

Information-processing demands in electrosensory and mechanosensory lateral line systems

Sheryl Coombs^{a,*}, John G. New^a, Mark Nelson^b

^a*Parmly Hearing Institute and Biology Department, Loyola University Chicago, 6525 N. Sheridan Rd., Chicago, IL 60626, USA*

^b*Beckman Institute for Advanced Science and Technology and Department of Molecular and Integrative Physiology
University of Illinois at Urbana-Champaign, IL 61801, USA*

Abstract

The electrosensory and mechanosensory lateral line systems of fish exhibit many common features in their structural and functional organization, both at the sensory periphery as well as in central processing pathways. These two sensory systems also appear to play similar roles in many behavioral tasks such as prey capture, orientation with respect to external environmental cues, navigation in low-light conditions, and mediation of interactions with nearby animals. In this paper, we briefly review key morphological, physiological, and behavioral aspects of these two closely related sensory systems. We present arguments that the information processing demands associated with spatial processing are likely to be quite similar, due largely to the spatial organization of both systems and the predominantly dipolar nature of many electrosensory and mechanosensory stimulus fields. Demands associated with temporal processing may be quite different, however, due primarily to differences in the physical bases of electrosensory and mechanosensory stimuli (e.g. speed of transmission). With a better sense of the information processing requirements, we turn our attention to an analysis of the functional organization of the associated first-order sensory nuclei in the hindbrain, including the medial octavolateral nucleus (MON), dorsal octavolateral nucleus (DON), and electrosensory lateral line lobe (ELL). One common feature of these systems is a set of neural mechanisms for improving signal-to-noise ratios, including mechanisms for adaptive suppression of reafferent signals. This comparative analysis provides new insights into how the nervous system extracts biologically significant information from dipolar stimulus fields in order to solve a variety of behaviorally relevant problems faced by aquatic animals.

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1. Introduction

The peripheral distribution, innervation and outward appearance (e.g. pits, pores, canals etc.) of electrosensory and mechanosensory lateral line systems are so similar that they had been historically regarded as one and the same ‘lateral line’ system until the discovery of the electrosensory function approximately 40 years ago [10,16,40,62]. Since that time, observations of morphological similarities at the periphery have been extended centrally to include the cytoarchitecture and interconnections of first-order brain stem nuclei and their ascending and descending connections (reviewed in 80; see also Section 6). Despite these striking similarities, it is now abundantly clear that the two systems have separate, although largely parallel, pathways in the

CNS [69,70], each dedicated to the processing of different stimuli with unique physical properties. Key differences in their functional organization—e.g. efferent innervation of mechanosensory (reviewed in [100]), but not electrosensory receptors, are also apparent. In recognition of these fundamental differences, the term ‘lateral line’ is now commonly reserved for the mechanosensory system alone, a convention that will be followed in this paper to distinguish it from closely-allied electrosensory systems.

Although the prevailing view is that many of the similarities are due to common phylogenetic and ontogenetic histories [70], the roles of stimulus attributes and information-processing demands in shaping both similarities and differences is perhaps less-widely understood and appreciated. Using the lateral line as a focal point for comparison, this paper reviews some of the similarities and differences between the two systems with respect to behavior and how the nervous system extracts

* Corresponding author. Tel.: +1-773-508-2720; fax: +1-773-508-2719.

biologically significant information from stimulus sources in order to solve fundamental problems—e.g. how to locate prey. For earlier treatments on the relationship between the two systems from a phylogenetic, ontogenetic and functional point of view, the reader is referred to the excellent overviews of Bodznick and Kalmijn [12,55–57]. From a phylogenetic perspective it is perhaps worth emphasizing that although both the lateral line sense and electroreception are primitive characters among non-teleost, anamniotic vertebrates, electroreception was lost with the advent of the Neopterygian fishes and has reevolved a number of times in various teleost taxa [17,87], whereas the lateral line system, so far as we know, is ubiquitous among all fish taxa [93]. Thus, the selective pressures for maintaining the lateral line system, whatever they may be, are perhaps greater and more pervasive than those for maintaining electroreception. Alternatively, major evolutionary events, like the movement of fish from marine to freshwater environments, may have had more serious consequences for the electrosense than for the lateral line. For example, the loss of an electrosense may have been pleiotropically linked to functional constraints that directly affected the electrosensory system, such as changes in skin resistance resulting from the changing osmoregulatory burdens imposed by freshwater environments. Another possibility is that the decreased conductivity of the freshwater environment resulted in a paucity of available and useful information.

2. Electrosensory and lateral line-mediated behaviors

Both electrosensory and lateral line systems have been experimentally implicated in a number of similar behaviors, one of the most common being prey capture behavior [28,44,54,75,79 for review]. As would be expected, the importance of these two sensory systems in this and other behaviors is greatest when vision is limited. For example, the prey-orienting and approach behavior of the nocturnally-active Lake Michigan mottled sculpin (*Cottus bairdi*) requires lateral line, but not chemosensory or auditory input when vision is absent [26,47]. The prey-capture behavior of many non-electrogenic species (e.g. some cartilaginous fishes and the paddlefish, *Polyodon spathula*) as well as weakly electric fish (e.g. the ghost knifefish, *Apteronotus leptorhynchus*) also relies predominantly if not exclusively on electrosensory systems [53,65,114]. The extent to which the lateral line system contributes to prey capture behavior in these and other electroreceptive species is unknown, but it is likely that it plays a complimentary, if somewhat subtle role, as it apparently does in the visually-dominated prey-capture behavior of non-electroreceptive species (e.g. the muskellunge, *Esox masquinongy*) [90,92]. Determining the nature of the

information extracted by the electrosensory and lateral line systems and how that information is functionally combined during prey capture behavior are interesting questions that deserve further attention.

Rheotaxis is another orienting behavior, in this case to the direction of a uniform water current in which the lateral line plays a dominant role at low current speeds (<10 cm/s) [81]. Positive rheotaxis (going against the current) has been implicated in the ability of fish to find upstream odor sources and to intercept prey drifting downstream, whereas both positive and negative rheotaxis plays a role in spawning migrations to and from natal streams or lakes [3,82]. Use of the lateral line system to orient to uniform water flow may be considered functionally equivalent to the ability of catfish [96] and stingray [56] to use information from the electrosensory system to orient to uniform electric fields and more generally, to the idea that fish can use electric fields induced from the earth's locally uniform magnetic field for orientation and navigation [56,78,95].

The lateral line system plays an important role in the coupling of motor acts between neighboring fish. For example, the lateral line is involved in the ability of fish to match their own swimming speeds and directions to that of their neighbors during tight schooling formations and maneuvers, which presumably functions as anti-predator strategies [94]. The lateral line also plays a pivotal role in elaborate, interactive courtship dances, which lead to the synchronous release of male and female gametes during spawning [102]. This coupling between individuals is possible because body movements of one animal can serve as a potent hydrodynamic stimulus to the lateral line of another animal. In the case of the electrosensory system, there is also the possibility of coupling behaviors between neighboring animals because the electromotor output of one animal serves as a potent electrosensory stimulus for the other. Examples of this sort of coupling between two fish via the electrosense include the jamming avoidance response (see [46] for review) in wave-type electric fish and the echo response in pulse-type fish [101].

Although both schooling and courtship behaviors may qualify as communication behaviors [49], other lateral-line mediated behaviors known to function in social communication are few and understudied relative to electro-communication behaviors in weakly electric fish. Furthermore, there is presently no evidence for a specialized class of communication effectors or receptors for sending and receiving hydrodynamic signals. In contrast, weakly electric fish have evolved a specialized effector for generating electric fields and in some cases, classes of sensors dedicated to the sole purpose of communication (e.g. the Knollenorgans of mormyrids) (see [49] for review). Furthermore, electric organ discharge (EOD) repertoires are quite rich and diverse, as are the many different functions they serve (e.g. sex and

species recognition, mate assessment, appeasement etc.) [49,50]. The nearly instantaneous transmission of electric signals and their minimal distortion by the environment make them especially well-suited for communication purposes [49–51] (see also Section 4). Thus, although additional hydro-communication behaviors may be discovered in the future, the physical attributes of electric signals may favor a relative abundance and diversity of electro-communication behaviors over hydro-communication behaviors. Nevertheless, effective communication in both channels is generally thought to be limited to short ranges, typically on the order of a few body lengths [55–57].

Both electrosensory and lateral line systems are undoubtedly used in the more general function of forming hydrodynamic and electric images of the environment. That is, fish use electrosensory and lateral line information to help determine the size, shape, identity and location of both animate and inanimate entities in their immediate vicinity. Moreover, both modalities can potentially operate in active and passive modes. As is the case with prey capture behaviors, hydrodynamic and electrical imaging abilities are most highly developed in species that have evolved under conditions where visual input is limited or absent (e.g. nocturnal species or those living in turbid environments). Indeed, visual limitations appear to be a potent selective pressure in the evolution of weakly electric fish and their active electrolocation abilities. Non-electroreceptive, blind cavefish (*Astyanax jordani*) perform a kind of active, hydrodynamic imaging of stationary, inanimate objects that is analogous to the active electrolocation abilities of weakly electric fish [18,34,45]. They do so by producing a relatively stable flow field around their bodies as they glide through the water past stationary objects, allowing them to detect the distortions in this self-generated flow field due to the presence of the object. This ability is so exquisite that blind cavefish can make spatial discriminations on the order of 1 mm [45]. By the same token, behaviors like obstacle-entrainment or station-holding by fish like trout [107] may involve a kind of passive imaging of stationary objects in which distortions or vortex trails created by the object in the on-going flow of the surrounding water can also be detected by the fish's lateral line system. Finally, the detection of water currents created by animate sources (e.g. a swimming fish or a filter-feeding bivalve) fit into this general category of passive hydrodynamic imaging and this ability is analogous to the passive abilities of electroreceptive fish to detect externally generated bio-electrical potentials from other animals (e.g. the modulated DC potentials across gills).

To summarize, the lateral line system can provide behaviorally relevant information on the movements of nearby animals (supporting prey capture, schooling, courtship behaviors and passive hydrodynamic imag-

ing) and inanimate objects (active hydrodynamic imaging). The lateral line also provides information on ambient water flow conditions (rheotaxis and navigation). The electrosensory system provides different, but complementary, information about the electrical properties of nearby animals (prey capture, jamming avoidance, echo response, electrocommunication and passive electrolocation) and inanimate objects (active electrolocation). The electrosensory system can also provide information on ambient electrical currents, including those induced by movement through the Earth's magnetic field (orientation and navigation). The major difference in terms of supported behaviors is that the electrosensory system supports a more elaborate system for social signaling and communication.

3. Structure, innervation and function of receptor organs

As mentioned in the Introduction, peripheral sense organs associated with the mechano- and electrosensory systems have many structural and functional similarities. Obviously there will be differences in the transduction mechanisms of individual receptor cells due to the nature of the physical stimulus, but it is interesting to explore other peripheral specializations that reflect similarities and differences in how sensory information is processed by these two systems.

Receptor organs in the lateral line system consist of superficial neuromasts found directly on the skin surface and canal neuromasts found in fluid-filled canals just under the skin and coupled to the surrounding water through a series of discrete pores (generally one canal neuromast between every two pores). The sensory epithelium of both superficial and canal neuromasts is a patch of directionally sensitive hair cells [42]. At the apical surface of each hair cell is a bundle of stereovilli and one eccentrically placed and elongated kinocilium. The location of the kinocilium determines the directional response properties of the cell such that bending of the stereovilli toward the kinocilium results in an excitatory response (i.e. a depolarization of the hair cell membrane and an increase in the firing rate of its innervating fiber) and bending in the opposite direction results in an inhibitory response [42]. Moreover, each canal or superficial neuromast contains two populations of oppositely-oriented hair cells, each with separate innervation. In canal neuromasts, the axis of best sensitivity is parallel to the canal such that water motion in one direction along the canal will excite roughly half of the hair cells while simultaneously inhibiting the other half.

The functional purpose of this bi-directional arrangement is unclear, but flow sensors in other aquatic animals (e.g. crayfish) have similar organizations, whereas air current sensors in terrestrial animals (e.g. crickets)

do not [113]. Wiese [113] argues that aquatic sensors are more closely coupled to the surrounding medium than air sensors and as a result, their displacement-detecting components (e.g. cilia or setae) are less likely to rebound to their resting position in the presence of a sustained DC stimulus. Thus, the bi-directional sensitivity of aquatic sensors might help to preserve their ability to respond to AC signals—especially in the presence of DC flows. Such an arrangement might also serve as the basis for a common-mode rejection mechanism in the CNS to filter out hair cell responses to biologically irrelevant, common-mode signals like monovalent cations [60] and/or for a lateral-inhibitory network for enhancing directional sensitivity [30]. In any event, electroreceptive organs do not have the same organization, as all of the receptor cells within a given endorgan display an identical excitability to either inward or outward current [117]. Furthermore, even though tuberous electroreceptors in *Hypopomus* show polarity preferences and directional sensitivities as a function of body location, these preferences are shaped largely by skin resistance and best directions for trans-epidermal current flow, rather than any intrinsic properties of the receptor cells themselves [71,116]. Although electroreceptive endorgans themselves do not exhibit a bipolar organization, bipolar sensitivity is nevertheless achieved in many electroreceptive teleosts at the level of the first-order brainstem via two different types of principal cells (e.g. basilar vs. non-basilar pyramidal cells)—one that receives direct excitatory input on its basilar dendrites from primary afferent terminals and the other that receives indirect input via an inhibitory interneuron (see [80] for review).

Superficial and canal neuromasts have different response properties owing largely, but not exclusively, to the biomechanical filtering properties of the structural interface (e.g. cupula and canal) between the hair cells and the surrounding water (see Section 4). This response dichotomy, based largely on frequency-responsiveness, loosely parallels that between ampullary and tuberous electroreceptive organs. Thus, afferent fibers from both ampullary organs of electrosensory systems and superficial neuromasts of the mechanosensory lateral line show sustained or tonic responses to low frequency signals (<30 Hz). In contrast, afferent fibers from canal neuromasts of the lateral line system and the so called tuberous class of electroreceptors, which includes the knollenorgans and mormyromasts of weakly electric mormyrids, respond best to higher frequencies. High frequency in this case ranges from 40 to 16,000 Hz [48,85,117], but the majority of tuberous organs are tuned above 200 Hz, whereas lateral line canal neuromasts are tuned below this value.

An upper frequency limit of 400 Hz for a supraorbital canal neuromast in but a single species, the African knifefish, *Xenomystus* [39], is an exception to this gen-

eral rule and is at least 4 times higher than the highest frequency measured for canal neuromasts in most temperate water species [85] and approximately 10 times higher than the highest frequency reported for cold-adapted (antarctic) species [77]. This anomalously high frequency can be attributed to the temperature-dependent tuning properties of hair cells and the relatively high temperatures (27 °C) at which *Xenomystus* lives [39]. Given that most, if not all, weakly electric fish are tropical or warm-water species, it is tempting to speculate that high temperatures may have been a prerequisite for the evolution of high-frequency, tuberous electrosensory systems in teleosts.

Low and high frequency subsystems in both lateral line and electrosensory systems also appear to differ in their innervation patterns, although the data in support of this notion are limited to a few species. Complicating the whole issue is the untidy fact that the absence or presence of a canal may not be the best or only criterion for distinguishing between the two subclasses of lateral line organs (see [32]). Nevertheless, in at least one case where the two classes have been unambiguously identified (the cichlid, *Sarotherodon niloticus*), it appears as if single afferent fibers may innervate up to 10 or so superficial neuromasts in a group, but rarely does a single afferent innervate more than one canal neuromast [83,84]. A similar dichotomy may apply to electrosensory systems as well, although an afferent fiber-to-sense organ ratio of 1:1 may not apply to all tuberous organs in all species. Zakon [117] reported a 1:1 ratio for tuberous organs in adult *Hypopomus* and *Apteronotus*, but a bimodal distribution of ratios (1:1–1:2 and 1:10) for tuberous organs in adult *Sternopygus*. In contrast, ampullary organs in adult *Sternopygus* have innervation ratios as high as 1:20–1:30. Most importantly, there is presently no evidence that organs in the two subsystems are innervated by the same fiber [83,84,118]. Thus, it would appear that information from the two subsystems is relayed to the brain along independent channels with no cross-coupling at the level of primary afferent fibers. Thus, afferent nerve fibers appear to integrate information from multiple endorgans in one subsystem (superficial neuromasts and ampullary organs), but to segregate information in the other (canal neuromasts and tuberous organs).

The story that has begun to emerge in recent years for the lateral line system is that superficial and canal neuromasts underlie different behaviors or behavioral tasks. Montgomery and colleagues, for example, have shown that superficial, but not canal neuromasts, are needed for rheotaxis to slow flows [5,6,81]. In contrast, canal neuromasts, but not superficial neuromasts, are required for the prey-orienting response of mottled sculpin [32,52] and the active hydrodynamic imaging abilities of blind cavefish [1]. The prey orienting response of mottled sculpin does not appear to involve a

simple approach algorithm like following or keeping a constant angle with the current lines [55,57], but rather an instantaneous snapshot or image of the prey, as encoded by the spatial excitation pattern along the lateral line sensory surface of the animal [24,27]. Thus, while superficial neuromasts appear to subserve behaviors that require the spatiotemporal integration of low-frequency information across multiple receptors (e.g. to determine the general direction of a uniform current), canal neuromasts appear to subserve behaviors requiring the spatiotemporal segregation of high-frequency information (e.g. to form hydrodynamic ‘images’ of current-generating or current-distorting sources) (see Section 5). This behavioral dichotomy may have some parallels to the ampullary-based abilities of sharks and catfish to orient to uniform electric fields [54, 96] and to the tuberous-based, active electrolocation and communication abilities of weakly electric fish [8]. This simple dichotomy may be challenged, however, by the passive ability of non-electrogenic fishes to detect and orient towards live planktonic prey [114,115] and the ability of weakly electric fishes to orient towards high-frequency, EOD-like sources by aligning their bodies along the current lines [33,61,103]. The central mechanisms for these electrosensory abilities are unknown. Active electrolocation abilities are presumed to rely on spatial patterns of EOD amplitude and phase along the body surface of the fish and their point-by-point representation in central, somatotopic maps, whereas electric field orientation and passive electrolocation abilities may rely on central computations of current direction.

Conspicuously absent is a parallel in the lateral line system for the two subclasses of tuberous organs specialized for encoding time (phase) and amplitude information in the electrosensory system [21]. While the tonic to slowly adapting responses of canal neuromast fibers might loosely be regarded as the equivalent of the amplitude-encoding fibers in tuberous electrosensory systems, there is no evidence at present for a separate phase- or time-encoding pathway in the lateral line system. That is, none of the features commonly associated with phase-sensitive pathways in the electrosensory sys-

tem of fishes or the auditory system of birds (e.g. minimal branching in the axonal arbor of primary afferents, large afferent terminals or calyceal synapses, round adendritic postsynaptic cells in the brainstem, calcium-binding proteins, separate ventral pathways in the CNS, etc.) [21,22] have been found. This is probably not too surprising, given that canal neuromasts generally operate at frequencies below 200 Hz and thus, in a range where the phase-locking abilities of afferent fibers are still quite good. Thus, at these low frequencies, both amplitude and phase can be adequately represented by the same fiber. Moreover, hydrodynamic signals, which travel at relatively slow speeds, do not place the same temporal processing demands on the system as do electrostatic fields, which are nearly instantaneous (see below).

4. The biophysical nature of electric and hydrodynamic stimuli

A generalized version of Ohm’s law provides a convenient framework for comparing the biophysical properties of electric and hydrodynamic stimuli (Table 1). Ohm’s law states that in an ideal conductor, the magnitude of the current (I) is directly proportional to the applied electromotive force, E and inversely proportional to the impedance, Z . In DC circuits, resistance, R , is the only thing that impedes the current, but in AC circuits, there is also inductive and capacitive reactance. The hydrodynamic equivalent of the electric current is incompressible flow and the equivalent of the electromotive force is a pressure drop per unit length. Although the movement of electrons or charged ions cause electrical currents, the actual currents are not the movement of charged particles per se, but rather the transfer of energy from one electron orbit to the next—at the speed of light. In contrast, incompressible fluid flow involves the transfer of mass or water molecules, which occurs at finite speeds (mm/s to m/s in the biologically relevant range of the lateral line). In reality, water is nearly, but not completely incompressible and as a

Table 1
Electric and hydrodynamic currents compared

	Electric Current	Incompressible Flow
Magnitude (I)	Coulombs/s (amps)	Cubic meters/s
Applied force (E)	Voltage gradient (V/m)	Pressure gradient (Pa/m)
Impedance (Z)	Impedance (ohms) <ul style="list-style-type: none"> • Resistance (dc, ac) • Inductive Reactance (ac) • Capacitive Reactance (ac) 	Viscosity (Pa s/m ⁴) Inertia
Current type	Transfer of energy	Transfer of mass
Current carriers	Electrons/charged ions	Water molecules
Transfer rate	Nearly instantaneous (speed of light)	Finite (mm/s–m/s)

consequence, energy, but not mass, can be transferred in propagated sound pressure waves at a relatively high rate of close to 1500 m/s. But incompressible flow is most important for the lateral line and flow opposition is due to the interplay of viscous and inertial forces, the closest analogy we have for electrical impedance. Unlike electrical impedance, however, viscosity and inertia (the resistance of mass to being accelerated), have consequences for the very nature and structure of the current.

Viscosity is simply a measure of how much a fluid resists distortion (see [110] for an excellent and more comprehensive treatment of this subject as it pertains to biological systems). Unlike solids, the shapes of fluid masses can be distorted by a shear stress (force per unit area). If the liquid mass interfaces with a solid surface, viscosity also results in what's called the 'no slip' condition, meaning that the fluid tends to stick to the surface when a shear stress is applied such that the velocity of fluid flow at the fluid–solid interface is always zero and at some distance away it is at its maximum, free-stream velocity. The region over which the velocity goes from zero to its free-stream velocity is called the boundary layer and this is a velocity-gradient region in which incompressible flow is impeded relative to its maximum value. Highly viscous fluids like molasses or ketchup resist distortion more than fluids of low viscosity like water or air and hence, their boundary layers are thicker and the viscosity contribution to flow resistance is greater.

To summarize, impedance in the hydrodynamic sense is the interplay between inertia and viscosity. This interplay is conveniently described by the Reynolds number, which is a dimensionless expression of the relative importance of inertial and viscous forces [110]. At low Reynolds numbers (~ 10), viscous forces dominate, boundary layers are thick and flow is laminar; at high Reynolds numbers ($>> 200,000$), inertial forces dominate, boundary layers are thin and flow is turbulent. Size and speed (or frequency of movement) also matter. The Reynolds number associated with the water motions created by a large whale swimming at 10 m/s is approximately 300 million, whereas that associated with the water motions of a small copepod swimming at 0.2 m/s is around 300 [110]. In general, small slow-moving prey objects will have low Reynolds numbers and will thus give rise to predictable flow patterns that should be relatively easy for the nervous system to analyze and interpret. In contrast, large fast-moving objects will have high Reynolds numbers and complex turbulent flow patterns which may make it more difficult for the nervous system to extract useful information about the source properties.

In addition, the interplay between viscous and inertial forces also underlies the biomechanical filtering properties of the lateral line system. Viscous opposition to flow

in large diameter pipes is less than that in small diameter pipes, where there is a larger surface area to volume ratio. When the water is accelerated, however, as is the case for high frequency motion, the viscous forces that normally oppose slow flow in small pipes are overcome by inertial forces. That is, the velocity of fluid motion inside the canal, the proximal stimulus to the enclosed canal neuromast, is reduced by viscous forces at low frequencies, but not at higher frequencies [36,37]. Thus, lateral line canals essentially operate as high pass filters—the smaller the canal, the more effective the filter and the higher the low-frequency cut-off. In contrast, superficial neuromasts on the skin surface are driven primarily by viscous forces or skin friction between the surrounding water and the gelatinous cupula, which covers the neuromast and couples the surrounding water motions to the underlying cilia. Because viscous forces decline at higher frequencies, the cupula/water interface of a superficial neuromast effectively acts as a low pass filter.

It turns out that one of the primary functions of lateral line canals may be to filter out unwanted low frequency noises, such as slow ambient water motions. Indeed, Engelmann and colleagues have recently shown that the responses of superficial neuromast fibers to a 50 Hz signal are completely degraded in the presence of slow, ambient DC flows, whereas those of canal neuromast fibers are preserved [38]. Similarly, Kanter and Coombs [59] have shown that Lake Michigan mottled sculpin are able to detect relatively weak 50 Hz signals in the presence of strong background flows and that detection thresholds are relatively stable over a 4-fold increase in background flow velocity. This feat is even more remarkable, considering how the fish's body, especially the broad pectoral fin, alters the flow field in the vicinity of the lateral line [32].

In summary, a number of different variables, including viscosity, frequency, size and speed can affect the fundamental structure of hydrodynamic flows associated with a mechanosensory stimulus as well as influencing the biomechanical filtering properties of the lateral line receptor organs. Flow regimes can vary from laminar, uniform and predictable to highly turbulent, non-uniform and unpredictable. Intermediate regimes often include structures like vortices, yet another consequence of viscosity. The whole notion of the lateral line as a vortex and turbulence detector is one that has only recently been explored and we now know from recent studies that both seals and fish are able to follow vortex trails at relatively far distances from the source using hydrodynamic sensors [35,97]. In any event, the different flow regimes represent a whole level of complexity to the signal structure of mechanosensory stimuli that has no counterpart in the electric sense.

5. Dipole fields and their consequences for information processing

Despite mass and viscosity-related differences in the transmission of hydrodynamic and electric signals, the spatial configuration of their stimulus fields can be quite similar and as Kalmijn [55–58] has frequently argued, often predominantly dipolar in shape. Dipole fields can be generated in one of two different ways: in an active sense, when the source itself produces the hydrodynamic or electric current (e.g. water currents generated by a moving prey or electric currents arising from the prey's bioelectric field), but also in a passive sense, when a non-current generating source (e.g. an inanimate object) is placed in a current field (e.g. a rock in a stream or a rock in the EOD field of an electric fish). Under certain conditions and with certain simplifying assumptions, the field around these sources can be approximated and mathematically modeled as a dipole field [55–58]. One important assumption—freedom from vorticity—is easily satisfied for bioelectric fields, but, as the previous section reveals, will be violated for hydrodynamic fields in boundary layer regions (e.g. at the animal–water interface) and other regions (e.g. in the trailing wake of a swimming fish or an object in a stream) where shear stresses and vortices predominate. Given that superficial neuromasts function largely within the viscous boundary layer, the dipole model is probably most useful for understanding information processing by canal neuromasts, which commonly respond to accelerated flows or pressure-gradients outside the viscous boundary layer. Indeed, canal neuromast fibers appear to follow, rather faithfully, the pressure-gradient direction and strength of dipole flow fields [27,29] (Fig. 1), but may be relatively insensitive to vortex wakes [74]. Moreover, the ability of mottled sculpin to orient toward a pure dipole source (oscillating sphere) that simulates live prey is heavily, if not exclusively, dependent on canal neuromasts [32].

In recent years, both electrosensory and lateral line researchers have converged upon several principles of information encoding and extraction based on the spatial configuration of dipole fields and the resultant stimulation patterns along the sensory surface of the animal's body [4,15,19,20,27,29,31,64,86,98,99,111] (Table 2). For the lateral line canal organs, the stimulation pattern arises from the spatial distribution of pressure-differences across canal pores, whereas in the electrosense, the pattern arises from transdermal voltage differences (Fig. 2). Using computational models based on a simple, linear arrays of sensors, these investigators have shown that the spatial distribution of both the amplitude and sign (polarity) of the pressure/voltage difference conveys important information about the source (Table 2). The location of the peak excitatory region carries information about the location of the

source relative to the fish, although this may be confounded by dipole orientation [25,98,115]. Because the peak amplitude in the pattern varies with several source parameters, including distance, size, shape and signal strength, it is not a very useful piece of information in and of itself. However, when the bandwidth of the peak excitatory region and/or its slope is normalized to peak amplitude, unambiguous information about source distance is provided [12]. The sign or the polarity of the

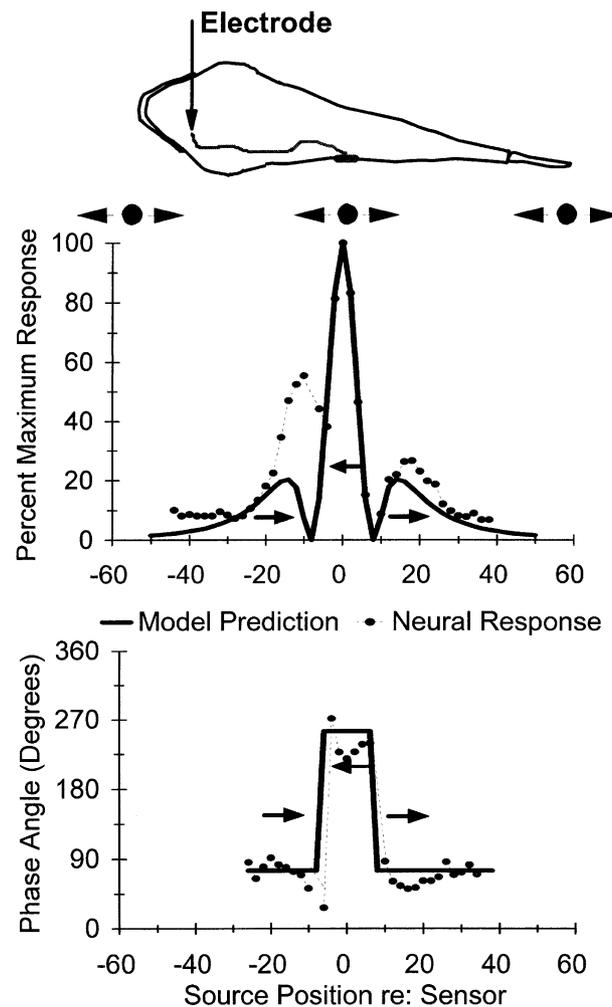


Fig. 1. Neural responses to a dipole source compared to modeled predictions. The spike activity of a posterior lateral line nerve fiber innervating a single canal neuromast on the trunk of a the mottled sculpin was measured in response to the slowly changing locations of a 50 Hz vibrating sphere. As the source changed its location, the increases and decreases in spike activity (thin line with symbols) follow the predicted changes in pressure-gradient amplitudes (thick line), modeled as the difference in pressure between two surrounding canal pores divided by the pore separation (2 mm) (A). The phase angle or preferred firing time of the fiber during a single sinusoidal cycle phase angle also follows the modeled predictions and shifts by a 180° for every predicted shift in pressure-gradient (flow) direction (see arrows). The asymmetry in the side lobes of the neural response is most likely due to the fact that the fish and consequently, the trunk lateral line, was slightly tilted with respect to the axis of linear source movement.

peak amplitude also carries information. In passively-generated hydrodynamic images of moving sources (e.g. oscillating sphere), the sign corresponds to the polarity of flow direction inside the canal and in combination with the shape of the pattern, carries information about the relative direction of movement between source and fish [25]. Similarly, in passively-generated images of live *Daphnia*, both the sign and shape of the image corresponds to the orientation of the *Daphnia* [15]. In actively-generated electric images of stationary objects, the sign (in this case, either an increase or decrease in EOD amplitude) corresponds to the conductivity of the object relative to the surrounding water [111].

The degree to which fish make use of this spatial information is largely unknown, but these models provide testable hypotheses of behavioral performance. Von der Emde and colleagues [112], for example, demonstrated that weakly electric fish appear to use the slope/amplitude cue for determining object distance by showing that fish erroneously judged spheres, which have smaller slope/amplitude ratios than most other

objects, as being further away than cubes at the same distance. Likewise, lateral-line based performances by mottled sculpin during prey capture behavior (e.g. the approach pathways taken by sculpin to dipole sources, the maximum distances at which the initial orienting response can be elicited, distances from which strikes are launched, strike success, and orienting accuracy) are all consistent with predictions based on modeled excitation patterns [31].

6. Organization and interconnections of first order brainstem nuclei

The medial octavolateralis nucleus (MON) of the lateral line and electrosensory regions of the brainstem [the dorsal octavolateralis nucleus (DON) of electroreceptive non-teleosts and the electrosensory lateral line lobe (ELL) of teleost fishes] all share several fundamental features that have been reviewed previously in great detail [80]. Briefly, these include (1) a superficial mole-

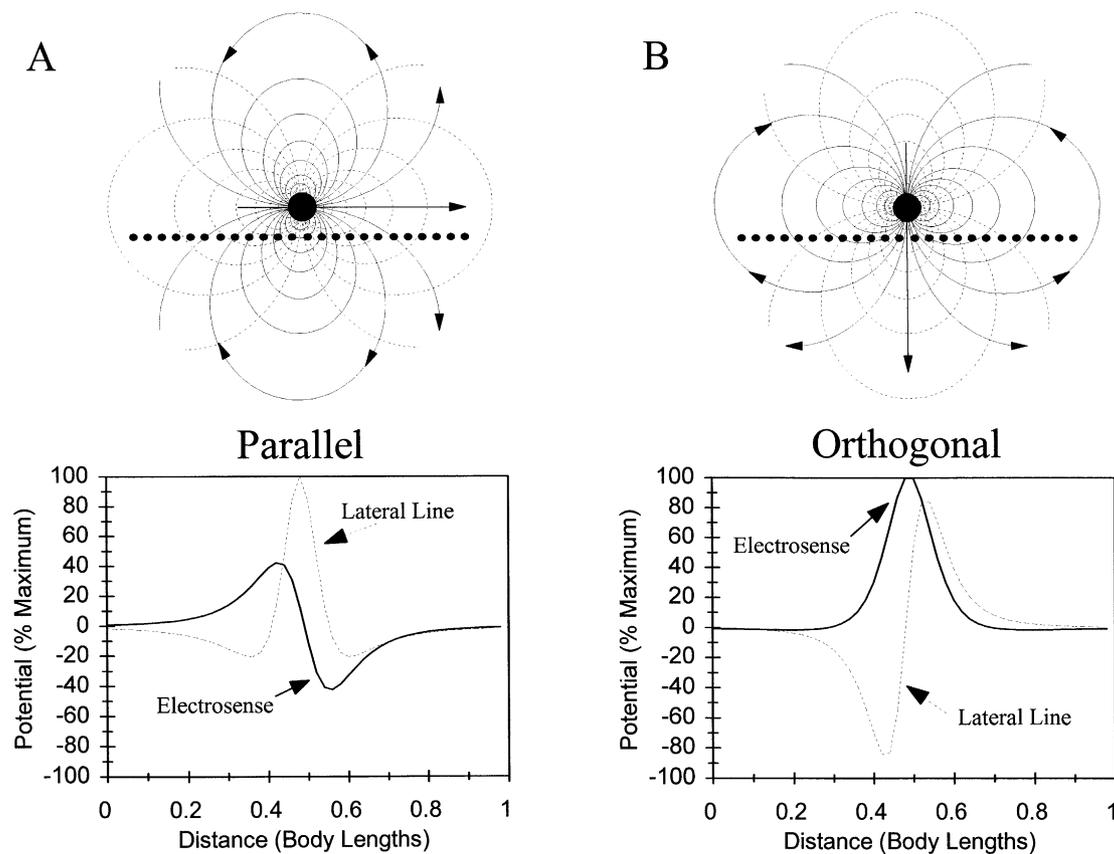


Fig. 2. Modeled stimulation patterns (bottom panel) along electrosensory (solid lines) and lateral line (dashed lines) sensor arrays for two dipole orientations, A and B (top panel). Current and iso-potential lines of the dipole field are depicted by solid and dashed lines, respectively. Electrosensory patterns are modeled as the voltage drop across a 1-cm thick slab of water to simulate the potential across the skin at sensor intervals of 0.02 body lengths (BL), whereas lateral line patterns are modeled as the pressure difference between canal pores separated by the same distance. Voltage and pressure potentials are normalized to the peak potential across dipole orientations for each system. These relatively primitive models rest on many simplifying assumptions, including that the dipole field imparts no motion to the fish and that voluntary movements of the fish are likewise absent. Note that the lateral line stimulation pattern and dipole orientation modeled in A corresponds to that in Fig. 1, but that the sign (direction) of the potential is represented by arrows and 180° phase-angle separations in Fig. 1.

cular layer of parallel fibers derived from granule cells, (2) a principal cell layer of large, multi-polar cells with apical dendrites that extend into the molecular layer and ventral dendrites that extend into deeper layers, and (3) deeper layers, where the terminals from primary afferent fibers contact the ventral dendrites of principal cells either directly or indirectly through inhibitory interneurons. Similarities in the interconnections of these nuclei include (1) ascending projections from principal cells to secondary brainstem nuclei and the midbrain, (2) indirect inputs from motor command, somatosensory and primary afferents via granule cells in the cerebellar eminentia granularis (teleosts) and dorsal granular ridge (elasmobranchs), and (3) descending projections from secondary brainstem nuclei. Many of these shared features, including the parallel fiber inputs from the granule cell regions, function as part of an adaptive filter mechanism for suppressing sensory reafference [9,80] (see Section 7). A variety of other functions have also been observed or proposed for the ELL circuitry and its recurrent feedback pathways. These include regulation of response sensitivity for adaptive gain control, regulation of receptive field properties for adaptive spatiotemporal filtering, a sensory searchlight mechanism for attentional control, coincidence detection for enhanced sensitivity to weak signals, common-mode rejection of background noise, and spike burst generation for feature extraction (see [11,43,109] for reviews).

Despite striking anatomical similarities, which are also present in the dorsal cochlear nucleus of mammals [80], there remain large differences in the level of complexity and number of cell types between tuberous electrosensory regions of the brainstem and the MON of the lateral line. Based on Golgi preparations in the goldfish, for example, there are at most four layers and five main cell types in the MON [91]. In contrast, the mormyromast zone of the ELL has 5–6 identifiable layers and approximately 14 main cell types [72] and like-

wise, the tuberous region of the ELL in weakly electric gymnotids has at least eight layers and 11 main cell types [66]. An additional factor that contributes to this overall level of complexity is the existence of multiple somatotopic maps in the tuberous ELL [23]. Each map is known to have different spatial and temporal tuning properties [104,105]. Although somatotopic mapping occurs in ampullary brainstem regions [13,63,89] and in the MON of the lateral line [2,89], there is presently no evidence of multiple maps in either system. Similarly, ampullary brainstem regions of both elasmobranchs [13], and teleosts [41] are more comparable to the MON than the tuberous ELL, having 3–4 layers with no more than 5–6 main cell types.

The absence of overall complexity, including multiple maps, in both the lateral line and ampullary electrosensory system, is consistent with the general idea that passive electro- and hydrodynamic detection abilities underlie simpler behaviors and require fewer central nervous system specializations than do tuberous electrosensory systems actively engaged in communication and electrolocation. Multiple maps, for example, may function in processing different stimulus parameters [64,86,104,105,106] and/or in controlling different behaviors [73]. The discovery of a species with increased repertoires of lateral line mediated hydrocommunication or active hydrolocation behaviors in association with MON hypertrophy in number of cell layers, cell types or somatotopic maps, would provide welcomed evidence for this general idea. Alternatively or in addition, the increased specializations and behaviors associated with tuberous electrosensory systems may be enabled or facilitated by the nature of the stimulus itself, including its rapid transmission characteristics and relative resistance to distortion by the environment. This would be especially true when other modes of rapid signal transmission and reception (e.g. vision) were absent. As previously discussed, the evolution of a dedicated, central timing pathway is an example of a

Table 2
Object features corresponding to spatial image features

Spatial image features	Object features
Location of peak amplitude on sensory array	2-d Projected location (X, Y)
Bandwidth or peak slope	Distance (Z)
Peak amplitude	Distance Size Shape Signal strength <ul style="list-style-type: none"> • conductivity (active electrosense) • acceleration (lateral line)
Sign (polarity)	Signal polarity <ul style="list-style-type: none"> • orientation • conductivity (active electrosense) • direction of movement (lateral line)
Shape (uni-, bi- or tri-modal)	Orientation (passive electrosense, lateral line)

specialization that is likely to be associated with rapidly transmitted signals. If increased behavioral repertoires are enabled by stimulus characteristics such as these, then the potential for an evolutionary expansion of lateral line-mediated hydrolocation and/or hydrocommunication behaviors should be extremely low—even in the absence of vision. Although characid blind cavefish clearly exhibit active hydrolocation behaviors and abilities, there is currently no information on the structure or organization of the MON in this species. Likewise, many deep-sea fish have clear and obvious specializations of the lateral line periphery [67,68], but data on behaviors and CNS anatomy are unfortunately lacking.

7. Central and peripheral mechanisms for improving signal-to-noise ratios

One of the most interesting comparative stories in recent years is the range of strategies and mechanisms for reducing sensory reafference and in general, for improving signal-to-noise ratios. Given that the same source (e.g. ventilatory movements of the gills) may serve as either a signal or noise source, depending on the context and the receiver, it is not surprising that there are a number of potential strategies and mechanisms that fish might use to reduce or filter out different kinds of noises in different behavioral contexts. These range from relatively simple and static biomechanical or electrical filters at the level of the sensory organ (e.g. lateral line and ampullary canals) to more complex and dynamic mechanisms involving complex neural circuits and overt behaviors (e.g. the jamming avoidance response). Many of these strategies and mechanisms are employed by both electro- and mechanosensory systems. Of these, perhaps the most exciting and revolutionary is the adaptive filter in the first order brainstem nuclei of both electrosensory and lateral line systems for suppressing unwanted, self-generated noises [see 9,80 for review]. The principal cell types and cerebellar-like infrastructure of brainstem nuclei in several different taxa (see Section 6) have now been shown by a number of investigators to support an adaptive filter or modifiable efference copy mechanism like that first discovered in the electrosensory lateral line lobe (ELL) of weakly electric mormyrids [7]. This adaptive filter constructs a negative image of the expected temporal pattern of reafferent input and then uses this negative image to cancel or suppress the components of the sensory input associated with the animal's own expected movements (e.g. the animal's own breathing movements). This negative image can be slowly modified, typically over a time course of several minutes, to adapt to changes in the reafferent signal.

The octavolateralis efferent system is also capable of suppressing sensory reafference, but this mechanism is

completely absent from electrosensory systems and differs from the adaptive brainstem filter in several ways. One, it operates directly and rapidly on the peripheral nervous system by inhibiting lateral line receptor cells and their afferent fibers before and during movements of the animal [100]. Two, it can be activated by unexpected or highly arousing visual stimuli (e.g. prey) [108] or by vigorous and rapid, self-body movements [100]. As Bodznick [12] points out, the striking absence of efferent innervation in many, independently-evolved electrosensory systems argues for a functional, rather than phylogenetic or ontogenetic explanation. That is, efferent systems are absent in the electrosense because they serve no useful function. Whereas vigorous, self-movements are likely to create potent hydrodynamic stimuli that compromise the sensitivity of the lateral line system to exogenous stimuli, the electric potentials generated by such movements may not be so intense as to severely compromise the sensitivity of the electrosensory system [12]. Alternatively, the spatially-complex and often turbulent and unpredictable nature of mechanosensory reafference may require a more direct and in some respects, simpler “all or none” mechanism for suppressing reafference. Such a mechanism may be unnecessary or even undesirable in the electrosense, given the availability of both adaptive filter and common-mode rejection (see below) mechanisms that are more specific and controllable in their actions. Finally, visual activation of the efferent system in the context of arousal and early warning may not offer significant advantages to the electrosense, as signal transmission is equally rapid in both visual and electrosensory systems.

Common-mode rejection is a third mechanism by which sensory reafference may be reduced. This mechanism appears to play an important role in electrosensory systems, but a less significant role, if any, for the lateral line system. This mechanism takes advantage of the fact that reafference due to ventilatory movement of the gills is common mode among ampullary receptors at different locations and on different sides of the body [54,76]. In the little skate, *Raja erinacea*, commissural cells, in the DON have inhibitory connections for subtracting out the common mode signal [14,88]. Inhibitory commissural cells like these are a common feature in deep layers of both ampullary and tuberous regions of the brainstem nucleus in many different taxa, but are conspicuously absent from the MON of the lateral line. Furthermore, hydrodynamic reafference due to ventilatory motion is unlikely to be common mode between receptors organs at different locations on the body. That is, both the direction and amplitude of the self-induced flow will vary as a function of location along the fish's head and body. Thus, common-mode rejection mechanisms for suppressing lateral line reafference, if they exist at all, may not be as well-developed nor play as significant a role as they do in electrosensory systems.

Nevertheless, some self-induced flows (e.g. ventilatory flows) will vary along each side of the body in a bilaterally-symmetrical way and inhibitory, commissural connections between large, pyramidal-shaped neurons in the principal cell layer of the MON [119] could provide the neural substrate for a point-by-point common-mode subtraction of symmetrical flows.

8. Future directions

Although there has been progress in achieving an understanding of the anatomical organization of the lateral line system and the response properties of the receptor organs, study of the lateral line has lagged behind that of electrosensory systems in many aspects. It is therefore difficult to make direct comparisons between the mechanisms of central neural processing between the two systems (but see Bleckmann in this volume for a review of CNS processing in the lateral line). Furthermore, what is known suggests that the ampullary electrosensory system may provide a more applicable model for comparisons. Phylogenetic evidence suggests that in teleosts the ampullary system evolved as a specialization of lateral line systems and that the tuberous electrosensory system evolved as a further specialization of the ampullary system. Nevertheless, even at our current level of understanding, significant differences exist between ampullary and lateral line systems and these may prove useful indicators of the functional constraints imposed upon systems dedicated to processing stimuli with different physical properties.

The manner in which various properties of a stimulus source are encoded is poorly understood in both lateral line and electrosensory systems. What are the abilities of these systems to resolve small differences in stimulus ‘texture’? Mottled sculpin will direct a feeding strike at hydrodynamic dipole sources and elasmobranchs will direct strikes at electric dipoles, but what are the abilities, if any, of these fishes to resolve differences in stimuli that might represent a preferred prey item? Many fish species demonstrate prey preferences; do lateral line or electrosensory systems play roles in such discrimination? And if so, how are differences in the hydrodynamic or electrosensory ‘signatures’ of different prey species encoded by CNS cells?

The receptors of both systems comprise spatially distributed arrays of receptors, but as in most sensory systems the approach of a fish to a stimulus source is one that involves relative movement between fish and source such that the spatial and temporal characteristics of the stimulus source change continuously. How does the information content of such a stimulus change over the course of an approach (or avoidance) behavior and what are the central mechanisms for tracking these

changes over time? Although there is experimental evidence to indicate that the various submodalities of the lateral line system (canal vs. superficial neuromasts) play roles in different behaviors, the actual extent to which afference from these two subsystems are segregated centrally is also unknown. There is no clear distinction between canal and superficial neuromast centers in MON of the hindbrain, as there are between ampullary and tuberous subdivisions of the ELL in weakly electric fish, in which the different submodalities play distinctly different behavioral roles. What then are the degrees of overlap or convergence between afference from the different receptors in the lateral line?

Additionally, the manner in which afference in electrosensory and lateral line systems is used to direct motor behaviors (striking, schooling, etc.) also remains to be discovered. Clearly that information from lateral line receptors must provide information to areas of sensorimotor integration, altering the activity of central pattern generators to produce a desired motor output. The mechanisms by which this occurs is not known, nor is the manner in which afference from other modalities is integrated centrally with lateral line or electrosensory afference in order to provide a richer and more accurate picture of the surrounding environment.

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