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Electroreception: Extracting Behaviorally Important Signals from Noise

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Abstract

Sharks, skates, and rays exploit a marine environment rich in bioelectric and motional electric fields, which are very weak but nevertheless very useful for prey capture, predator avoidance, social interactions, and orientation in the sea. The elasmobranchs' appreciation of these fields is made possible by two distinct specializations. The first of these is an array of extraordinarily sensitive receptors, the ampullae of Lorenzini, which derive much of their sensitivity from positive feedback mechanisms held delicately balanced at threshold. The second specialization is a sophisticated set of filter mechanisms in the brain for extracting the weak electrosensory signals from much stronger background noise. A large portion of this background noise is created by the fish's own movements. Recent experiments show that a remarkable adaptive filter mechanism implemented by the cerebellar-like circuitry of the medullary electrosensory nucleus accounts for much of the noise suppression. The specializations of receptors and CNS so well developed in these fishes allow us to recognize important general principles operating in other sensory systems and in other vertebrates.

1. Introduction

Despite its relatively recent discovery, electroreception is widespread in aquatic vertebrates. Furthermore, the distribution of electroreception indicates that an original system based on receptors like the ampullae of Lorenzini evolved very early in vertebrate phylogeny, and that the electrosense has been lost and reevolved several times in vertebrates (Bullock et al., 1982). This chapter reviews our knowledge of Lorenzinian electroreception as exemplified by elasmobranchs, with a particular emphasis on recent advances. Like all sensory systems, the electrosense has its own peculiar set of physical and biological potentialities and limitations, but unlike many other sensory systems, these lie outside our own sensory experience. So the particular challenge of electroreception is to understand and depict an electrosensory world unfamiliar to us. To do this requires an understanding of the behaviorally important signals in the environment and the ways in which these are detected, encoded, and

processed by the sensory periphery and central nervous system. Perhaps more than in other sensory systems, the electrosense has the potential to be corrupted by environmental and self-generated noise, so recent studies have focused on the strategies and mechanisms that exist for the fish to extract the behaviorally important signals from this noise.

2. Behaviorally Important Signals

2.1. Predation and Mate Detection

The most significant source of behaviorally relevant signals for elasmobranch electroreception is other animals in the environment. All aquatic animals pump ions to maintain the integrity of their body fluids and in doing so separate ionic charges. This creates electrical fields that are short-circuited by the surrounding seawater, forming quasi-dipolar sources. Other currents are generated by muscle action potentials but these do not appear to be significant sources for the elasmobranch electrosense since their frequency composition is largely higher than the sensitivity range of the electroreceptors. The fact that natural local dipole sources in the marine environment are exclusively of animate origin may well be one of the most important features of the electrosense. In effect, the electrosense "sees" only other animals in the environment, and it is other animals that form the most salient behaviorally relevant stimuli as potential prey or predators, or as conspecifics in social interactions. In visual terms, this is analogous to the infrared detectors of snakes or military snipers, which pick out the body heat of their mammalian targets against a uniform or featureless background. That local dipole sources can be equated with the presence of animals simplifies the central processing tasks for the electrosense. It is not necessary to distinguish relevant electrical image from complex background (or figure from ground in the terminology of visual psychophysics), and discrimination can be relatively straightforward.

In line with this expectation, behavioral studies show that sharks, rays, and skates make just the same orienting responses to either artificially produced or naturally occurring dipole electric fields (Fig. 20.1A). Sharks attracted to a bait source exhibit well-directed attacks at an adjacent small dipole source, ignoring the visual stimulus of the bait (Kalmijn, 1982). The calculated fields at the point the shark turns toward the source provide the often-quoted threshold sensitivity of the system of 5 nV/cm. Swell sharks use their electrosensory system to detect small fish being washed toward them in the subtidal surge zone on the reef; the shark's response to an approaching dipole is simply to open its mouth (Tricas, 1982). During mating season male Atlantic stingrays in the Sea of Cortez approach and investigate a buried plastic model of a female when the model is equipped with a synthesized bioelectric field (Fig. 20.1B) (Tricas et al., 1995). As is clear from these examples, the electrosense plays a major role in predation and in mate location and probably also in other social behaviors. Social and reproductive interactions, in some skates, incorporate pulsed discharges of an electric organ in their tails (Mikhailenko, 1971; Mortenson and Whitaker, 1973; Bratton and Ayers, 1987), though the behavioral importance of these discharges is yet unknown. Finally, it seems likely that the electrosense is also involved in predator detection and avoidance. Even skate embryos still within the egg capsule pause their normal respiratory tail undulations in response to weakly electric fields, one source of which could be a predator nearby (Sisneros et al., 1998).
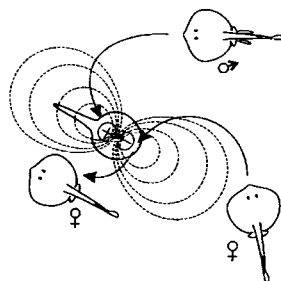
2.2. Orientation and Navigation

In addition to the relatively small-scale bioelectric fields, there are also large-scale electrical fields in the environment, and electrical fields produced by movements of the animal itself (Kalmijn, 1974). Both of these result from Faraday's Law of electromagnetic induction that specifies the electromotive force induced in a conductor moving within a magnetic field. In the case of large-scale environmental fields, these are induced by
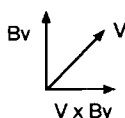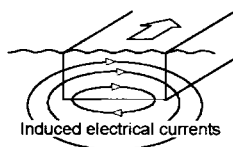
A Predation

B Mate detection

C Orientation & navigation
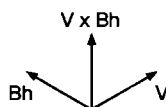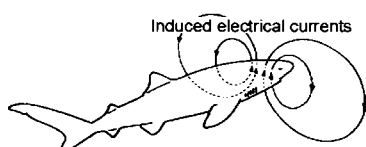
Passive mode   Active mode

FIGURE 20.1. (A) Little skate, *Raja erinacea*, aroused by food odor, orienting to a DC dipole electrical field of 0.2 μV/cm at the perimeter of the test area (20 cm from electrodes buried in the sand). Images from video frames are in left-to-right order. (B) Mating stingrays, *Urolophus halleri*, in shallow water of the Sea of Cortez orient to a buried plastic model during playback of the low-frequency bioelectric field recorded from a female. Males approach, explore, and sometimes dig up buried models (as they do actual females) in an attempt to mate. Females also locate and approach the model and often bury next to it. (After Tricas et al., 1995.) (C) Diagrams illustrating motional electric fields available to elasmobranchs for navigation in the ocean. Large-scale fields associated with ocean streams may be used by the fish to set a heading with respect to the stream (passive mode), or the fish's own swimming movements within the Earth's magnetic field create fields whose polarity and intensity depends on the fish's compass heading and velocity (active mode). Abbreviations: Bh, Bv—Earth's magnetic field horizontal, vertical vector; V—velocity vector. (After Kalmijn, 1974.)

movements of oceanic and tidal streams in the Earth's magnetic field, and are well within the sensitivity of the elasmobranch electrosense. Because of boundary conditions at the water surface, the most relevant are horizontal fields produced by the horizontal movement of the stream through the vertical component of the earth's magnetic field (Fig. 20.1C). The relatively constant direction of these fields may provide a directional reference, allowing elasmobranchs to maintain a constant heading. Kalmijn (1997) refers to this as the passive mode of electronavigation. In the active mode, the animal's own movements induce an electric field across its body. Close to the surface, these self-induced fields could be distinguished from environmental fields by concentrating on the vertical fields induced by the horizontal movement of the animal through the horizontal component of the Earth's magnetic field. It is clear that as the horizontal heading changes, so too would the strength and polarity of the vertically induced field. As Murray (1962) suggested, this available cue could provide the basis of an electrosensory-mediated compass sense (Kalmijn, 1982). One complication is that the electro-

receptors themselves do not encode purely DC potentials, but as Paulin (1995) has shown, the compass-heading cue could still be available from the modulated field produced by the shark's head undulations during swimming.

3. Electrosensory Periphery

3.1. Ampullae of Lorenzini and Distribution of Receptors

The ampullae of Lorenzini are the electrosensory organs in elasmobranchs. Thin-walled, conductive jelly-filled canals open onto the body surface at one end, and terminate in swellings, called ampullae, at the other (Fig. 20.2A,B). The electroreceptor cells line the walls of the ampullae, and each of these has a synaptic contact with a primary afferent electrosensory nerve fiber. There are 4–5 ampullary swellings at the base of each canal, and 5–10 afferents each receiving their input from several thousand electroreceptor cells. The canals are arranged in 3 or 4 clusters on each side, with the ampullary swellings close together, and the canals radiating outward various distances to their pore terminations on the body surface. As discussed below, the long canals of some of the receptors make a contribution to sensitivity in large-scale electric fields, but they also permit clustering of the ampullae of the different receptors so that they share a common internal reference potential (Kalmijn, 1974). This is important for electrosensory noise suppression in the brain. In skates and rays, there are generally many canal pores on the leading edge of the pectoral fin, and ventrally on the snout and around the mouth. In sharks, the receptor distribution is restricted to the head (for details see Chu and Wen, 1963; Bodznick and Boord, 1986). Although the general patterns of pore distributions of batoids and sharks are described, only recently have these been interpreted in relation to the fish's natural ecology and behavior. Raschi (1986) examined the distributions of ampullary pores in 40 species of skates and found that different patterns were associated with different diets and habitats. This "neuroecological" approach was used to analyze the projection vectors of canals from ampullary clusters in the white shark and barndoor skate by Tricas (2001). Distinct projection patterns were found both among and within ampullary groups (Fig. 20.2C), and were postulated to serve different biological functions, including aspects of prey capture and orientation to uniform electric fields.

3.2. Receptor Sensitivity and Frequency Response

The electroreceptors of elasmobranchs are the most sensitive known biological detectors of electrical potential, responding to small fractions of a microvolt. What factors might account for this extreme sensitivity? The long conductive canal of some receptors, in conjunction with the fish's relatively low skin resistance, allows sampling over widely spaced points in an external voltage gradient. The high resistance of the sensory epithelium compared to the negligible resistance along the canal length assures that most of the available voltage drop takes place directly across the receptor cells (Waltman, 1966). In an external uniform field of 5 nV/cm, the potential drop across the sensory epithelium of a receptor organ with a 20-cm canal may be nearly 0.1 μV. But this is still an exceedingly small potential and detecting it would seem to require much greater sensitivity than could be provided by the familiar voltage-gated ion channels of nerve or muscle cell membranes.

Positive feedback and spontaneous activity may be the keys to this puzzle. The sensory epithelium at rest shows regenerative electrical activity, and even the dissociated receptor cells exhibit spontaneous impulses in the absence of stimulation (Araneda and Bennett, 1993). The apical, lumen-facing membranes of the receptor cells bear voltage-gated calcium (Ca) channels. According to the model proposed first by Obara and Bennett (1972), the apical faces of the individual receptor cells in the unstimulated receptor organ are held by a bias current at a membrane potential on the brink of threshold for a regenerative Ca spike, occasionally exceeding threshold. Excitatory cathodal electrosensory stimuli then increase the amount of this regenerative activity, which in turn
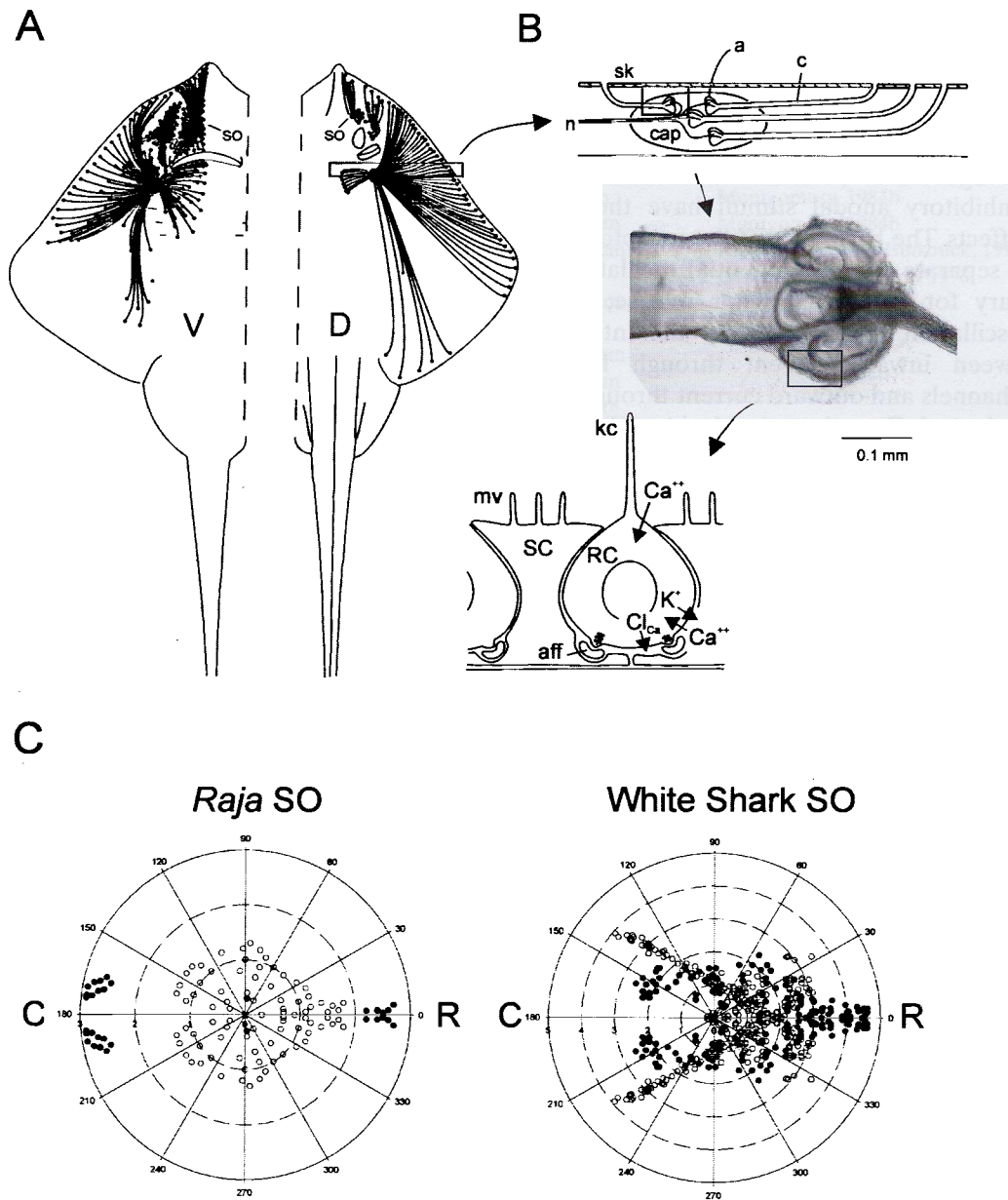
FIGURE 20.2. Ampullae of Lorenzini. (A) Distribution of receptors on the dorsal (D) and ventral (V) surface of *Raja erinacea*. (B) Schematic of receptor organs in cross section (*top*); high-contrast photo of a receptor ampulla and canal in wholemount (*lower left*); and electrosensory epithelium with known receptor cell ionic conductances (arrows) (*lower right*). (C) Polar plot of projection vectors of superficial ophthalmic (SO) receptor canals in the horizontal plane for the skate. Projections of dorsal group (filled circles) are distinct from those of canals that project ventrally (open circles). In skate, dorsal canals project in the rostral (R) and caudal (C) directions. Projections of canals on the ventral surface are omnidirectional. Dorsal superficial ophthalmic

canals in the white shark project almost parallel with the rostrocaudal axis, whereas the ventral canals project obliquely toward the edges of the head. These different projections may subserve different behaviors such as orientation to uniform fields (long canals with projections parallel to the body axis) vs. detection of prey (short omnidirectional canals near the mouth). Radius units are centimeters. Data are from Raschi (1986) and Tricas (2001). Abbreviations: a—ampulla; aff—afferent nerve ending; c—canal; cap—capsule; kc—kinocilium; mv—microvilli; n—nerve; RC—receptor cell; SC—support cell; sk—skin; SO—superficial ophthalmic ampullae. (Fig. 20.2B is extensively modified after Murray, 1974).

increases the depolarization of the basal face, and consequently the level of ongoing synaptic transmitter release and afferent nerve discharge rate (Clusin and Bennett, 1979). Inhibitory anodal stimuli have the opposite effects. The basal face of the receptors exhibits a separate ongoing potential oscillation necessary for neurotransmitter release; the basal oscillation is generated by the interplay between inward current through L-type Ca channels and outward current through K channels and Ca-activated chloride (Cl) channels (see Fig. 20.2B) (Lu and Fishman, 1995a,b). Voltage clamp studies (Clusin and Bennett, 1979) indicate that the channels of the electroreceptor cells are just the same as those of other excitable cell membranes and show no extraordinary sensitivity. Instead, the great sensitivity of the individual electroreceptor cells is just that which is inherent in a positive feedback system poised at threshold.

Although positive feedback systems at threshold are extremely sensitive, they generally gain that sensitivity at the cost of nonlinearity. Nevertheless, the firing rate of the electrosensory afferent fibers is a linear function of stimulus intensity over the natural stimulus range and this is probably because the individual receptor cells in most circumstances operate independently and fire asynchronously (but see Lu and Fishman, 1994). The number of receptor cells that are concurrently active determines the afferent firing rate at any given time, and electrosensory stimuli increase or decrease this proportion of active receptor cells.

One final factor contributing to receptor sensitivity is the great convergence of hundreds to thousands of receptor cells onto each afferent fiber. This convergence can lead to a $\sqrt{N}$ improvement (ca. 30× for a 1,000:1 convergence ratio) in the signal-to-noise ratio in the afferents for stimuli generating coincident activity among receptor cells. In summary, the extreme sensitivity of the receptors is achieved by the length and passive electrical properties of the canals, the spontaneous activity of sensory epithelium and afferent fibers, and the high convergence ratio of receptor cells to afferents.

Elasmobranch electroreceptors accommodate to mV changes in DC level without losing their absolute incremental sensitivity (Bodznick et al., 1993). A dipole stimulus of $1\,\mu V$ causes a similar change in afferent firing rate whether riding on a DC level of $2\,mV$ or $0\,mV$. The value of this accommodative mechanism to the skate is likely to be in adjusting to its own transcutaneous DC potentials such as those generated by osmoregulatory ion pumping. These can be $0.2\,mV$ or more in amplitude (i.e., about a thousand times the receptor threshold).

The physiology of elasmobranch electrosensory afferents has been extensively studied in a number of species, especially skates and stingrays. The afferents effectively respond to the voltage gradient developed between the pore opening on the skin and the interior of the animal adjacent to the base of the canal. As stated, the afferents are spontaneously active with an electrical gradient sensitivity of 1–25 I/s/μV/cm depending on species (Table 20.1). In the clearnose skate, afferent sensitivity increases as the animals grow (Sisneros et al., 1998). Since the afferents are spontaneously active, there is no discernible threshold in their response; however, the behaviorally determined threshold must correspond to a change in firing rate of only about a tenth of an impulse per second. Sinusoidal electric stimuli can be encoded by primary afferent neurons in the round stingray at levels as low as 10–20 nanovolts/cm (Tricas and New, 1998), which is near the behavioral response threshold of 1–5 nanovolts/cm. The enhanced sensitivity observed in the secondary processing cells known as ascending efferent neurons (AENs) of the dorsal nucleus may be at least partially due to convergence of primary afferents (Tricas and New, 1998).

The frequency sensitivity of the electroreceptors has also been determined for a number of different elasmobranch species (Fig. 20.3) and essentially exhibits a bandpass characteristic with a bandwidth (50% of maximal response) between about 0.1 and 10 Hz. The filter properties of the afferents appear to be determined largely by the properties of the receptor cells themselves, but canals longer than about 10 cm may contribute a low-pass characteristic to receptors (Waltman, 1966).

TABLE 20.1. Spontaneous activity (SA) and gain of elasmobranch electroreceptors and second-order neurons.

Animal	Cell type	SA (I/s)	Gain	Reference
P. triseriata	Afferent	18	4 I/s/μV/cm	Montgomery, 1984b
	Secondary cells	10	32 I/s/μV/cm	Montgomery, 1984b
R. erinacea	Afferent	14	0.9 I/s/μV/cm	Montgomery and Bodznick, 1993
	AENs	0	2.2 I/s/μV	Conley and Bodznick, 1994
U. halleri	Afferent	33	24 I/s/μV/cm	Tricas and New, 1998
R. eglanteria				Sisneros et al., 1998
Embryo	Afferent	12	2.5 I/s/μV/cm	
Juvenile		45	13 I/s/μV/cm	
Adult		45	19 I/s/μV/cm	

The frequency response curves of the clearnose skate change during ontogeny; the upper frequency range extends in juveniles, and then contracts in adults (Sisneros et al., 1998). The broad peak of frequency sensitivity in reproductively active adults is near the normal discharge rate of this species' electric organ. In Atlantic stingrays, increased sensitivity to low frequencies (0.5–2 Hz) takes place in wild males during the reproductive season and in the laboratory after exogenous testosterone treatment (Sisneros et al., 1998; Sisneros and Tricas, 2000), perhaps to enhance detectability of the female's standing or ventilatory potentials.

3.3. Reafference

In paralyzed animals (the default condition for most electrophysiological experimentation), the spontaneous activity of electrosensory afferents is relatively steady. This situation changes dramatically in freely breathing animals with the afferent nerves often driven over most of their dynamic range in time with the breathing movements (Fig. 20.4) (Montgomery, 1984a). This ventilatory self-stimulation (reafference) is driven by the standing potential that exists between the inside and the outside of the animal and that is modulated by changes in resistance pathways caused by opening and closing of the mouth and spiracle. The "inside/outside" origin of the potential determines that ventilatory reafference is very similar in all of the electroreceptors irrespective of where their pore openings are on the body surface. Thus ventilatory reafference is "common mode" across the afferent population. As we shall see, this has implications for the removal of ventilatory reafference by the electrosensory circuits of the hindbrain.
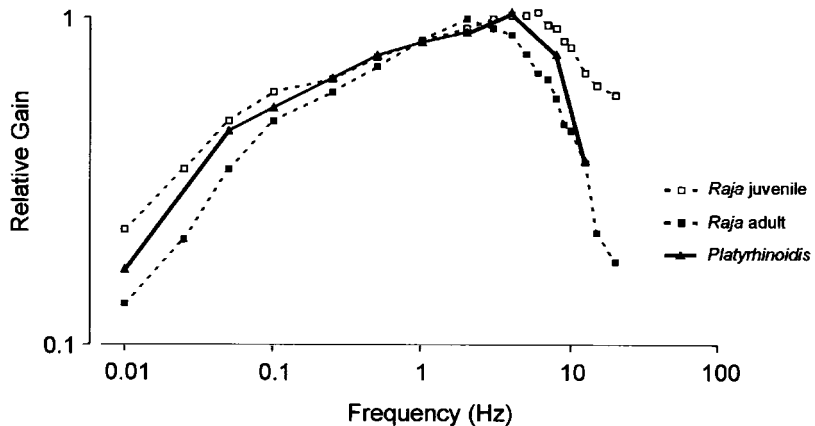

FIGURE 20.3. Frequency response functions of electrosensory primary afferents. Note the broader response in *Raja* juveniles than adults (Sisneros et al., 1998). *Platyrhinoidis* data from Montgomery (1984b).
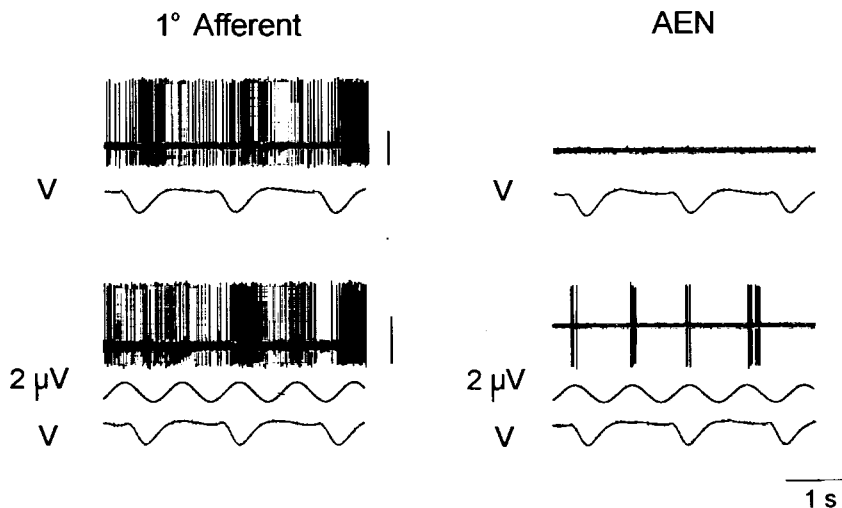
1° Afferent

AEN

FIGURE 20.4. Reafference comparison for primary afferent and AEN. The ventilatory reafference in a primary afferent recorded from a freely breathing skate (top) masks the response of the same unit to a 2-µV, 1-Hz sinusoidal dipole field (bottom). AEN recorded about the same time was unaffected by ventilatory activity (*top*) but still very sensitive to the 2 µV dipole field (*bottom*). The traces just below the spike records in each case are the output of a force transducer monitoring ventilatory movements. The sinusoidal traces indicate the dipole field stimulus. (From Bodznick et al., 1999. Reprinted by permission of Company of Biologists Ltd.)

4. Central Processing

4.1. Hindbrain Circuits

The electrosensory nerves enter the dorsal octavolateral nucleus (DON) on the dorsolateral wall of the hindbrain. The DON has a distinct molecular layer cap composed of axons of granule cells from the auricular lobes of the cerebellum. Below the molecular layer, in what is termed the peripheral zone of DON, is a band of neuronal cell bodies, many of which are the so-called AENs. The rest of the nucleus is termed the central zone. The principal circuits of the DON are illustrated in Figure 20.5. Afferents enter the DON and course rostrally and caudally through the central zone of the nucleus. They make contact with the ventral dendrites of the AENs, and also with interneurons of the central zone. Many of these interneurons are GABAergic and in turn make inhibitory synaptic contacts with the AENs (Montgomery and Bodznick, 1993; Duman and Bodznick, 1996, 1997). AENs also have extensive dorsal dendrites that receive multiple inputs from parallel fibers and stellate interneu-
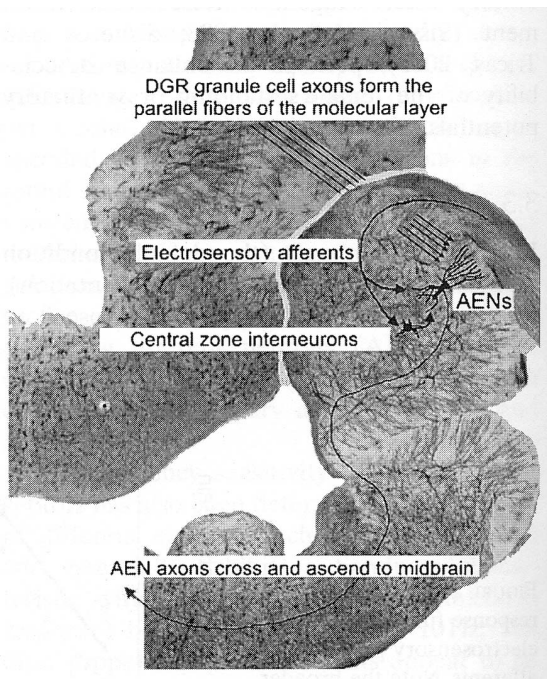

FIGURE 20.5. Principal neuron (AEN—ascending efferent neuron) and circuits of the dorsal octavolateralis nucleus (DON) are shown overlaying Golgi-stained transverse sections.

rons of the molecular layer. The stellate cells are inhibitory and GABAergic. The AEN axons cross the midline and ascend to the contralateral midbrain. Crossed inhibitory pathways (not illustrated in Fig. 20.5) also join the bilateral dorsal nuclei.

4.2. Receptive Fields and Common Mode Rejection

The responses of AENs differ from primary afferents in several respects. The spontaneous activity of AENs is much lower and less regular, they are more sensitive to extrinsic electrical fields (Table 20.1), they have complex receptive fields, and, most strikingly, they show very little response to the animal's own ventilatory movements. The low spontaneous rate and the lack of response to ventilation are illustrated in Figure 20.4. Whereas in the typical primary afferent it is difficult to see the spike-rate modulation of an external $2\mu V$ stimulus over the top of the ventilatory modulation, the typical AEN, with its zero spontaneous activity and no ventilatory modulation, provides a very clear modulation to the external stimulus. If one considers the ventilatory modulation to be "noise," then the clear modulation to the external stimulus coupled with the zero response to ventilation represents an effectively infinite improvement in the signal-to-noise ratio between the primary afferent and the AEN illustrated in Figure 20.4. One of the main factors in this dramatic improvement in the signal-to-noise ratio is that the AENs have balanced excitatory and inhibitory components to their receptive fields. Whereas primary afferents are activated by a stimulus applied to a single electrosensory canal pore, AENs have an excitatory receptive field consisting of one or several canal pores, and an inhibitory receptive field that can be either focal (one or several pores) or diffuse including components from the contralateral side. Because the ventilatory modulation in afferents is similar across the whole afferent population, balanced excitatory and inhibitory inputs onto the AEN can cancel most of the ventilation by simple subtraction (Montgomery, 1984b; New and Bodznick, 1990; Bodznick and Montgomery, 1992; Bodznick et

al., 1992). This is the principle of common-mode rejection (CMR) that is used in differential electronic amplifiers to remove common-mode noise present at the positive and negative input terminals. Inhibitory receptive field input to AENs is mediated by GABAergic interneurons and commissural neurons of the DON (Duman and Bodznick, 1996, 1997).

Modeling studies show that CMR can remove most, but not all of the ventilatory reafference due to differences in the dynamics of the excitatory and inhibitory pathways (Nelson and Paulin, 1995). In addition, significant reafference from the fish's swimming and other movements is generally not common mode but rather affects different parts of the receptor array differently. Common mode rejection is ineffective against such noise. For these reasons, an additional more sophisticated filter is required to fully remove reafferent modulation in the AENs. This so-called adaptive filter is a property of the molecular layer of the DON and is described below.

Balanced excitatory and inhibitory receptive fields are required for CMR of ventilatory input. However, the precise nature of the receptive field structure also has a major impact on how external electric field stimuli are encoded at the level of the hindbrain (Salypongse et al., 1992). AENs with a focal excitatory receptive field and a diffuse inhibitory field do not respond well to uniform external fields. Widespread focal excitatory and inhibitory fields would be best suited to encode uniform fields. Kalmijn's (1997) approach algorithm and electronavigational hypothesis both require the animal to determine its angle with respect to the external field; however, in the little skate and in the carpet shark, widespread focal receptive fields appear to be the exception rather than the rule. From this we can conclude that, for these species, the spatial localization of small external dipoles, such as prey, is probably the most important function of the electrosense. As an aside, it is interesting that *R. erinacea* orienting to small dipoles ignore the vertical dimension. Dipoles held above the pectoral fin produce a positioning of the mouth to the position on the substrate below where the stimulus was presented (M. Jarnot and D.

Bodznick, unpublished). The skate has reduced source localization to a two-dimensional problem.

4.3. Adaptive Filter

The molecular layer of the DON provides the substrate for an adaptive filter that can cancel any self-generated noise. The presence of this additional filter is demonstrated in Figure 20.6. The experiment is to record from an AEN in a freely ventilating animal. A stimulus is presented to the excitatory receptive field triggered by the animal's own breathing movements (Fig. 20.6A). The AEN initially responds strongly to this stimulus, but over a time course of 10 minutes or so, the response declines (Fig. 20.6B). The AEN has learned to suppress the response to a stimulus that is correlated with its own movements. A control stimulus presented at about the same rate, but not triggered by ventilation, shows no decline over the same period. The mechanism underlying the cancellation of the ventilation-triggered stimulus is revealed when the stimulus is turned off; a negative image of the initial response remains (Fig. 20.6B, poststimulation). Where the AEN was initially excited it is now inhibited; where the AEN was inhibited, it is now excited. During the course of the coupling, a cancellation signal input to the AEN has developed that suppresses the AEN's response in an apparently additive fashion. After the stimulus has ended, the cancellation signal is removed with a similar time course to its development.

How could the AEN learn to cancel inputs associated with its own movements? What is the source of the cancellation signal, and how is it constructed and modified? The answers to these questions lie in the molecular layer circuitry. The parallel fibers of the molecular layer are the axons of granule cells from the auricular lobe of the cerebellum—specifically from an area termed the dorsal granular ridge (DGR). Recordings from this area show that DGR cells receive a variety of inputs, including efference copy signals from the motor control centers (Hjelmstad et al., 1996). In other words, the neural circuitry that drives ventilation, and presumably other movements, sends a copy of all the motor signals to the DGR. In addition, DGR cells receive information from proprioceptors activated by movement, and other inputs including descending electrosensory feedback. In effect, the molecular layer provides a rich matrix of information related to, among other things, self-generated movement. The parallel fibers of the molecular layer contact the spiny dendrites of the AENs, with many thousands of excitatory parallel fiber synapses on each AEN. In addition, parallel fibers contact stellate interneurons in the molecular layer that in turn make inhibitory connections with the AENs. So in theory, excitatory and inhibitory selections of the molecular layer information could be combined onto one AEN to generate the required cancellation signal in the molecular layer dendrites. The cancellation signal then would null the sensory reafference impinging on the ventral dendrites of the AEN. This description still begs the question as to how the selection of molecular layer information is made. How does each particular AEN, through experience, come to be selectively affected by just those molecular layer inputs that comprise an effective cancellation signal? It turns out that two simple learning rules are sufficient to make the selection of molecular layer inputs (Montgomery and Bodznick, 1994):

1. Each time the AEN is activated by the electrosensory inputs, turn down the gain of coincidentally active excitatory parallel fiber synapses (and/or conversely turn up the gain of coincidentally active inhibitory stellate cell synapses).

2. If parallel fiber synapses are active in the absence of AEN activity, increase their synaptic gain (and/or decrease the gain in the case of inhibitory synapses).

In effect, the changes in synaptic strength directed by these learning rules result in a reduction of molecular layer excitatory drive to the AEN to compensate for the increase in excitatory electrosensory input on the AEN's ventral dendrites. A net increase in the molecular layer excitatory drive compensates for an increased inhibitory electrosensory input ventrally.
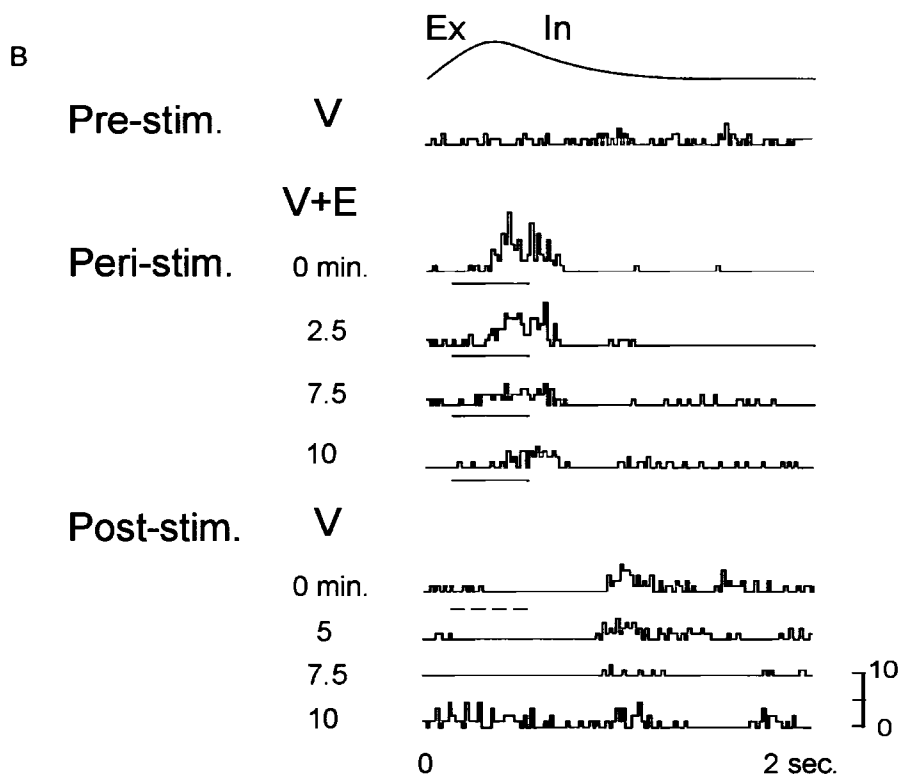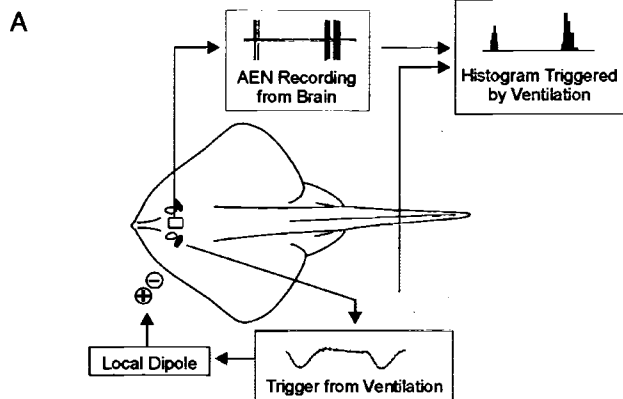
FIGURE 20.6. Adaptive filter experimental setup and results. (A) A monitor of branchial ventilatory movements of a partially immobilized and decerebrated skate triggers the computer-generated histogram of AEN spike activity recorded from the brain. The same trigger synchronizes presentation of a local dipole E field stimulus with the onset of ventilation. (B) Histograms of the AEN spiking activity during the ventilatory cycle recorded before (pre-stim.), during (peri-stim.), and after (post-stim.) the presentation of a 2-μV dipole time-linked with the ventilatory movements. Top trace schematically illustrates the ventilatory cycle, and the line beneath each trace indicates dipole stimulus timing. Note the decline in the E field response during the period of coupling (compare peri-stim. 10 vs. 0 min.), and the presence of a negative image of the initial response at stimulus offset (compare post-stim. 0 min. with pre-stim.) No such decline in response is observed if the stimulus is given at a similar rate but not time-linked to ventilation. Abbreviations: Ex—exhalation; In—inhalation; V—ventilatory movements alone; V+E—dipole field stimulus coupled with ventilation.
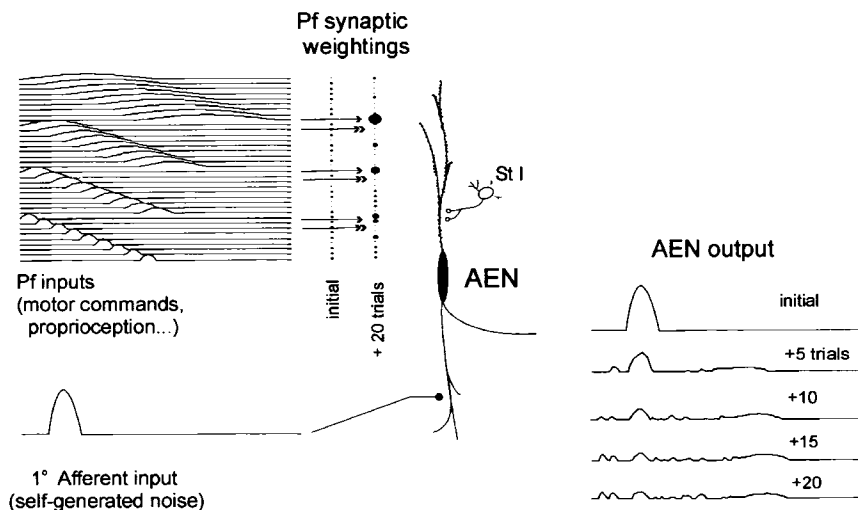
FIGURE 20.7. Adaptive filter model of Montgomery and Bodznick (1994). Following learning rules described in the text, the relative strengths (or weightings) of the excitatory parallel fiber (Pf) synapses to the apical dendrites of the AEN are altered through experience in order to construct a cancellation signal input that is the inverse of the expected self-generated noise brought in by the 1° afferents. The cancellation signal then adds with the 1° afferent input in order to eliminate the self-generated noise from the AEN output. In this model, molecular layer stellate interneurons (St I) provide a steady background of inhibition against which Pf excitation can be added or removed. Filled circles at the center of the figure denote by their size the strength of the synapse of each parallel fiber onto the AEN. Note that after 20 trials the learning rules result in a strengthening of the Pf synapses from those parallel fibers whose activity is consistently out of phase with the noise (single-headed arrows), and a reduction in the weighting of synapses of parallel fibers whose activity is consistently coincident with the noise (double-headed arrows). Please see text for additional details.

A simple computer model demonstrates the utility of these synaptic learning rules to generate reafference cancellation (Fig. 20.7). In this model, the parallel fiber signals are a series of different half-period sine waves staggered through the ventilatory cycle. Although these are clearly artificial, they can be thought of as the sequential motor signals that would drive the sequential movements of ventilation, along with the resulting propriosensory feedback. Below the parallel fiber signals is a representative half-sinusoid reafference, or self-generated noise, that has been constructed so as not to match any one of the parallel fiber signals. Initially the parallel fibers are connected with random, low synaptic weightings to the AEN, and the AEN output has a strong component of the self-generated noise. The computer program simply steps through the files applying the learning rules. If the AEN is silent, each of the parallel fiber files is examined to see which are active and which are not. Those that are active have their connection strengths incremented by a small amount (rule 2). If the AEN is active, coincidentally active parallel fibers have their connection strengths decreased (rule 1). With successive passes through the files (or with each ventilatory cycle), the "self-generated noise" in the AEN output is successfully canceled. In this simple model, stellate cell inhibitory synapses have been represented as fixed and they provide a constant background level of inhibition against which the parallel fiber excitatory inputs can be added or removed to achieve net shifts in the molecular layer excitatory and inhibitory input to the AEN. The anatomical arrangement with stellate interneurons receiving convergent input

from thousands of different parallel fibers seems to suggest such a role for them in providing nonspecific background inhibition. However, models in which both inhibitory and excitatory molecular layer synapses are adjustable also work well (Nelson and Paulin, 1995).

As Figure 20.7 illustrates, this simple model is robust, and cancels arbitrary waveforms provided they are not too dissimilar to those in the parallel fibers. In essence, the model does a generalized inverse Fourier transform, synthesizing an arbitrary wave out of a series of quasi-sinusoids. The only reason that the filter does not also cancel extrinsic electrosensory signals is that they are not consistently linked with any of the molecular layer inputs; they are not predictable.

Since the learning rules are based on the activity of each individual AEN, the adaptive filter mechanism results in the development of a neuron-specific cancellation signal. Each AEN receives its own unique cancellation signal input that is fitted to the particular form of the reafference that the neuron experiences during a particular behavior (Fig. 20.8).

Experimental tests of the model have been conducted showing that the correlation of intracellular depolarization with breathing produces an appropriate cancellation signal, and that correlation of DGR stimulation with excitatory input to an individual AEN also effects a cancellation (Bodznick et al., 1999). Anti-Hebbian synaptic learning and a similar adaptive filter have also been clearly demonstrated in the electrosensory lateral lobe of weakly electric fishes (Bell et al., 1993, 1997; Bastian, 1995).

4.4. Ascending Projections and Midbrain Maps

Noise cancellation forms an important first stage to sensory processing in the nervous system. The AEN receptive field structures and adaptive filter precondition the signals before they are sent further up the neuraxis. Much less is known about these higher electrosensory areas in elasmobranchs. Ascending information is sent to a number of nuclei en route to the midbrain, but the functional correlates of these pathways is as yet unknown (Bodznick and Boord, 1986). At the midbrain level, electrosensory information is mapped into the regions of the tectum and the lateral mesencephalic nucleus (LMN) (Bodznick, 1991) and also into the anterior mesencephalic nucleus (AMN) in *Platyrhinoidis* (Schweitzer, 1986).
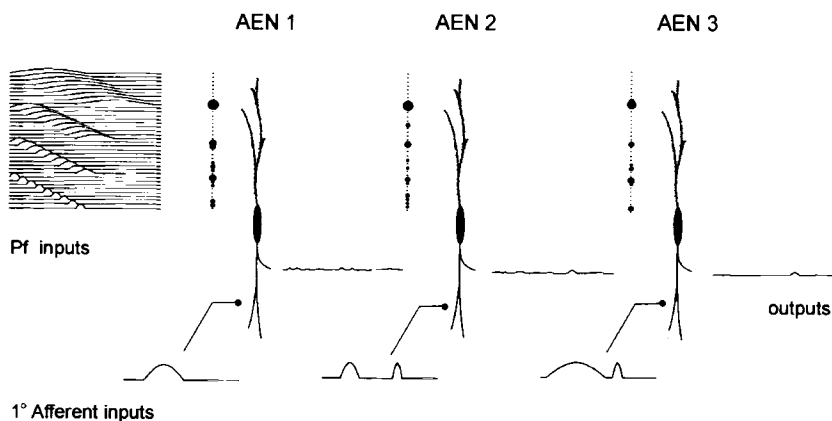
FIGURE 20.8. The adaptive filter is neuron-specific. The ouput of the model illustrates that since changes in the synaptic weightings are directed by the activity of each individual AEN, different patterns of reafference associated with a particular behavior result in a unique set of synaptic weightings for each AEN. That is, after the learning each AEN receives its own unique cancellation signal matched to eliminate the particular form of reafference it receives.

The electrosensory maps in the tectum in skates are in register with the visual maps, and both form an extensive overrepresentation of the lateral fin margin and the animal's horizon. Thus, like the skate's orienting responses to dipoles, the tectal sensory representation is largely a two-dimensional map of the horizontal plane. The electrosensory map of the LMN covers the ventral surface of the animal for which there is no visual equivalent from the dorsally placed eyes. Forebrain targets of the ascending electrosensory pathway include two separate nuclei in the diencephalon and at least one area in the medial pallium of the telencephalon (Schweitzer, 1983; Bodznick and Northcutt, 1984), but an examination of the physiology of these areas must await future studies.

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