Chapter 41

Electroreceptors and Magnetoreceptors

Timothy C. Tricas and Bruce A. Carlson

Chapter Outline

I. SUMMARY

Many animals have the ability to detect electric and magnetic fields. Although many species respond and orient to magnetic stimuli, only recently were putative vertebrate receptor systems identified. All organisms generate weak electric fields in water, due to an uneven distribution of ions between the interior of the organism and the external aqueous environment. Ampullary electroreceptors are an ancestral vertebrate trait that allows for the passive detection of these electric fields, which is useful for detecting prey, predators and mates. Although ampullary electroreceptors were lost during vertebrate evolution, they subsequently re-evolved several times independently. In two groups of teleost fishes, both ampullary and tuberous electroreceptors evolved, the latter specialized for the detection of actively generated electric organ discharges, or EODs. These fish generate EODs to communicate in the electrosensory domain, as well as actively to sense their environment by detecting distortions in the self-generated EOD. Many physiological mechanisms involved in electrosensory processing are unique.

II. INTRODUCTION

The production of potent shocks by the electric catfishes (*Malapterurus*), eel (*Electrophorus*) and rays (*Torpedo*) to capture prey were reported in antiquity but it was much later that the shock from these animals, and the imperceptible discharges of others, were found to be electrical in nature (Moller, 1995). Further, the production of weak electrical discharges in the millivolt range indicated that weak electrical signals serve functions other than attack or defense (Lissman, 1958; Lissman and Machin, 1958). Because these weak electrical discharges offered a possible system for sensing the environment and communication among conspecifics, scientists sought the identity of the sensory receptors that detected them. Thus, the study of electroreception arose and has since produced much information on electroreceptors, electrogenic organs and their physiology.

Electroreception is an ancient vertebrate sense that occurred in the predecessors of jawless and jawed vertebrates (Bullock et al., 1983). The electrosense is retained in numerous extant taxa (Fig. 41.1) including lampreys, chondrichthyan fishes, bichirs, sturgeon and paddlefishes, lung-fishes, coelacanths and non-anuran amphibians (salamanders and caecilians). Phylogenetic analysis of character traits indicates that the electrosenses of these animals are homologous, reflecting their common phylogenetic origin (Bullock et al., 1983; Bullock and Heiligenberg, 1986). Electroreception, however, was lost in the vast majority of teleosts, the lineage to which most modern bony fishes belong. Most teleosts, together with their sister groups of gars and bowfin, which collectively comprise the Neopterygii, lack an electrosense. Remarkably, only two distantly related lineages of teleost fishes do possess electroreceptors and it is apparent from character analysis that

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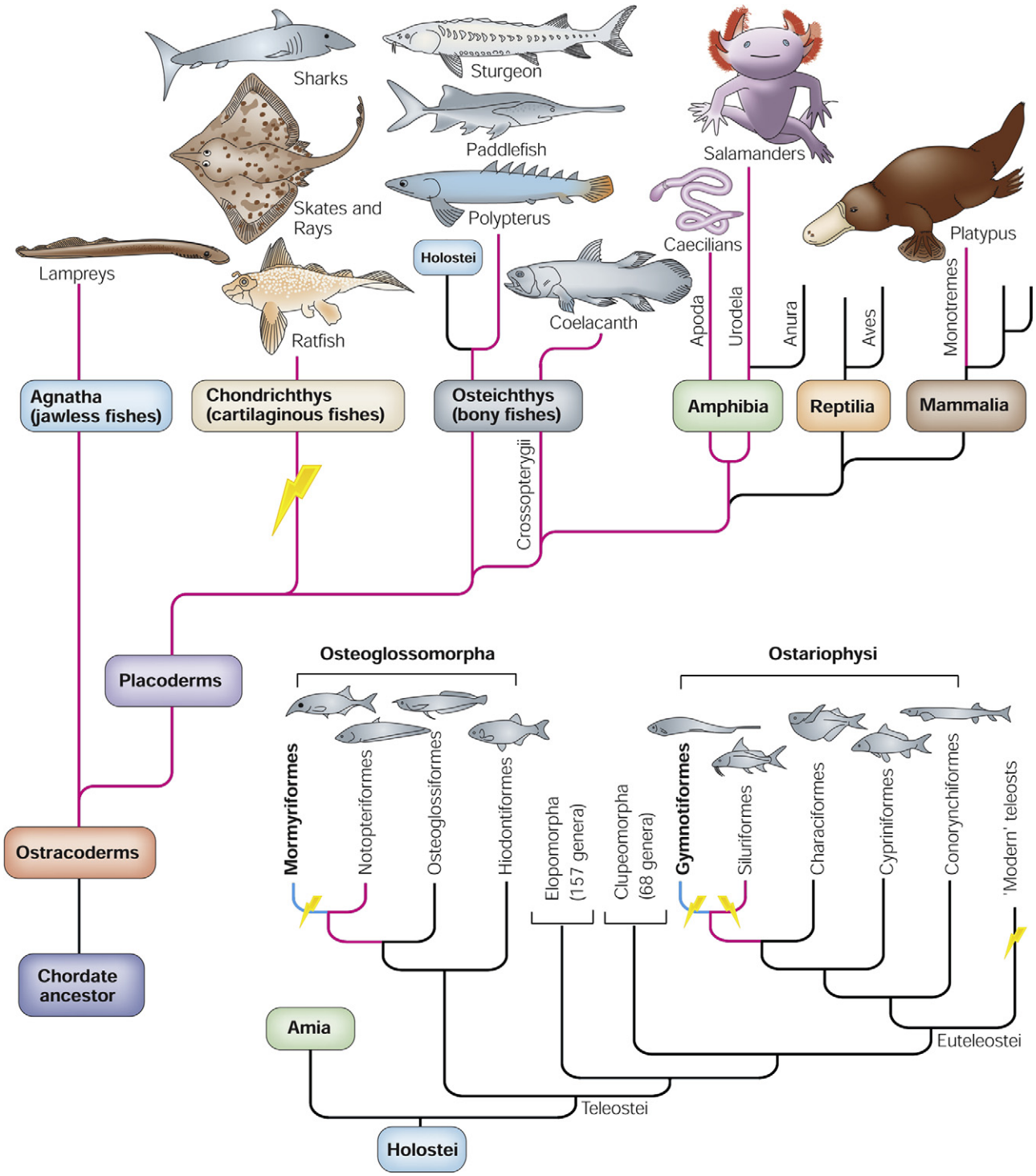


FIGURE 41.1 Cladogram showing the phylogenetic distribution of electroreception and electric organs. Clades with ampullary electroreceptors are indicated by magenta lines, clades with both ampullary and tuberous electroreceptors are indicated by cyan lines (and bold lettering), and clades with electric organs are indicated by lightning bolts. *(Modified from Rose, 2004).*

these have evolved independently (Fig. 41.1). In addition, two species of monotreme mammal, the semiaquatic platypus and the truly terrestrial echidnas, are electroreceptive (Fig. 41.1). Because electrosenses are not present in most other tetrapod lineages, this clearly represents yet another "reinvention" of electroreception.

Electroreceptors of most aquatic vertebrates are classified as either ampullary or tuberous (see Zakon, 1986,

1988). *Ampullary receptors* respond to low-frequency stimuli with best sensitivity to varying electric frequencies between 0.1 and 20 Hz. This range of frequencies includes the detection of standing (DC) bioelectric fields produced by other aquatic organisms that are experienced by a swimming electrosensitive animal as well as those produced by non-living physicochemical sources in aquatic environments. Detection of these extrinsic sources by ampullary receptors is often referred to as electroreception in the *passive mode* (Kalmijn, 1974, 1988). *Tuberous electroreceptors* are tuned to much higher frequencies, with best frequencies in the 0.1−10 kHz range. Tuberous organs are found in fishes possessing weak electric organs of the sort initially described by Lissman (1958) and these receptors have best frequencies that correspond closely to the peak spectral frequency of the discharge of the animal's electric organ. The tuberous organs detect changes in the intensity and temporal pattern of the electric field produced across the body by the electric organ discharge (EOD), whether by the presence of items in the field of objects with different conductances than the water, or by the addition of the electric organ discharges of another individual. Such forms of electrodetection that respond to alterations of the self-generated EOD and the detection of induced electric fields caused by swimming through the Earth's magnetic field are referred to as electroreception in the *active mode* (Kalmijn, 1988). In this chapter, we consider current information on the morphology and physiology of ampullary and tuberous electroreceptors. Space limitations preclude a discussion of the central processing of electrosensory information, which remains one of the most captivating stories in modern neuroethology. The reader is referred to several excellent recent reviews on this topic (Bullock and Heiligenberg, 1986; Bell and Maler, 2005; Kawasaki, 2005).

The ability directly to detect geomagnetic fields is known as *magnetoreception* and the ability to sense and respond to magnetic stimuli is known for a number of animal groups and bacteria (for reviews see Tenforde, 1989; Wiltschko and Wiltschko, 1995). These studies are primarily behavioral, with incomplete information on magnetoreceptor organs and receptors in most taxa. The direct identification of a magnetoreceptor cell has many technical challenges because direct magnetoreception is believed to be associated with localized deposits of magnetite crystals (Fe_3O_4) which are extremely small, easily contaminated, degrade easily in preserved tissues and are difficult to verify. Localized magnetite domains are described in tissues of bees, salmon, tuna, turtles, pigeons, dolphins, humans and many other species (Wiltschko and Wiltschko, 1995). In several birds and one species of fish, candidate magnetoreceptor cells were identified in close association with small rostral branches of the trigeminal nerve. In the homing pigeon, superparamagnetic crystals occur along the surface of afferent nerve terminals of the somatosensory branch that innervates the upper beak (Fleissner et al., 2003) and this arrangement is similar in other migratory and non-migratory species (Falkenberg et al., 2010). Neurophysiology experiments show that fast adapting trigeminal neurons in bobolinks respond to changes in applied magnetic fields as low as 30−50 nT, whereas slow adapting units respond as amplitude detectors (Beason and Semm, 1987; Semm and Beason, 1990). Potential receptor cells that contain single-domain magnetite exist in the lamina propria of the rainbow trout olfactory rosette and are in close association with endings of a rostral branch of the trigeminal nerve that penetrates the olfactory epithelium (Walker et al., 1997; Diebel et al., 2000). Single cell neurophysiology bench experiments show that units respond to rapid changes in applied magnetic fields (Walker et al., 1997). Indirect magnetoreception is also possible in some electroreceptive taxa via the detection of electric fields induced by an animal's movement through a geomagnetic field or drifting in an oceanic current (see discussion later). Evidence for chemical magnetoreception that involves magnetic actions on correlated spin states of radical ions is also proposed for the bird visual system (Ritz et al., 2000) but is not covered here. For recent reviews of the waning magnetoreception controversy, readers are referred to Johnsen and Lohmann (2005) and Walker et al. (2007).

III. AMPULLARY ELECTRORECEPTORS

The wide phylogenetic distribution of ampullary electroreceptors among extant vertebrate taxa indicates that this class of electroreceptor has served important biological functions for hundreds of millions of years and has subsequently "re-evolved" several times (see Fig. 41.1). With the exception of weakly-electric fishes that also possess tuberous electroreceptors, most species with ampullary electroreceptors lack electric organs. Thus, behaviorally relevant ampullary stimuli are thought to originate primarily from extrinsic sources. Ampullary electroreceptors are known to be important for the detection of prey (Kalmijn, 1971; Tricas, 1982; Wilkens et al., 2001), mates (Tricas et al., 1995), potential predators (Sisneros et al., 1998) and orientation to local inanimate electric fields (Kalmijn, 1982; Pals et al., 1982). In addition, the ampullary electroreceptor system is theoretically capable of mediating navigation by detecting electric fields induced by movement of the animal through the Earth's magnetic field (Kalmijn, 1974, 1988; Paulin, 1995), which would represent a form of electroreception in the *active mode*.

IIIA. Development and Morphology

Information on the ontogeny and development of electroreceptors is based largely on descriptive studies and we

refer readers to the excellent recent discussion provided by Northcutt (2005). Ampullary electroreceptor cells in non-teleost aquatic vertebrates develop from ampullary primordia that are derived from the neural crest in the shark (Freitas et al., 2006), associated with the lateral line placodes and sensory ridges (Northcutt et al., 1994, Gibbs and Northcutt, 2004) and possess either a kinocilium, microvilli or both. In teleosts, it remains to be experimentally demonstrated whether tuberous electroreceptors arise from induction in the general ectoderm (Vischer, 1995) or from lateral line placodes (Northcutt, 2003). In contrast, the electrosense of monotreme mammals evolved as a specialization of the trigeminal nerve associated with dermal mucus glands of the snout (Gregory et al., 1989; Pettigrew, 1999).

The lampreys possess an electroreceptor known as an *end bud* that differs considerably in morphology from the ampullary electroreceptors of other fishes (Ronan and Bodznick, 1986). Each end bud consists of numerous support cells and three to 25 sensory cells in the epidermis that are in direct contact with the surrounding water. Individual receptor cells have numerous small microvilli on the apical surface but lack a kinocilium. Small groups or lines of end buds are distributed over the head and body surface with multiple buds being innervated by a single sensory lateral line nerve fiber (Bodznick and Preston, 1983; Ronan, 1986). The excitation of end bud electroreceptors by cathodal (−) stimuli indicates a possibly similar transduction mechanism as the ampullary receptors of more derived non-teleosts (see discussion below). However, it is not known whether end buds represent the ancestral electroreceptor state or whether they are a derived condition unique to the lampreys.

Elasmobranch fishes (rays, skates and sharks) and rat fishes (Fields et al., 1993) possess ampullary electroreceptor organs of a similar morphology. In elasmobranch fishes, the electroreceptive unit is a highly specialized structure known as an *ampulla of Lorenzini* (Fig. 41.2). The ampulla proper in the marine skate is composed of multiple *alveolar sacs* or diverticulae which share a common lumen (Waltman, 1966). The apex of each ampulla chamber is connected by a highly insulated *marginal zone* to a single subdermal *canal*, which is approximately 1 mm in diameter and terminates as a small epidermal pore. The canal wall is 1−2 μm thick and composed of two layers of flattened epithelial cells, which are separated by a basement membrane to which the lumenal layer is also united by tight junctions. Both the canal lumen and the ampullary chambers are filled with a K^+-enriched, mucopolysaccharide, jelly-like matrix that is secreted by the superficial layer. While the resistivity of the gel (25 ohm cm) is similar to that of sea water and has similar responses as seawater to standing DC fields, recent work shows that the electrical properties of the gel exhibit reduced electrical admittance to varying electric stimuli. In combination with long canals

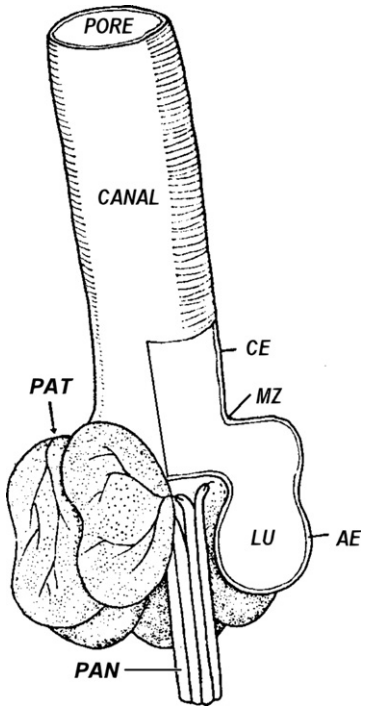
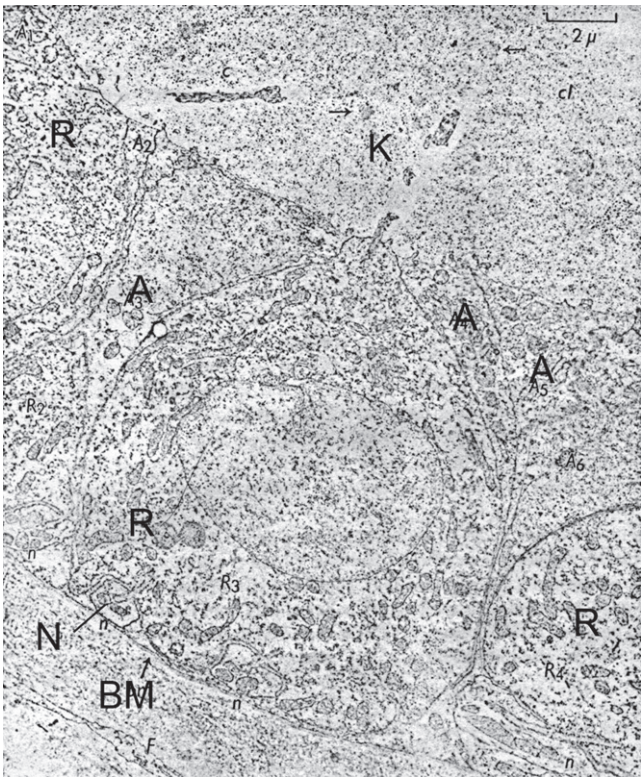


FIGURE 41.2 Ampulla of Lorenzini from the marine skate, *Raja.* The ampulla proper consists of multiple alveoli formed by the alveolar epithelium (AE). A high-resistance marginal zone (MZ) connects the sensory walls of the ampulla to the high-resistance canal epithelium (CE), which projects to the surface of the skin and terminates as a small pore confluent with the surrounding water. The ampulla lumen (LU) and canal are filled with a gel that provides electric conductivity along the length of the canal. Myelinated primary afferent neurons (PANs) innervate the base of the ampullae and their unmyelinated primary afferent terminals (PATs) receive chemical excitation from the basal region of the sensory cells in the epithelial layer. *(Modified from Waltmann, 1966, with permission).*

of narrow 1 mm diameter, the high resistance ampulla−gel−canal complex promotes detection of differences along the length of the canal rather than direct isopotential contact between the ampullary electroreceptors and seawater at the location of the surface pore (Brown et al., 2002, 2005). The sensory epithelium within the alveolus is composed of two cell types, which form a monolayer that is approximately 15 μm thick (Fig. 41.3). The vast majority of the alveolar surface is formed by accessory cells that are highly resistive to transmembrane currents and are bound together by tight junctions that prevent ionic leakage across the lumenal and basal surfaces of the epithelium. Interspersed among the accessory cells are flask-shaped receptor cells (thought to be modified hair cells), which possess a single kinocilium on the apical surface and lack microvilli. This physical arrangement results in only a small fraction of the receptor cell surface being exposed to the ampullary chamber.

The basal membrane surface of the receptor cell forms a ridge seated in a postsynaptic invagination that is separated by a distance of 100−200 Å (Waltmann, 1966).



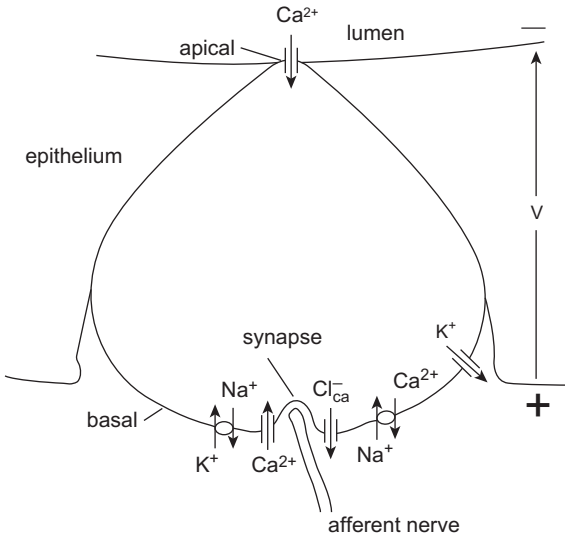


FIGURE 41.3 Receptor cell of the ampulla of Lorenzini in the skate, *Raja*. Top figure is photomicrograph of flask-shaped receptor cells (R) and adjacent accessory cells (A) that are united by tight junctions to form the alveolar epithelium. A single kinocilium (K) projects from each receptor cell into the lumen and, together with a small portion of the apical surface, is exposed to electric stimuli. Primary afferent neurons (N) innervate the basal portion of the receptors. The basement membrane (BM) is located beneath the sensory epithelium (*modified from Waltmann, 1966*.). Bottom figure shows ion channels and transporters involved in steady state conductance and sensory transduction. The excitable region of the cell is the apical membrane that has a partially activated inward bias current. The apical conductance is thought to work with oscillations created by exchangers and channels in the basal membrane that produce regular afferent discharges at the postsynaptic neuron. A weak electric stimulus in the ampulla that is more negative than the potential at the outside basal surface results in excitation of the cell and increased discharge potential in the afferent nerve. *(Top figure from Waltmann, 1966 with permission from Wiley Press and bottom figure modified from Lu and Fishman, 1994 with permission from Elsevier Limited, Kidlington, Oxford.)*

A *synaptic ribbon* about 250 Å wide and 2 μm in length is located within the presynaptic ridge. A single layer of synaptic vesicles covers the ribbon and exocytotic release of chemical neurotransmitter contained within these vesicles depolarizes the postsynaptic membrane of the innervating fibers of the anterior lateral line nerves. Unlike the hair cell receptors of the mechanosensory lateral line and octaval systems, all ampullary electroreceptors, both primitive and derived, lack efferent innervation.

Chondrichthyan fishes typically possess hundreds (or thousands) of ampullae that are associated in specific *ampullary clusters* associated with specific branches of the anterior lateral line nerve and are often closely bound by a dense matrix of connective tissue (Fig. 41.4A). From these clusters the subdermal canals radiate omnidirectionally and terminate in surface pores on the head and on the enlarged pectoral disk of batoids (Rivera-Vicente et al., 2011). The multiple orientations of the receptor canals and the copious distribution of the ampullary pores over the cephalic surface provide an extensive array of receptors with a high degree of spatial resolution. The morphology of the ampullary electroreceptors in freshwater elasmobranchs is thought to reflect sensory adaptations to their highly resistive environment (Kalmijn, 1974; Raschi and Mackanos, 1989). The freshwater rays, *Potamotrygon* and *Dasyatis garouaensis*, have a hypertrophied, thick epidermis that functions to increase transcutaneous electrical resistance. The ampullary electroreceptors are greatly reduced in size and are referred to as *miniampullae* or *microampullae*, which are distributed individually across the skin rather than in clusters and which have very short canals (about 0.3−2.1 mm long) that traverse the integument.

The anatomy and organization of ampullary electroreceptor organs in other non-teleost fishes and amphibians are generally similar to those of elasmobranch fishes, with which they are believed to be homologous. Ampullary electroreceptors in chondrostean (sturgeon and paddlefishes), cladistian (bichirs) and dipnoan fishes (lungfishes) share in most respects a similar morphology among alveoli, canals and ampullary pores. However, the ampullary organs in these freshwater fishes are most commonly arranged as single units or small groups (as opposed to large clusters) and have very short (generally <0.25 mm) and small diameter (generally <0.14 mm) canals. The abundance of receptors are distributed in the head region, with the exception of the lungfishes, in which there are single ampullary electroreceptors on the head and small groups consisting of three to five ampullae scattered widely over the body (Pfeiffer, 1968). Ampullary electroreceptors of the head are innervated by a ramus of the anterior lateral line cranial nerve, while those on the body are innervated by

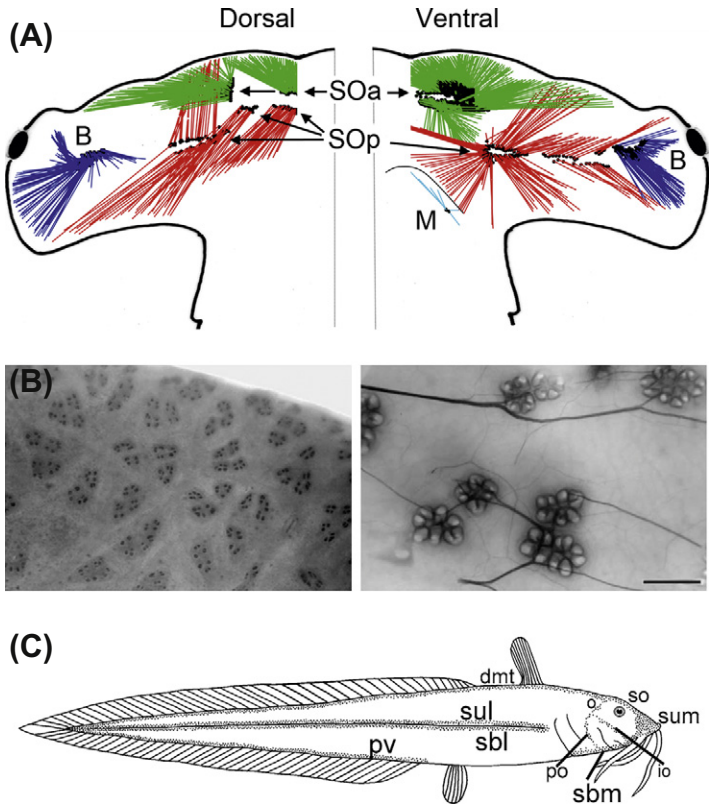


FIGURE 41.4 Distribution of ampullary electroreceptor canal pores in fishes. (A) The scalloped hammerhead shark, *Sphyrna lewini*, has more than 2800 ampullary pores on the dorsal and ventral surfaces of head many of which have long canals that project to the sensory ampullae. Ampullae (small black dots) are grouped into clusters that are associated with branches of the anterior lateral line nerve. Canals and associated clusters are B = buccal (blue), SOa = superficial ophthalmic anterior (green), SOp = superficial ophthalmic posterior (red), M = mandibular nerve (light blue). (*From Rivera-Vicente et al., 2011, with permission from PLoS One.*) (B) Ampullae in the paddlefish, *Polyodon spathula,* have transdermal pores that occur in small clusters. Left photo shows arrangement of pores across the ventral surface of the rostrum. Scale bar = 2 mm. Right photo is a cleared and stained preparation that shows innervation of primary afferent fibers. Scale bar = 1 mm. (*From Wilkens et al., 2002 with permission from Elsevier Limited, Kidlington, Oxford.*) (C) Ampullary pore distributions in the estuarine catfish, *Euristhmus lepturus* (Plotosidae). Each spot represents a single ampullary pore or cluster. Pore distributions are associated with nerve branches: dmt = dorsal midtrunkline, io = infraorbital, o = otic, po = preopercular, pv = posterior ventral, sbl = sublateralis, sbm = submandibular, so = supraorbital, sul = supralateralis and sum = supramandibular. *(From Whitehead et al., 2009, Copyright Springer-Verlag, Inc. Reprinted with permission.)*

a recurrent branch of the anterior lateral line nerve complex. In the bichir, *Polypterus* (Cladistia), there are about 1000 ampullae on the head region (Northcutt, 1986). In sturgeon, the electroreceptor organs are arranged in about 1300 clusters of about 20 ampullae each whereas, in the related paddlefish, *Polyodon*, there are 50 000 to 75 000 ampullae on the elongate rostral "paddle" (see Fig. 41.4B) which are also arranged in small clusters (Wilkens et al., 2001; Jørgensen, 2005). In the marine coelacanth, *Latimeria*, the "rostral organ" located between the eye and olfactory organ represents a complex of three principal canals that end centrally in small sensory crypts (Millot and Anthony, 1956) and is thought to be a homologous structure to the elasmobranch ampullae of Lorenzini (Bemis and Heatherington, 1982).

There is significant variability also in ampullary receptor cell morphology, particularly at the level of the apical membrane (Jørgensen, 2005). Ampullary receptor cells in bichirs and reedfish possess both a single kinocilium and 8–10 microvilli, whereas those of chondrostean sturgeons and paddlefish possess only a kinocilium as in the elasmobranchs. The receptor cells in lungfishes lack a kinocilium, but possess microvilli as in the jawless lampreys. The receptor cells of the urodele amphibians (salamanders) are highly variable in morphology, whereas the tropical subterranean gymnophion have only microvilli. The ancestral condition for non-teleost electroreceptors is generally thought to be one possessing both kinocilium and microvilli (like other hair cells), but the reason for the loss of either kinocilium or microvilli in the various taxa and possible physiological ramifications is not known. These receptors also possess synaptic ribbons in the basal cell region, although some variation in synaptic morphology occurs.

Ampullary canals of marine teleost species are often long as in marine elasmobranchs, although morphological differences associated with habitat may occur within species (Whitehead et al., 2000). Ampullary pores are concentrated on the head and may also occur across the body (see Fig. 41.4C). The fine structure of ampullary electroreceptors in freshwater teleost fishes closely resembles that of the freshwater elasmobranchs (Szabo, 1974) (Fig. 41.5). These receptors, however, are not homologous to non-teleost receptors rather they represent a case of parallel homoplasy, presumably the result of developmental and functional constraints necessary for the detection of extrinsic electric fields and their derivation from the hair cell receptors of the lateral line. The organs are located at the level of the basement membrane of the epidermis with a very short canal (usually about 200 µm)

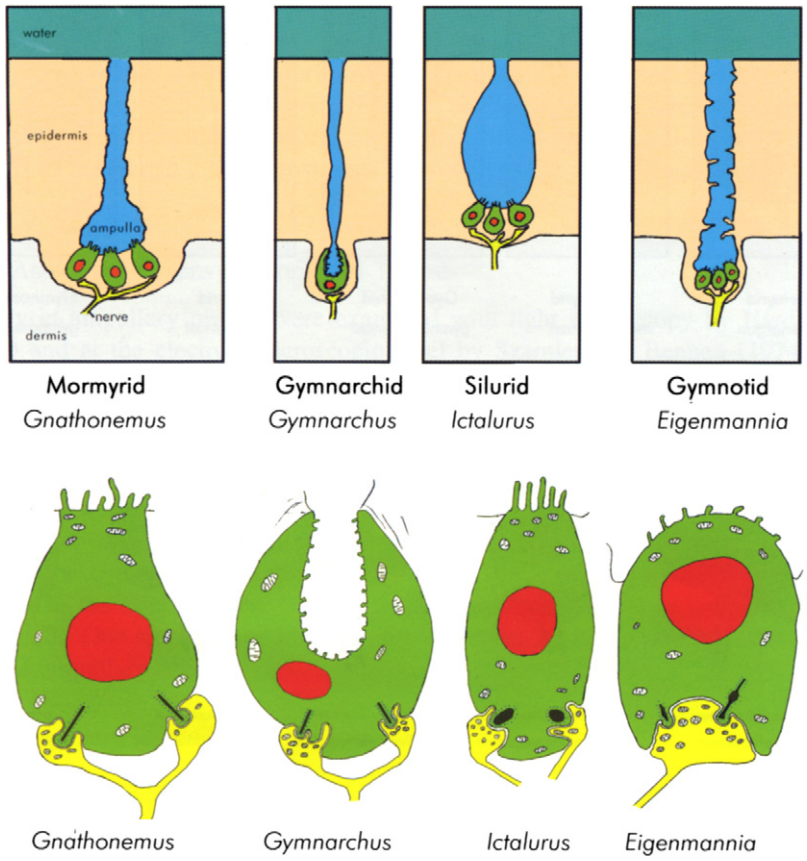


FIGURE 41.5 Diagrammatic representation of ampullary receptor organs in four families of freshwater teleosts. Top row shows cross-section of ampulla pores in contact with water, short canals and the receptor epithelium in the epidermis. Bottom row shows representative differences in receptor morphology and innervation. *(Modified from Jørgensen, 2005.)*

connected to a pore on the skin surface. The cells of the inner walls of the ampulla and canal consist of three to five layers of flattened epithelial cells connected by tight junctions preventing current leakage across the canal wall and the canal is filled with a conductive jelly that provides a low-resistance pathway through the lumen (Pfeiffer, 1968). The parallelism of ampullary electroreceptors among both ancient and derived groups is further demonstrated in the few existing species of electroreceptive marine teleosts. In the marine catfish, *Plotosus*, the ampullary canals are elongated, forming long subdermal tubules terminating centrally in alveolar clusters strikingly similar to the ampullae of Lorenzini in marine elasmobranchs (Obara, 1976). These teleosts can detect electric field stimuli at 80 μV/cm (Kalmijn, 1988), which is much more sensitive than the ampullary system of freshwater species.

The ampullary receptor cells of teleosts are located in the base of the alveolus and are connected to the supporting cells via tight junctions, with only a small portion of their apical face exposed to the lumen. Teleost electroreceptor cells generally possess only microvilli with the exception of the African knifefish *Xenomystus* (Notopteridae) that shows a single short cilium on the electroreceptor (Jørgensen, 2005). The synaptic structure of receptors in more recently derived fishes is similar to those of the more primitive species, in which synaptic ribbons and presynaptic membrane evaginations are surrounded by a prominent postsynaptic "cup" (Szabo, 1974). Unlike most non-teleost ampullary electroreceptor cells, ampullary receptors in teleosts may be innervated by either anterior or posterior lateral line nerves, depending upon location on the body surface. Like most other non-teleost fishes, the ampullae are distributed widely over the head, but differ in that they are usually distributed across the trunk in distinct patterns that are species-specific.

IIIB. Physiology

For marine elasmobranches, such as the thornback ray, *Platyrhinoides*, the resistance of the skin is moderately higher than that of the body tissues (Kalmijn, 1974). When the body encounters a weak external dipole source, such as that produced by small prey, penetration of the electric field into the body is limited and makes the voltage drop across the skin in the region of the pore the effective stimulus. In contrast, external uniform fields, such as those produced by geomagnetic induction in streaming ocean currents, invade the body along the length of the canal and detection may be enhanced by long canal length under these conditions. In freshwater elasmobranches, such as *Potamotrygon*, the resistance of the skin is relatively high compared to marine species and the resistance of the internal tissues is relatively low, presumably as a result of osmoregulatory constraints. In these fishes, the internal environment is essentially at a common reference potential. Individual ampullae detect the transepidermal voltage drop between an applied external field and the internal tissue reference. Hence, most strictly freshwater elasmobranchs, as well as most other ampullary-bearing taxa, have short ampullary canals that cross only the dermis.

Technical challenges make it very difficult to obtain detailed intracellular single-cell recordings from ampullary electroreceptor cells. The membrane biophysics of ampullary receptor excitation for non-teleosts is best described for the skate, *Raja*, in which the voltage stimulus could be clamped or controlled near the sensory epithelium of the ampulla (see Obara and Bennett, 1972; Bennett and Clusin, 1978; Lu and Fishman, 1994, 1995a,b). The excitability of the electroreceptor cell results from voltage-gated Ca^{2+} channels located in the apical membrane (see Fig. 41.4). In unstimulated electroreceptors, there exists a steady-state inward current by L-type Ca^{2+}-channels. The basal membrane has a net outward current that involves K^+ and Ca^{2+}-dependent Cl^- channels that produce an oscillation thought to drive presynaptic neurotransmitter release. In addition, intracellular Ca^{2+} concentrations and the basal membrane voltage are tightly regulated and maintained by Na^+-K^+ and Na^+-Ca^{2+} ion transporters (Lu and Fishman, 1995b). Electric stimuli applied to the ampulla lumen that are more negative than those at the basal outside surface will depolarize the apical membrane and promote additional inward Ca^{2+} conductance. This results in a net outward current across the basal surface of the cell, an influx of Ca^{2+} that promotes presynaptic neurotransmitter release and subsequent depolarization of the postsynaptic afferent fiber. Weak anodal stimuli applied to the lumen decrease apical Ca^{2+} conductance and neurotransmitter release. This model is supported by electric models and empirical measurements (Fig. 41.6A). Voltage clamp experiments provide data on complex admittance (the reciprocal of impedance) at different frequencies and indicate the real part of the admittance at low frequencies is negative and is consistent with inward current at the apical membrane (Lu and Fishman, 1994).

The membrane biophysics of the teleost ampullary electroreceptor also involves several ion channels that also include voltage-sensitive Ca^{2+} channels, but the excitable membrane is at the basal surface of the receptor cell. In the marine catfish (*Plotosus*) and likely in other teleosts, the electroreceptors are excited by anodal potentials in the ampulla chamber near the low resistance and passive apical membrane. Voltage and current clamp experiments on isolated ampullae reveal the existence of an electrogenic Na^+-K^+ pump in the basal receptor membrane (Sugawara, 1989a). This provides a steady outward bias current that activates a sustained non-inactivating inward Ca^{2+} L-type

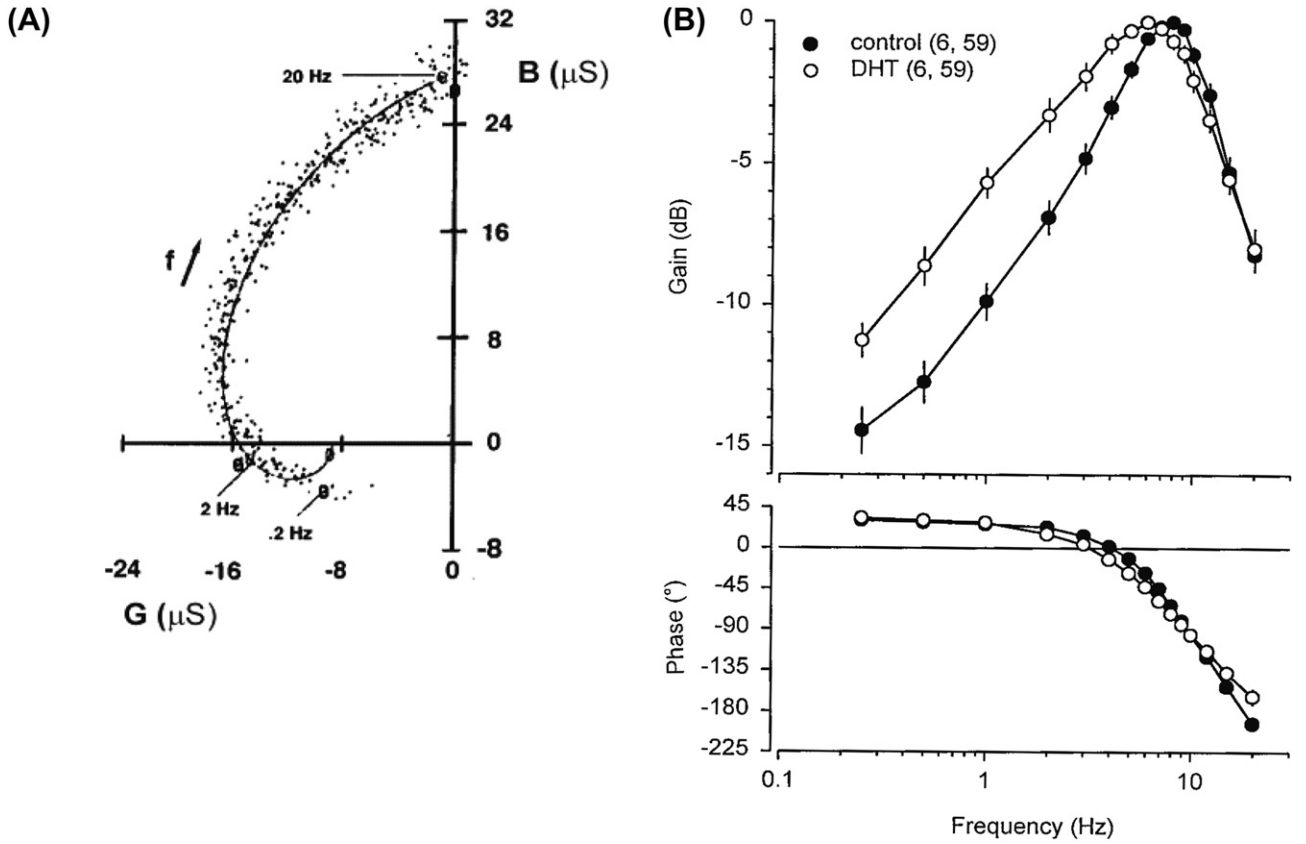


FIGURE 41.6 Frequency response of ampullary receptors and primary afferent neurons in elasmobranch fishes. (A) Locus of the admittance function of complex frequency as determined by voltage clamp experiments on an ampullary organ of the skate, *Raja*. The locus of 400 data point at low frequencies from 0.05 to 20 Hz are plotted in the complex plane [*B(f)* vs *G(f)*] and fall in the left half plane. This describes a negative conductance in this low frequency range. Also, note that the locus plot intercepts the real axis (B(uS) = 0) at 2.1 Hz which indicates solely negative (inward) conductance. (*Reproduced from Lu and Fishman, 1994 with permission from Elsevier Limited, Kidlington, Oxford.*) (B) Bode plot and phase diagram for frequency response of electrosensory primary afferent neurons recorded from adult male Atlantic stingrays, *D. sabina*, after DHT implants. Peak frequency sensitivity decreased from 7−8 Hz to 5−6 Hz for DHT-treated fish and also the low frequency response. The numbers of animals and electrosensory primary afferent neurons tested are indicated in parentheses. Data are plotted as mean and SE. *(Modified from Sisneros and Tricas, 2000.)*

current that maintains the tonic release of neurotransmitter and the regular resting discharge firing rate of afferent neurons (Sugawara, 1989b). This Ca^{2+} conductance is enhanced by an anodal (positive) stimulus in the ampulla to create a superimposed fast Ca^{2+} N-type current that initiates an outward transient Ca^{2+}-gated K current. The conductances are inhibited by phasic cathodal stimuli in the ampullary lumen (Bennett, 1971a; Bennett and Obara, 1986). Primary afferents that innervate ampullary electroreceptors in freshwater fish show regular resting discharges that are excited by anodal stimuli at the lumen and have a dynamic range of ±1 mV in *Gymnotus* (Bennett, 1968) with thresholds that can range from tens to hundreds of microvolts (see Zakon, 1986). The low frequency response of primary afferents in the paddle fish are efficient detectors of bioelectric stimuli from single plankton (Wilkens, 2004) and have proved an intriguing model for detection of signals in noisy environments and sensory oscillators (Neiman and Russell, 2004; Neiman et al., 2007).

The high sensitivity of electrosensory primary afferent neurons was first established for the elasmobranch at a voltage gradient of about 1 μV/cm (Murray, 1962) and has recently been extended to near 20 nV/cm applied to ampullae with long canals by Tricas and New (1998). The neural response to a prolonged, constant current field is sustained for a duration of a few seconds before it begins to adapt back to the resting discharge rate. Prolonged, constant stimulation results in a return to resting levels and accommodation of the receptor, resulting in no change in the overall sensitivity of the receptor (Bodznick et al., 1993). Work on a variety of species with both non-teleost and derived ampullary electrosenses shows a maximum response to sinusoidal electric fields at frequencies of 1−10 Hz (Andrianov et al., 1984; Montgomery, 1984b; Peters and Evers, 1985; New, 1990; Tricas and New, 1998). Sensitivities of primary afferent fibers innervating ampullary electroreceptors to a sinusoidal uniform field are 0.9 spikes per second per μV/cm for the little skate, *Raja*

erinacea (Montgomery and Bodznick, 1993), four spikes per second per μV/cm for the thornback guitarfish, *Platyrhinoidis triserata* (Montgomery, 1984a) and 24 spikes per second per μV/cm average for the round stingray, *Urolophus halleri* (Tricas and New, 1998). The frequency response of primary afferents neurons were shown in the stingray *Dasyatis sabina* to vary across the reproductive season in association with natural surges in serum androgens (Sisneros and Tricas, 2000). In wild males, there was an increased sensitivity to low frequency stimuli from 0.01 to 4 Hz. Experimental implants of dihydrotestosterone induced a similar increased sensitivity in the band of 0.5−2 Hz. These androgen dependent shifts in sensitivity may serve to enhance the detection of potential female mates or other reproductive-related behaviors.

Recordings from the lateral line nerve in behaving elasmobranchs and bench preps show that the regular discharge of primary afferent neurons is modulated in rhythmic bursts that are in phase with the ventilatory movements of the fish. This reafferent neuromodulation is explained by the standing (DC) bioelectric field that arises from the differential distribution of ionic charges in the animal which, in the skate, is a result of both diffusion potentials and osmoregulatory ion pumping at the gills (Bodznick et al., 1992). The modulation of this standing field occurs as the animal opens and closes the mouth, gills or spiracles during the ventilatory cycle, which changes the resistance pathway between the animal's internal tissues and surrounding seawater. The resultant transcutaneous potential is the source of electrosensory self-stimulation or *ventilatory reafference* (Montgomery, 1984b), by which a change in the internal potential of the animal (and basal regions of the ampullary receptor cells) proportionately modulates the regular discharge of all primary afferent neurons. Thus, electrosensory receptors and primary afferents exhibit common mode noise and also a central adaptive filter in the hindbrain circuit, which has important implications for noise rejection and central processing of electrosensory information (see Bodznick and Montgomery, 2005).

IV. TUBEROUS ELECTRORECEPTORS

Tuberous electroreceptors have only been found in teleost fish, though they have evolved multiple times independently (Bullock et al., 1983). They are found only in fish that also have ampullary electroreceptors and the phylogenetic distribution of ampullary and tuberous organs suggest that tuberous organs are evolutionarily derived from ampullary organs (see Fig. 41.1). Within the Osteoglossomorpha, both ampullary and tuberous organs are found within the African Mormyriformes (Zakon, 1986). However, within the closely related Notopteridae, the African subfamily Xenomystinae has only ampullary organs, whereas the Asian subfamily Notopterinae lacks electroreceptors altogether (Braford, 1986). Within the Ostariophysi, the South American Gymnotiformes (knifefishes) possess both ampullary and tuberous organs (Zakon, 1986). The closely related Siluriformes (catfish) generally possess only ampullary organs, although tuberous organs have been described in one species. Despite the independent origins of tuberous electrosensory systems, there are many remarkable similarities in receptor morphology and physiology (Zakon, 1986; Jørgensen, 2005), as well as in the anatomy and physiology of the central sensory systems (Finger et al., 1986).

In general, tuberous electroreceptors are found in fish that have specialized electric organs for actively generating electric fields (see Fig. 41.1), underscoring their functional role in the detection of these fields. However, there is one exceptional case, the blind catfish *Pseudocetopsis* spp., which does not appear actively to generate electric fields and yet has both ampullary and tuberous electroreceptors (Andres et al., 1988). In all other cases, tuberous electroreceptors are tuned to the power spectrum of the species-specific electric organ discharge, or EOD (Carlson, 2006). EODs can be categorized as "wave-type" or "pulse-type": for wave-type EODs, the duration of each pulse is equal to the interval between pulses, resulting in a quasi-sinusoidal, continuous electric field; for pulse-type EODs, the duration of each pulse is much shorter than the intervals between pulses, resulting in discrete pulses of electricity. Both pulse- and wave-type species are found within the African Mormyriformes and South American Gymnotiformes (Fig. 41.7). EODs serve two functions (Fig. 41.8): communication, which is based on detecting the EODs of other individuals (Hopkins, 1986, 2005; Carlson, 2006) and active electrolocation, which is navigation and orientation based on detecting distortions in the self-generated electric field (von der Emde, 1999; Nelson, 2005). Both groups of fish are nocturnal and typically live in tropical rivers, streams and creeks. The electric sense thereby provides an effective sensory modality in conditions under which vision is of limited use. Studies on the neurobiology and behavior of these fish have generated many fundamental insights into neural structure and function (Moller, 1995; Rose, 2004).

IVA. Electric Organs

Strongly electric fish that use electricity as a weapon have electric organs capable of generating hundreds of volts. Weakly electric fish, those that use the EOD for active electrolocation and communication, generate much weaker electric fields (millivolts to a few volts). Electric organs have evolved independently at least six different times (see Fig. 41.1): once in the African Mormyriformes, once in the South American Gymnotiformes, once in the "modern" teleost order Perciformes (the stargazer *Astroscopus*), twice

in cartilaginous fishes (once in the torpedinoids or electric rays and once in the rajoids or skates) and at least once in the Siluriformes (catfish).

In nearly all cases, electric organs are of myogenic origin, i.e. they are derived from muscle (Bass, 1986). The excitable cells, termed electrocytes, are packed densely into the electric organ. They are driven to fire in synchrony by spinal electromotor neurons that receive input from a hindbrain command circuit, such that their individual action potentials (AP) summate to generate an external electric field (Caputi et al., 2005; Carlson, 2006). In wave-type species with a myogenic electric organ, the EOD frequency varies from about 100 to 500 Hz. Pulse-type species typically discharge at a lower rate (<100 Hz). In pulse-type mormyriforms, the EOD rate is highly variable, whereas in pulse-type gymnotiforms, EOD rates are quite regular. In general, the maximum energy in the power

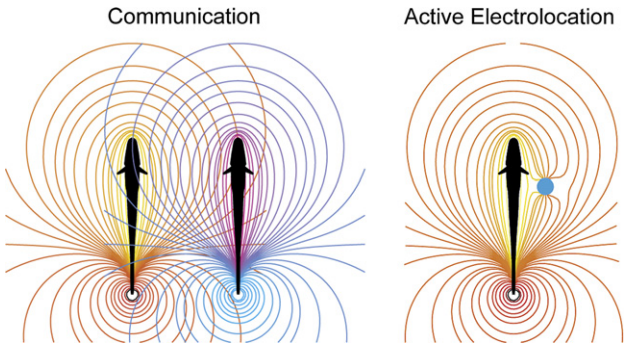


FIGURE 41.8 Electric organ discharges (EODs) serve two distinct functions: electric communication and active electrolocation. The EOD results in an electric field surrounding the fish, shown as isopotential field lines. Electric communication occurs when a fish enters the electric field of a neighboring fish. Active electrolocation occurs when nearby objects cause distortions in the self-generated electric field. The fish can detect these distortions and use them for orientation and navigation purposes. *(From Krahe and Gabbiani, 2004, with permission from Nature Publishing Group.)*

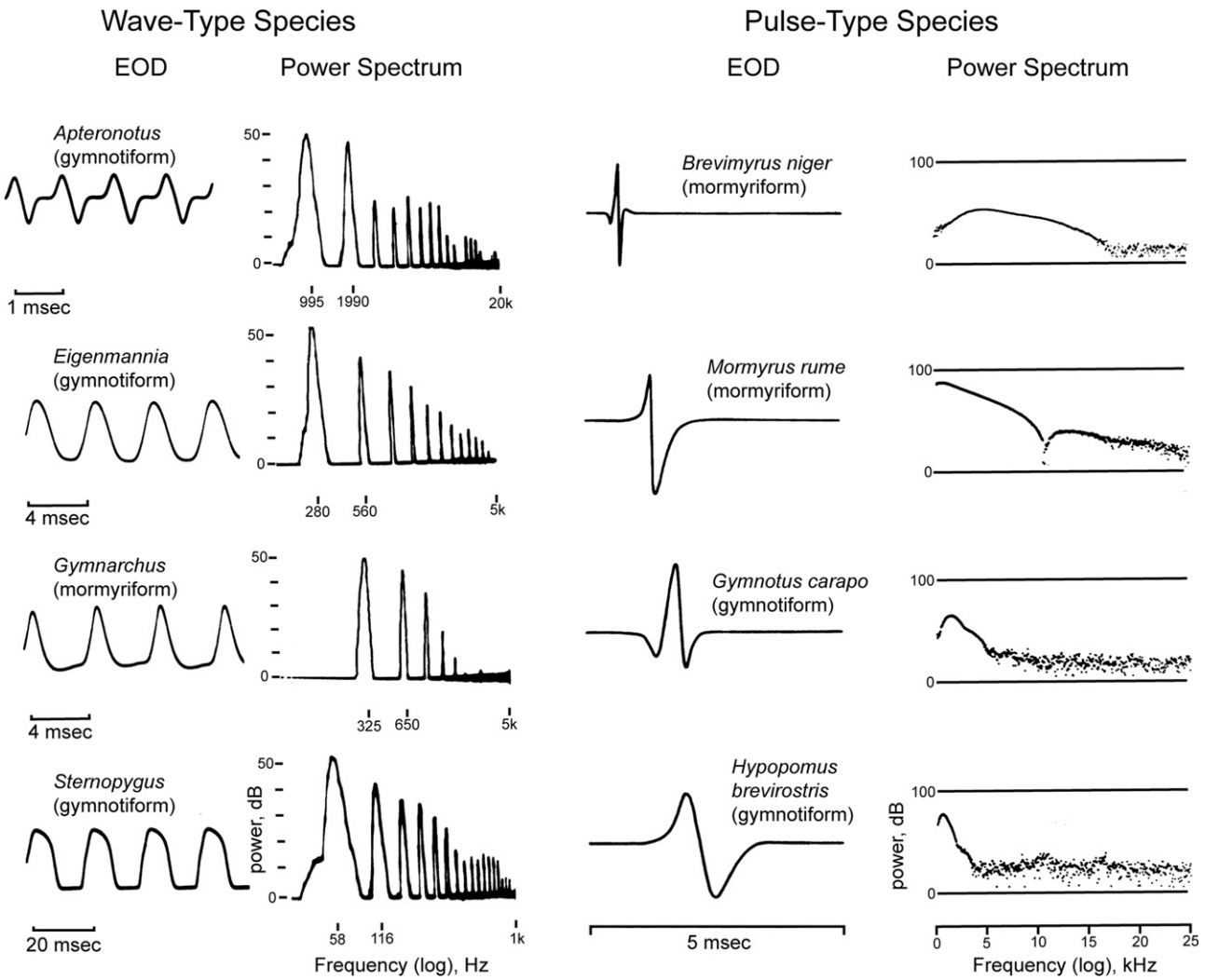


FIGURE 41.7 Electric organ discharges (EODs) and corresponding power spectra produced by several wave-type (left column) and pulse-type (right column) electric fish from the orders Gymnotiformes and Mormyriformes. *(Modified from Heiligenberg, 1991.)*

spectra of pulse-type EODs occurs in the range of about 100 to 10 000 Hz (see Fig. 41.7). Within the Gymnotiformes, one family, the Apteronotidae, possess a neurogenic electric organ that is composed of the axons of spinal electromotor neurons rather than derived from muscle (Bass, 1986). This may represent an adaptation to generating especially high EOD frequencies: the Apteronotidae generate wave-type EODs at frequencies ranging from about 650 to 1500 Hz (see Fig. 41.7). Detailed reviews of electric organ morphology, physiology and central control were published elsewhere (Bennett, 1971b; Bass, 1986; Caputi et al., 2005; Carlson, 2006).

IVB. Tuberous Electroreceptor Anatomy

In general, tuberous electroreceptor organs are distributed across the body surface (Szabo, 1974; Zakon, 1986; Jørgensen, 2005), although the distribution is not always uniform. High densities of tuberous receptors associated with improved electrosensory acuity have been described as electrical fovea, analogous to the visual fovea of the retina (Pusch et al., 2008). In addition, some tuberous organs in some species are organized into discrete clusters, or rosettes, that are localized to specific parts of the body surface (Zakon, 1986; Carlson et al., 2011). The organs themselves consist of a roughly spherical chamber located in the epidermis (Fig. 41.9). This chamber is connected to the external environment by a short canal that perforates the epidermis. Unlike ampullary organs, which have a mucous-filled duct that connects the receptor cells to the surface of the skin, the canals of tuberous organs are composed of a plug of loosely packed epithelial cells. This epithelial plug creates a capacitance in series with the receptor cells, which acts to filter out low stimulus frequencies (Bennett, 1965). Further, the walls of the canal and chamber consist of numerous layers of epithelial cells. These many

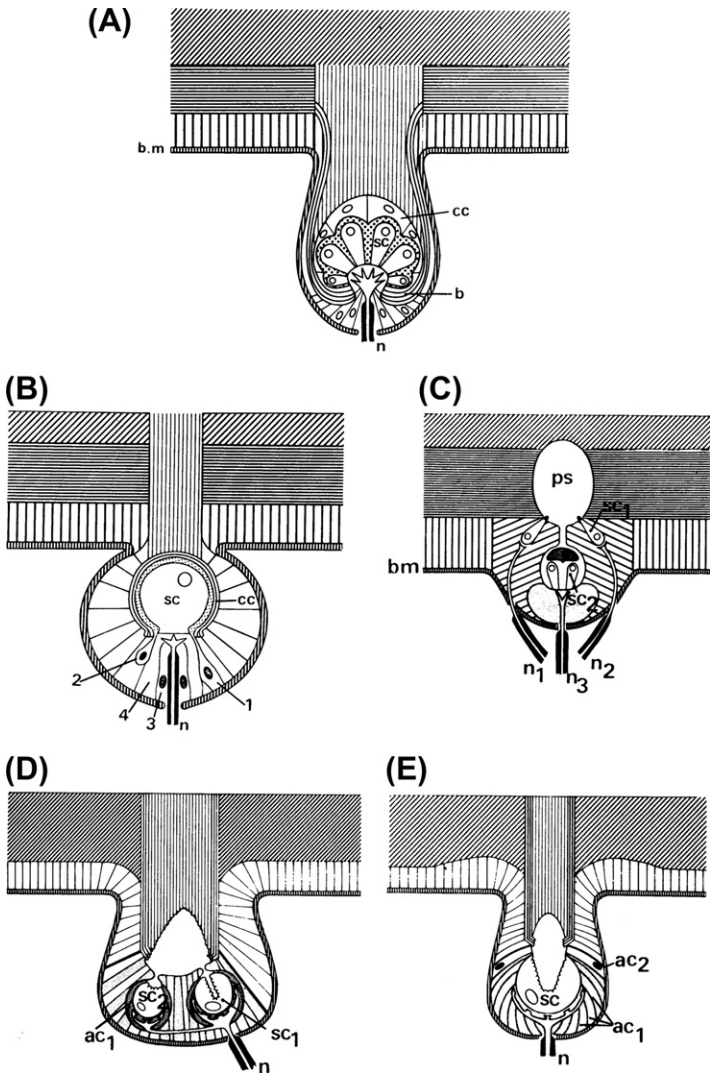


FIGURE 41.9 Schematics illustrating the anatomy of tuberous electroreceptor organs in (A) gymnotiform, (B, C) mormyrid and (D, E) gymnarchid weakly electric fishes. Abbreviations: ac1, ac2: accessory cells; b: capsule wall; bm: basement membrane; cc: covering cells; n#: afferent nerve fibers; ps: perisensory space; sc#: sensory cells. Numbers indicate different cell types within a given organ. *(From Szabo, 1974, with permission from Springer-Verlag, Berlin.)*

epithelial layers cause the wall to have relatively low capacitance, so that there is reduced shunting of high frequencies (Bennett, 1971a). These two distinguishing morphological features partly account for the tuning of tuberous receptors to much higher frequencies than ampullary receptors (Fig. 41.10). Indeed, EOD frequency correlates with the number of epithelial layers in the canal wall: species with low frequency EODs have fewer layers than those with high frequency EODs (Zakon, 1986).

At the base of the canal, the tuberous organ swells into a capsule within the corium. The sensory receptor cells themselves are located on the basal surface of this capsule, with their apical faces exposed to a mucopolysaccharide-filled receptor lumen. These apical faces contain either numerous microvilli or membrane foldings, both of which act to increase surface area, thereby increasing series capacitance while decreasing series resistance (Bennett, 1967, 1971b; Zakon, 1986). The number of receptor cells per organ varies from one to as many as 100, depending on the species and the type of tuberous organ. In all cases, the receptor cells are innervated by branches of the lateral line nerves, with primary afferent fibers that terminate within hindbrain electrosensory regions. In most cases, synaptic vesicles are found near the basal membrane of receptor cells and these mediate chemical synaptic transmission with primary afferent fibers. In one case, however, there may be an electronic junction between receptor cells and primary afferent fibers (see below). Details on the anatomy and physiology of central tuberous electrosensory pathways were reviewed elsewhere (Bell and Maler, 2005; Kawasaki, 2005).

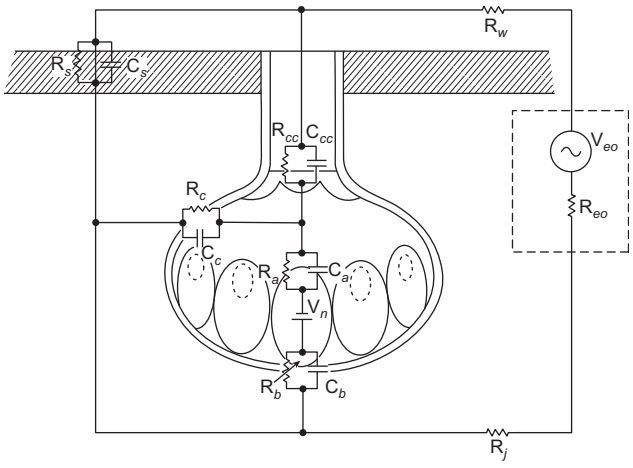


FIGURE 41.10 Electrical equivalent circuits of tuberous electroreceptors. Abbreviations: C_a: capacitance of the receptor cell apical membrane; C_b: capacitance of the receptor cell basal membrane; C_c: capacitance of the canal and capsule wall; C_{cc}: capacitance of the covering cells; C_s: capacitance of the skin; R_a: resistance of the receptor cell apical membrane; R_b: resistance of the receptor cell basal membrane; R_c: resistance of the canal and capsule wall; R_{cc}: resistance of the covering cells; R_{eo}: internal resistance of the electric organ; R_i: internal resistance of the fish; R_s: resistance of the skin; R_w: resistance of the water; V_{eo}: internal voltage of the electric organ; V_n: resting potential of receptor cells. Resistances and capacitances of supporting cells are not indicated and are believed to be passive. The resistance of the receptor cell basal membrane is thought to be voltage-gated. *(Modified from Bennett, 1967.)*

IVC. Tuberous Electroreceptor Physiology

Intracellular recordings from individual tuberous receptor cells have yet to be obtained; therefore, we know little about the underlying transduction mechanisms and much of what we do know about tuberous receptor physiology comes from recordings from their primary afferent fibers. While the apical membrane of receptor cells appears to act solely as a series capacitance that contributes to high-pass filtering, the basal membrane appears to be electrically excitable, generating graded potentials or, in some cases, even spikes (Bennett, 1971a). The receptor cells respond to inward current that creates a voltage drop across the basal membrane of the receptor cell (see Fig. 41.10). Thus, they effectively measure the difference in voltage between the interior of the receptor cell and the internal "reference" potential of the animal (Bennett, 1971a). Tuberous receptors are sensitive to much higher frequencies than ampullary receptors as they are generally tuned to the power spectrum of the species-specific EOD. In wave-type species, this tuning is typically quite sharp, whereas the tuberous receptors of pulse-type species are more broadly-tuned. Although some of this tuning relates to passive electrical filtering due to the morphology of tuberous organs and the apical face of the receptor cells (see above), active mechanisms also contribute substantially to frequency tuning (see Fig. 41.10). Tuberous receptors typically respond to stimulation with potentials that oscillate at a frequency equal to the best frequency of the receptor (Bennett, 1971a) and, in some species at least, this appears to be based on both inward Ca^{2+} and outward K^+ currents (Zakon, 1986). Across taxa, tuberous receptors can be divided into two broad classes based on their responses to electrosensory stimuli: "amplitude-coding" and "time-coding" receptors (Fig. 41.11). As their names suggest, amplitude-coding receptors function primarily in encoding EOD amplitude, whereas time-coding receptors function primarily in encoding the timing of EOD pulses or cycles (Zakon, 1986). Time-coding receptors may generally be distinguished from amplitude-coding receptors as having lower thresholds, greater response probabilities, reduced timing jitter and shorter response latencies.

IVD. Tuberous Electroreceptors in Gymnotiformes

There are currently five recognized families with the order Gymnotiformes, two of which have wave-type EODs (Sternopygidae and Apteronotidae) and three of which

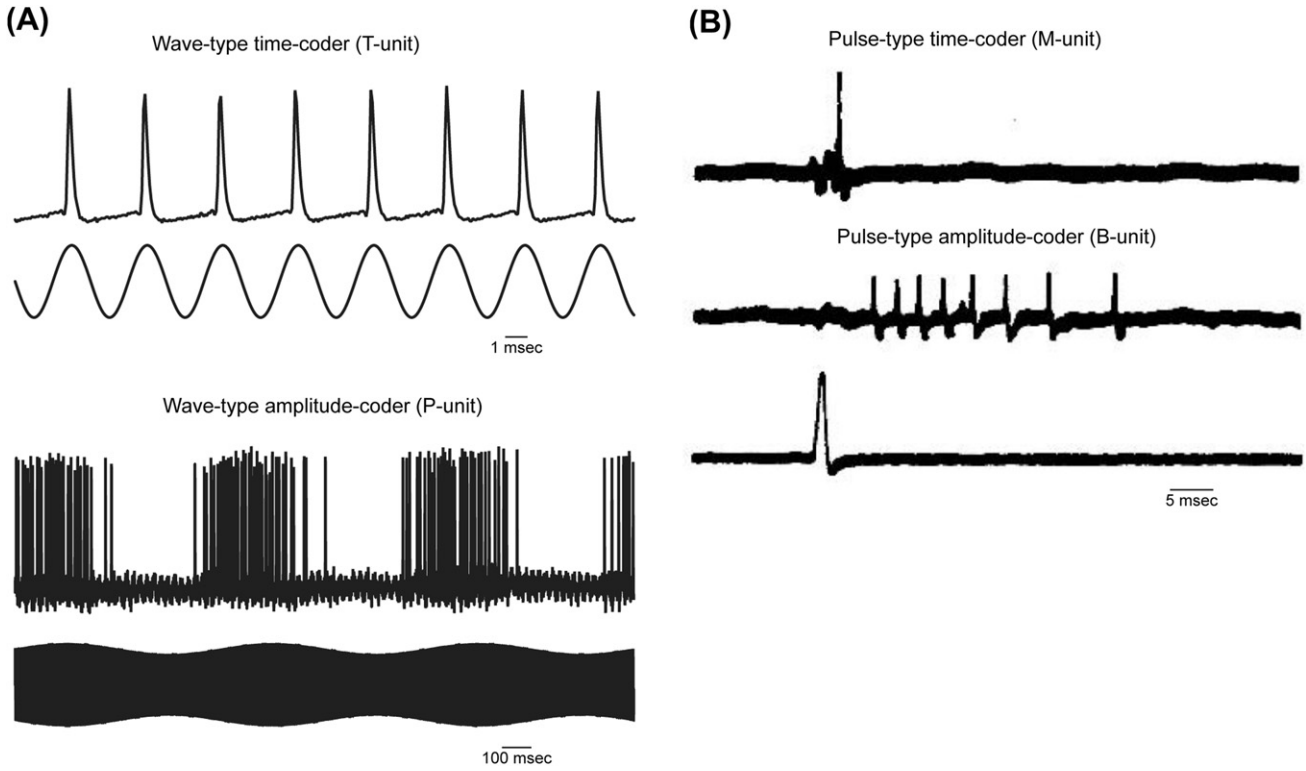


FIGURE 41.11 The primary afferent fibers of tuberous electroreceptors can be classified as either amplitude-coding or time-coding depending on which stimulus feature they respond most strongly to. (A) In the wave-type gymnotiform *Eigenmannia*, T-units fire a single, time-locked action potential (AP) in response to every cycle of an EOD (or a substitute sine wave as shown here), providing a precise marker of EOD timing. P-units do not fire an AP in response to every cycle; instead, their firing probability varies as a function of stimulus amplitude, as can be seen when a stimulus is modulated in amplitude over longer timescales. (*Unpublished recordings from Carlson, 2008a.*) (B) In the pulse-type gymnotiform *Hypopomus*, M-units fire a single, time-locked AP in response to each EOD pulse, whereas B-units fire a burst of spikes in response to each EOD pulse. The number of spikes in a B-unit burst varies as a function of stimulus amplitude. *(From Bastian, 1976.)*

have pulse-type EODs (Gymnotidae, Hypopomidae, and Rhamphichthyidae). The morphology of gymnotiform tuberous organs is essentially similar across all species studied (see Fig. 41.9A) (Szabo, 1974; Zakon, 1986; Jørgensen, 2005). Directly beneath the epithelial plug and above the sensory receptor cells, there is a layer of covering cells that extends across the capsule. These cells are joined to each other and to the walls of the capsule by tight junctions. The layer of covering cells maintains a constant ionic environment within the receptor lumen and also adds an additional series capacitance to the receptor organ.

The number of sensory receptor cells per organ typically varies from 20 to 30, but some tuberous organs can have as many as 100 receptors (Szabo, 1974; Zakon, 1986). The receptor cells are about 20−30 μm long. The apical region of the receptor cell has numerous microvilli exposed to the lumen and large numbers of mitochondria (Szabo, 1974). The receptors are attached to the base of the chamber via tight junctions only at the basal-most portion of the receptor cell's membrane. Thus, 95% of the membrane surface is exposed to the surrounding lumen. The remaining basal portion of the cell membrane is electrically isolated from the lumen via tight junctions with supporting cells (Szabo, 1974; Zakon, 1986). All of the receptor cells within a tuberous organ are innervated by a single afferent fiber, though one fiber may innervate either one or several organs. When an afferent fiber innervates several tuberous organs, those organs form a distinct cluster called a rosette, resulting from the division of a single organ with growth. The receptive field of each primary afferent fiber is centered on the pore of a single tuberous organ (Bennett, 1967; Zakon, 1986).

Two distinct physiological classes of primary afferent fibers have been described in wave-type gymnotiforms: T-units (for *Time-coder*) and P-units (for *Probability-coder*). Within the natural range of stimulus intensities, T-units fire one phase-locked spike per EOD cycle with less than 100 μs of timing jitter (see Fig. 41.11A), thus providing a precise marker of the timing of positive transitions in the EOD (Zakon, 1986; Heiligenberg, 1991; Carlson, 2006, 2008a,b). By contrast, P-units do not fire a spike during each EOD cycle and they have timing jitter greater than 500 μs (Zakon, 1986; Heiligenberg, 1991; Carlson, 2006, 2008a). The probability of P-unit firing

varies with amplitude; thus, the firing rate of P-units codes for EOD amplitude (see Fig. 41.11A). There are a number of additional distinguishing features between the two types of receptors (Zakon, 1986): T-units are more sharply frequency tuned and they are typically tuned to higher frequencies than P-units; P-units readily adapt to changes in steady-state amplitude, whereas T-units do not; although both types of units have dynamic ranges of about 20 dB, the threshold stimulus intensity for T-units is about 15−20 dB lower than that of P-units. Although it remains unclear, P- and T-units may correspond to two distinct anatomical classes of tuberous organs, one which is characterized by one to two receptor organs per axon with thick axon branches and a second which is characterized by four or more receptor organs per axon with thin axon branches (Zakon, 1986).

P- and T-units both play important roles in electrosensory-mediated behaviors (Heiligenberg, 1991). Interference between the EODs of neighboring fish results in modulations in both the amplitude and timing (i.e. phase) of the resulting electric field (Fig. 41.12). Information about the temporal relationship between amplitude and phase modulation is used to determine the EOD frequency of a neighboring fish, a determination that is important for both communication behavior and avoidance of electrosensory jamming (Heiligenberg, 1991; Carlson, 2006, 2008a). Further, wave-type gymnotiforms are able to distinguish purely resistive objects from capacitive objects having complex impedances by comparing the activities of P- and T-units (von der Emde, 1999). Although the two classes of units are clearly specialized for separately encoding the amplitude and timing of stimuli, the distinction is not complete: the spike times of T-units are affected by stimulus amplitude and the firing rate of P-units can be affected by stimulus timing, and this "cross-talk" can ultimately influence electrosensory perception (Carlson, 2008a).

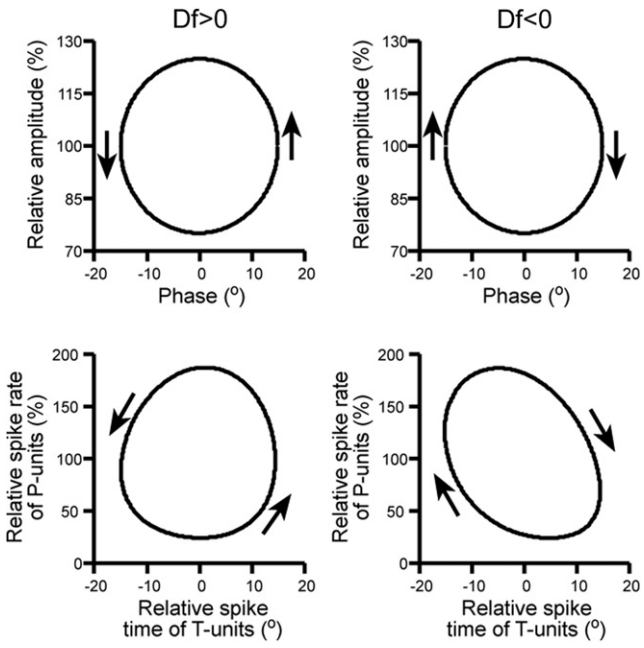


FIGURE 41.12 Neural representations of sinusoidal stimulus modulations caused by interference from a neighboring fish's EOD in the wave-type gymnotiform *Eigenmannia*. The top row shows Lissajous plots that illustrate the temporal relationship between amplitude modulation and phase modulation, with the sense of rotation indicating how these two variables change over time: when the neighboring fish has a higher EOD rate than the focal fish (Df > 0, left), the resulting plot has a counterclockwise sense of rotation. When the neighboring fish has a lower EOD rate than the focal fish (Df < 0, right), the resulting plot has a clockwise sense of rotation. The bottom row shows similar Lissajous plots, except that the average spike rate of P-units is plotted against the average spike time of T-units. Notice how the neural representations of the two different conditions exhibit the same sense of rotation as the stimuli themselves. *(Modified from Carlson, 2008a.)*

Pulse-type gymnotiforms also have two distinct physiological classes of primary afferents (see Fig. 41.11B): M-units (for *pulse Marker*) and B-units (for *Burst duration-coder*). Similar to T-units, M-units fire a single, short latency spike in response to each EOD pulse with little timing jitter; by contrast, B-units respond to each EOD pulse with a longer-latency burst of spikes (Bastian, 1976; Zakon, 1986). The duration of the burst increases with increasing EOD amplitude: at near threshold intensities, B-units may respond to an EOD with a single spike, whereas they respond with 20−40 spikes at higher intensities. Both units are sensitive to the direction of current flow, with greatest responses to stimuli at the best azimuth for transepidermal current flow (Hopkins, 2005).

The physiological distinction between M- and B-units is clearly linked to anatomical differences in the associated receptor organs (Szabo, 1974; Zakon, 1986). M-units have large-diameter axons with large myelinated terminal enlargements within the receptor capsule that give rise to boutons that innervate the receptor cells. By contrast, B-units have smaller-diameter axons that lose their myelination upon entering the capsule and give rise to several thin, unmyelinated terminal branches that innervate the receptor cells.

IVE. Tuberous Electroreceptors in Mormyriformes

The Mormyriformes consist of two distinct sister families, the Mormyridae and the monotypic Gymnarchidae, *Gymnarchus niloticus*. All of the mormyrids have pulse-type EODs, while *Gymnarchus* has a wave-type EOD (see Fig. 41.7). Two distinct physiological classes of receptors have been described in *Gymnarchus*: S- and O-units, which are remarkably similar to the T- and P-units of wave-type gymnotiforms, respectively (Kawasaki, 1997; Carlson, 2008a). S-units have lower thresholds, higher firing probabilities, reduced jitter and less adaptation to steady-state

changes in intensity than O-units. Thus, within the natural range of stimulus intensities, S-units fire 1:1 with each cycle of the EOD and provide a precise marker of the timing of positive transitions, whereas the firing rate of O-units codes for stimulus amplitude. As in the wave-type gymnotiforms, both units provide critical information for determining the EOD frequency of neighboring fish (Kawasaki, 1997). Further, S-units do respond to changes in stimulus amplitude and O-units can respond to changes in stimulus timing, similar to the effects seen in T- and P-units (Carlson, 2008a).

Anatomically, the tuberous organs of *Gymnarchus* are referred to as Gymnarchomasts (Szabo, 1974; Zakon, 1986; Jørgensen, 2005). Type I gymnarchomasts contain two distinct sensory receptor cell types; the organ may contain one or many pairs of these two cell types (see Fig. 41.9D). The larger of the two receptor cell types has a deep invagination filled with numerous microvilli. The microvilli located at the base of the depression are especially long and project upwards into the apical cavity. The smaller receptor cell type has only a slight depression at its apical surface, although it too has densely-packed microvilli. Both sensory cells are surrounded by numerous support cells and only a small portion of receptor cell membrane surface is exposed to the surrounding lumen. All of the receptor cells in an organ are innervated by a single afferent nerve fiber. Physiologically, type I gymnarchomasts have been linked to S-unit primary afferent fibers (Bennett, 1971a; Zakon, 1986). Type II gymnarchomasts consist of several (12−13) sensory receptor cells that are innervated by a single primary afferent fiber. Each individual receptor cell is separated from the surrounding receptor cells by a ring of accessory cells. Thus, the type II organ can be thought of as composed of multiple sensory "units", each with a single receptor cell and multiple accessory cells (see Fig. 41.9E). The receptor cells are similar in morphology to the larger receptor cell of the type I gymnarchomast in having a deeply invaginated apical surface filled with microvilli that project upwards. Type II gymnarchomasts are thought to correspond to O-unit primary afferent fibers (Bennett, 1971a; Zakon, 1986).

The pulse-type mormyrids also have two distinct classes of tuberous receptor organs, amplitude-coding mormyromasts and time-coding knollenorgans (Bennett, 1965, 1971a; Szabo, 1974; Zakon, 1986). Knollenorgans typically have one to 10 sensory receptor cells, although some species have especially large knollenorgans with as many as 60 receptor cells. The receptor cells are large (40−50 μm in diameter) and each is enclosed in its own cavity within the receptor capsule (Szabo, 1974; Zakon, 1986; Jørgensen, 2005). Only the basal-most portion of the receptor cell's membrane is attached to the base of the chamber, similar to the tuberous receptors of gymnotiforms (see Fig. 41.9B). The apical cell membrane is densely packed with microvilli, below which is a dense band of mitochondria. Knollenorgans are unique among tuberous receptors in that the receptor itself generates APs rather than only graded receptor potentials. Further, physiological evidence suggests an electrotonic synapse between the receptor cell and primary afferent fiber (Bennett, 1971a), a conclusion supported by the small numbers of synaptic vesicles and close apposition of pre- and postsynaptic membranes (Zakon, 1986). However, gap junctions have never actually been observed. All of the receptor cells within a knollenorgan are innervated by a single primary afferent fiber that divides to form several terminal boutons onto each individual receptor cell.

Like the pulse marker primary afferents (M-units) of pulse-type gymnotiforms, knollenorgans have a relatively low threshold and fire a single AP in response to an EOD (Bennett, 1965, 1967; Bell, 1990; Carlson, 2008b). The primary afferents of knollenorgans terminate in the hindbrain, where an inhibitory input arising from the electromotor pathway blocks ascending knollenorgan responses whenever the fish generates its own EOD (Carlson, 2008c). Thus, the downstream knollenorgan pathway never "hears" the fish's own EOD, strongly suggesting that knollenorgans function solely in communication behavior (Carlson, 2006). The timing of the knollenorgan AP is tightly phase-locked to the timing of outside-positive positive transitions in the stimulus waveform (Bennett, 1965; Hopkins and Bass, 1981). In response to natural stimuli, different knollenorgans receive EODs with different polarities, resulting in small differences in spike timing across the population of knollenorgans (Fig. 41.13). Behavioral, anatomical and physiological evidence suggests that these spike timing differences mediate the detection of species-specific EOD waveforms (Hopkins and Bass, 1981; Xu-Friedman and Hopkins, 1999; Carlson, 2006), although certain clades of mormyrids appear to lack this ability (Carlson et al., 2011).

Mormyromasts have a distinctive morphology (Jørgensen, 2005). Although the pore and epithelial plug are similar to other tuberous organs, the organ itself consists of two separate chambers, one superficial and one deep, connected to each other by a short duct (see Fig. 41.9C). The two chambers each have their own distinct type of sensory receptor cell: the sensory cells in the upper chamber are referred to as A-type receptor cells, whereas those in the lower chamber are referred to as B-type receptor cells. The number of receptor cells in the two chambers is nearly always equal, varying from two each in the smaller mormyromasts to more than 12 in the larger ones (Jørgensen, 2005). The A-type cells lack microvilli and have only a small portion of their apical surface exposed to the receptor lumen. By contrast, the B-type cells have microvilli and, like knollenorgan receptors, nearly the entire receptor surface area is exposed to the surrounding lumen. The A-cells are contacted by two to three primary

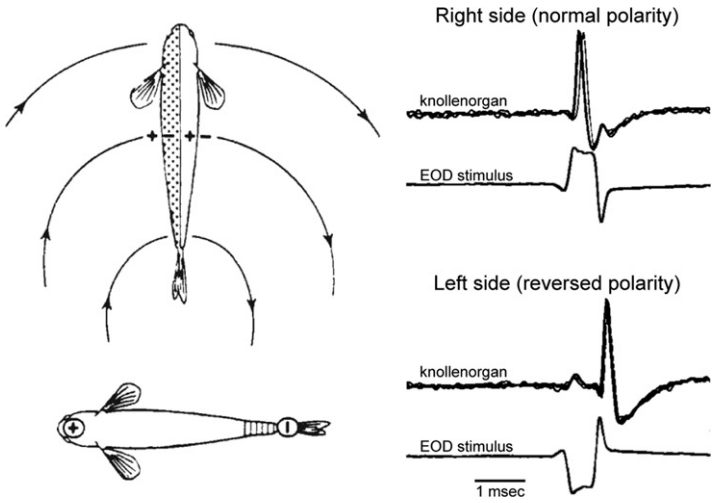


FIGURE 41.13 Knollenorgan electroreceptors in mormyrids mediate species recognition during electric communication. On the left, a signaling fish and receiving fish are viewed from below. The signaling fish is modeled as a simple dipole with "+" and "−" poles at the head and tail, respectively. This causes current to flow into the right side of the receiving fish and out the left side. (*Modified from Hopkins, 1986.*) On the right, the responses of a single knollenorgan to opposite polarity EOD stimuli are shown. Knollenorgans respond to outside-positive changes in voltage. As a result, knollenorgans respond to the start of a normal polarity EOD (simulating the response of a knollenorgan on the right side of the body), but they respond to the end of a reversed polarity EOD (simulating the response of a knollenorgan on the left side of the body). The resulting difference in response latency is used to determine EOD duration. *(Modified from Hopkins and Bass 1981.)*

afferent fibers, whereas all of the B-cells are always contacted by a single primary afferent fiber. The A- and B-cell primary afferents terminate in separate portions of the hindbrain electrosensory lateral line lobe, forming two distinct maps of the body surface (Bell and Maler, 2005). Interestingly, in one genus of mormyrid, *Stomatorhinus*, both the A- and B-cells are present, but only the A-cells receive innervation from primary afferent fibers and this is associated with a complete loss of the associated electrosensory lateral line map (McNamara et al., 2005). This may be related to the extremely short duration (≈250 μs) and high peak power spectral frequencies (≈14−26 kHz) of the EODs in these species, which may preclude the detection of complex impedances based on waveform distortions (see below).

Both A- and B-cell afferents may be classified as amplitude-coding. Like the burst duration coders of pulse-type gymnotiforms, they respond to suprathreshold stimuli by generating a burst of spikes (Bennett, 1965; Bell, 1990). Increases in stimulus amplitude cause both a decrease in first-spike latency, as well as an increase in the number of spikes (Fig. 41.14) (Bennett, 1965; Bell, 1990), although behavioral and physiological evidence suggests that first-spike latency appears to be the critical feature for stimulus coding. In contrast to the knollenorgan sensory pathway, mormyromast input to the hindbrain is gated by an excitatory input arising from the electromotor pathway, rather than inhibited (Carlson, 2008c). As a result, the downstream mormyromast pathway is selectively responsive to the fish's own EOD, indicating that mormyromasts function solely in active electrolocation behavior (von der Emde, 1999).

Compared to knollenorgans, mormyromast primary afferent fibers have higher thresholds and they tend to be

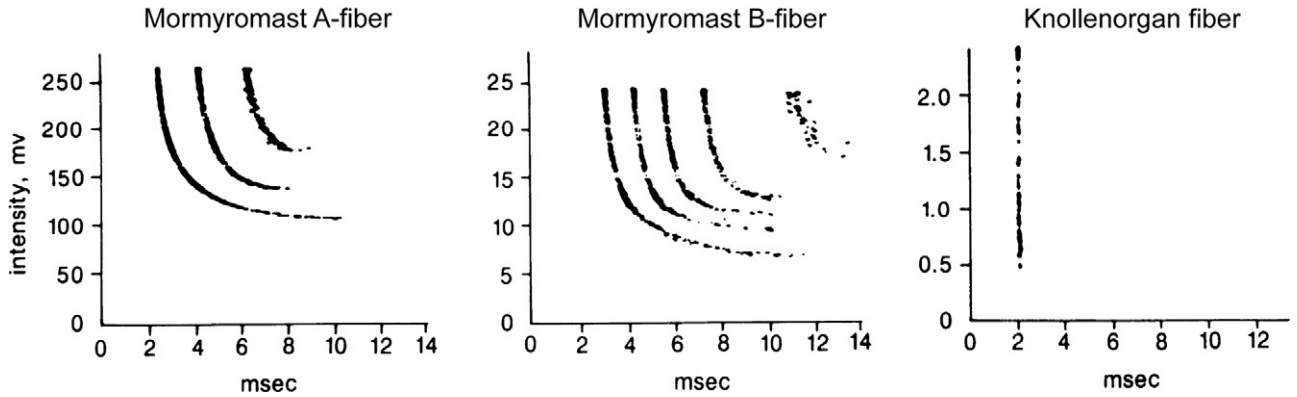


FIGURE 41.14 Differences in the coding of electrosensory stimuli among tuberous electrosensory primary afferent fibers in mormyrids. Stimulus intensity is plotted against the latency of action potentials (Aps) relative to the stimulus. The minimum stimulus intensity required to elicit a response (i.e. threshold) is indicated by the lowest intensity at which any APs occurred. Mormyromast fibers have a much higher threshold than knollenorgan fibers. Further, increases in stimulus intensity cause a decrease in the latency to the first spike, as well as an increase in the number of spikes in mormyromasts, whereas knollenorgans fire only a single spike at a relatively fixed latency. Mormyromast B-fibers tend to have a lower threshold and greater number of spikes per burst compared to A-fibers. *(Modified from Bell, 1990.)*

tuned to frequencies below the peak power frequency of the species-specific EOD (see Fig. 41.14) (Bell, 1990). B-cell afferents tend to have a lower threshold, smaller dynamic range and greater maximum burst number than A-cell afferents. Further, A-cells tend to be tuned to higher frequencies and show more variation in frequency tuning than B-cells. Most importantly, B-cell afferents respond to subtle changes in EOD waveform caused by complex impedances, whereas A-cell afferents do not (von der Emde, 1999). Thus, comparing the responses of the two types of primary afferents may be the mechanism by which mormyrids distinguish simple from complex impedances during active electrolocation (von der Emde, 1999).

IVF. Tuberous Electroreceptors in Siluriformes

Compared to the mormyriformes and gymnotiforms, we know very little about the tuberous receptors found in siluriforms (catfishes). Tuberous organ morphology has been described only in the blind catfish *Pseudocetopsis* spp. (Andres et al., 1988). Compared to tuberous organs in other taxa, this tuberous organ, referred to as a siluromast, is located superficially within the epidermis (Jørgensen, 2005). Each organ has a single sensory receptor cell with a diameter of $\approx$25 μm and an apical surface covered with microvilli. A single primary afferent fiber loses its myelin sheath within the supporting cell layer and then synapses onto the receptor cell with a flattened terminal face. The function of this tuberous organ is unclear, as these fish are not known actively to generate EODs. One intriguing possibility is that these tuberous organs serve a predatory function by allowing the blind catfish passively to electrolocate sympatric gymnotiforms by detecting their EODs (Andres et al., 1988).

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