input from sense organs on their ventral dendrites, but parallel fiber input from granule cells on their apical dendrites. Parallel fibers in the molecular layer convey information from granule cells, which receive multiple inputs, including motor corollary discharge to inform animals about self-generated noises. [Adapted from Montgomery et al. (1995)]

octavolateralis systems have fueled recent advances in our understanding of the underlying circuits and adaptive filter mechanisms in these brain stem structures (reviewed in Requarth & Sawtell, 2011).

5 Gems of the Future

There is no doubt that lateral line research will continue to be an integral part of the hearing sciences. Current research on the lateral line system of the zebrafish (*Danio rerio*) is a stellar example. The zebrafish lateral line serves not only as a useful bioassay for screening ototoxic agents (Ou et al., 2010), but also as a powerful model system for molecular, cellular, and genetic studies of hair cell loss and regeneration (reviewed in the chapter by Coffin, Brignull, Raible, & Rubel), as well as pattern formation, development, and morphogenesis (e.g., Dambly-Chaudiére et al., 2003; Nagiel et al., 2008; Ma and Raible, 2009).

Research on the lateral line has clearly made (and will continue to make) significant contributions to the hearing sciences. However, it is well worth remembering that lateral line research makes equally important contributions to our understanding of how flow information is utilized by fish and aquatic amphibians in a wide range of amazing behaviors, from simple (e.g., orientation to currents) to more complex (e.g., synchronized schooling maneuvers (reviewed in the chapter by Montgomery, Bleckmann, & Coombs). Given that there are more than 30,000 species of fish, the structural variations in the lateral line across species is a veritable gold mine of structure–function relationships to explore (see the chapter by Webb). Moreover, there is the growing promise that future research on structure–function relationships, as well as on the processing of flow information by the central nervous system (see the chapter by Bleckmann & Mogdans), will inspire novel flow-sensing technologies (e.g., Yang et al., 2006, 2010) and engineering applications, such as the sensory guidance of autonomous underwater vehicles to explore foreign and hostile environments. Thus, this fascinating system will continue to inspire classic research for years to come and in ways not yet imagined.

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